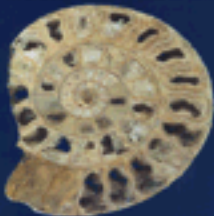


Marine Palaeoenvironmental Analysis from Fossils

edited by

Don W. J. Bosence and Peter A. Allison



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EDITED BY

DAN W. J. BOSENCE

Royal Holloway University of London, Egham

AND

PETER A. ALLISON

The University, Reading

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A review of marine palaeoenvironmental analysis from fossils

DAN W. J. BOSENCE¹ & PETER A. ALLISON²

¹*Department of Geology, Royal Holloway University of London, Egham, Surrey,
TW20 0EX, UK*

²*Postgraduate Research Institute for Sedimentology, The University, PO Box 227,
Reading RG6 2AB, UK*

The papers in this volume critically review the use of fossils, including their inorganic skeletal tissue or their soluble organic remains, for the analysis of palaeoenvironments. The contributions are not limited to traditional palaeontological techniques but are multi-disciplinary, drawing on a host of geochemical, palaeoecological and palaeontological methods. This holistic approach is essential if the potential pitfalls of a strictly uniformitarian approach are to be avoided. If a range of methods are used, and the results compared, then different environmental controls can be isolated. This methodology is of importance to sedimentologists, stratigraphers and palaeontologists who need to maximize their palaeoenvironmental interpretations from palaeontological data. The implications of this work are fundamental to correct interpretations of depositional environments, facies models, sequence stratigraphy and palaeoclimates.

The approach taken in the volume is analytical rather than taxonomic. As such, the techniques used to analyse the effects of different environmental parameters are focused on, rather than what can be learnt from the study of particular fossil groups. This approach is therefore different to that found in many texts (e.g. Dodd & Stanton 1981; Clarkson 1986), where the emphasis is on the palaeoecological value of different taxonomic groups and is more similar to the short reviews of 'Fossils as environmental indicators' in Briggs & Crowther (1990). This analytical approach leads to a more thorough analysis of palaeoenvironments. By using a range of techniques, from the traditional taxonomic uniformitarianism to the more recently developed geochemical and isotopic analyses of mineralized skeletons and soluble organic tissue from plants, more information may be obtained of the record of past environmental parameters.

The common thread in this volume is that it is palaeontological material that is being analysed;

whether it be identifiable body fossils, trace fossils, distinctive fossil associations, diagenetically unaltered skeletal material or organic compounds. Palaeoenvironmental analysis is also largely undertaken through sedimentological investigation, and although some papers in this volume overlap with sedimentology (e.g. Goldring this volume; Allison *et al.* this volume), it is the data which may be obtained from organisms and their remains which are focused upon.

Approaches to palaeoenvironmental analysis

Taxonomic uniformitarianism

In the past much reliance has been made on the approach known as **taxonomic uniformitarianism** which relates the environmental requirements of fossils to those of their taxonomically nearest living relatives. This relies heavily on Hutton's and Lyell's Uniformitarianism, i.e. 'the present is the key to the past'. This technique does have serious drawbacks, the main of which was pointed out by Lyell himself (1875 pp. 214–215) that the ecology of organisms may well have evolved through time.

There are different ways of dealing with the problems of taxonomic uniformitarianism which lead to more precise palaeoenvironmental interpretations.

The first is by studying the entire assemblage, rather than individual fossils, as it is unlikely that all will have changed their ecological requirements synchronously. Examples of such studies, from the Mesozoic on palaeosalinity determinations are those of Hudson (1963, 1990) and Fursich (1994). Hudson & Wakefield (1992) stress the significance of studying more or less *in situ* molluscs, conchostracans, ostracods and palynomorphs from the same section. If the same signature is found in all these low diversity biotas, which have present-day relatives indica-

tive of low salinity environments, then the evidence for ancient low salinities is that much stronger.

The second is to develop geochemical or isotopic indicators of environmental conditions which are independent of taxonomy. A number of chapters in this volume review these techniques (e.g. Corfield; de Leeuw). Similarly, comparisons should always be made with sedimentological data and this is stressed by Allison *et al.* and Goldring.

Thirdly, such changes in the environmental preferences of organisms, or associations of organisms, should be documented and tested with physical and chemical techniques and against their sedimentological setting, so that their changing ecology can be understood and used appropriately in palaeoenvironmental analysis (Bottjer *et al.* this volume).

Development of new analytical techniques

Whilst the development of accurate mass spectrometers in the 1940s gave H. C. Urey and his colleagues the potential to explore the palaeoenvironmental uses of carbon and oxygen isotopes (Urey 1947; Urey *et al.* 1951; reviewed by Corfield this volume), techniques developing in the 1990s are paving the way for a similar breakthrough in the palaeoenvironmental uses of solvent soluble organic matter as reviewed by de Leeuw *et al.* (this volume). de Leeuw and his co-workers review the separation and analytical techniques of gas and liquid chromatography-mass spectrometry (GC-MS, LC-MS) and spectroscopic methods of analysing soluble organic matter from plants. Their review examines how the carbon skeletal structure, the positions of functional groups and the stable carbon isotope ratios may be used in identifying a large range of precursor plant sources from *Archaeobacteria* to aquatic higher plants, and diatoms to dinoflagellates. These techniques are also shown to be useful in identifying palaeoenvironments such as shorelines, and the terrestrial input into marine environments and environmental conditions such as palaeotemperature, palaeosalinity or sulphate reduction or methanogenesis.

Identification and isolation of different controls

It is well known that there will be a number of different environmental factors influencing organism distribution in any one habitat. For example, it has been argued that particular growth forms of bryozoa indicate either shallow

turbulent settings or deeper quieter waters, but Smith (this volume) in her review of palaeoenvironmental interpretations from bryozoa indicates that there is no agreement in the literature on this and still no experimental data exist on this problem. Similarly, Brasier (this volume, second contribution) highlights the problem of using bioerosion on reefs as a proxy for increased nutrient levels. Whilst some authors have indicated that high levels of bioerosion may relate to nutrient levels (Hallock 1988) it is also well known that amounts of bioerosion relate to reef accumulation rates (Adey & Burke 1976) and the nature of the reef framework (Bosence 1985) which are controlled by a number of parameters unrelated to nutrients.

The problem, therefore, stands as how to identify different controls and whether any of the controls can be isolated from each other. Techniques used include an independent geochemical, isotopic or sedimentological assessment of controlling parameters in addition to traditional palaeontological techniques. Examples include the recognition by Phleger *et al.* (1953) of supposed low, mid and high latitude groups of planktonic foraminifera (as reviewed by Murray this volume), based on taxonomic uniformitarianism, which have subsequently been shown by $\delta^{18}\text{O}$ analyses to relate to surface water temperatures (Corfield this volume).

Similarly, the palaeontological analysis of Hudson (1963) on possible salinity or substrate control on reduced diversity benthic associations may be tested independently by analyses of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values as indicators of fresh and marine water mixing (Hudson 1990) in order to assess effects of salinity as opposed to substrate effects on the fauna.

Low diversity marine benthos is also used to identify episodes of low oxygenation. However, Allison *et al.* (this volume) argue that on its own this approach is unreliable because a paucity of benthos may also be a function of other environmental parameters, such as environmental stability, substrate, or nutrient flux. However, low oxygenation may also be defined by independent geochemical signatures (e.g. carbon isotopes, rare earth element content, degree of pyritization, carbon/sulphur ratios) which can also be used to identify the likely controls.

An alternative approach to this problem is presented by Perrin *et al.* (this volume) for determination of depth zonation of corals and algae down ancient reef fronts where a range of physical (e.g. light, hydrodynamic energy, temperature) and biological (predation, competition, grazing) factors are known to influence

reef communities. Although the effects of these controls may sometimes be identified, their relative importance in delineating different depth zones cannot be established for ancient reefs. An alternative approach in such a complex situation is to select outcrops preserving reef crest and slope where the bathymetric ranges of the different organisms can be directly measured. This provides data on the existence of depth related zones for different periods of time which can be used in environmental analysis and bypasses the near impossibility of fully understanding what is controlling the depth zones.

Palaeoenvironmental factors reviewed

Temperature

Corfield (this volume) in his review of palaeothermometry based on oxygen isotope ratios concentrates on analyses from fossil foraminifera, which when appropriately identified and separated, can be used to infer temperatures of surface, deep and bottom waters. Drawbacks to this method are the uncertainties in the isotopic composition of ancient oceans, the occurrence of non-equilibrium fractionation in organically precipitated calcite and diagenetic alteration of the isotope values of carbonate fossils. Nevertheless, secular trends in palaeotemperatures, such as the Cretaceous–Tertiary climatic cooling, the early Eocene and mid Miocene climatic optima (see also Plaziat this volume for independent floral evidence of these events) and Pleistocene glaciations are discernible from carbonate fossils. The low negative oxygen isotope ratios of the Palaeozoic are reviewed but no consensus explanation emerges for this phenomenon and current explanations include lower ^{16}O content of sea water, greatly decreased water temperatures, or, sequestration of ^{18}O into deeper saline waters. However, there are good arguments against each one of these explanations.

Palaeotemperatures have also been inferred from organism distribution as reviewed for the Tertiary by Adams *et al.* (1990). However, the data from isotopes and from fossils are inconsistent and Adams *et al.* (1990) document palaeontological evidence for higher palaeotemperatures in intertropical low-latitude regions for the Tertiary than has been published from $\delta^{18}\text{O}$ analysis. Plaziat (this volume) suggests this anomaly may be explained through the existence of the large Tethyan seaway of the Eocene which may have facilitated greater ocean mixing and milder high-latitude climates in northwest Europe. This may then have resulted in both

the lower intertropical water temperatures (as evidenced by the isotopes) as well as the greater latitudinal spread of warm water biotas.

Low latitude shorelines

Mangroves have long been used as indicators of shorelines experiencing equatorial and tropical climates. However, their potential use in palaeoenvironmental analysis may be greatly extended if the considerable climatic and palaeogeographic variability is better understood (Plaziat this volume). Considering their despositional setting it is surprising that there are very few well-documented examples of ancient preserved mangrove shorelines, although their pollens and fruits may be widely distributed. Even the distinctive molluscan assemblages of mangrove environments, or mangals, are rarely preserved *in situ* because of extensive early dissolution. An independent indication of the proximity of mangrove shorelines is given by Frewin in de Leeuw *et al.* (this volume), where it is shown that terrestrial higher plants have a distinctive organic biomarker indicating the former presence of shorelines.

Oxygen levels

Oxygen is one of the ecological factors which has held the greatest fascination for sedimentologists and palaeontologists alike. For the sedimentologist the association of oxygen deficient facies with accumulations of organic-rich sediment has led to the notion that anoxia is a prerequisite for the formation of hydrocarbon source rocks. For the palaeontologist, oxygen is recognized as an essential requirement for the existence of metazoan life. Thus, variations in levels of past oceanic oxygenation can potentially influence global marine biotic diversity.

Allison *et al.* (this volume) review the geochemical and palaeontological methods used to define depositional palaeo-oxygenation and the effect this has on both the biota and carbon preservation. This review discusses the advantages and limitations of the different indicators of palaeo-oxygenation and the geological conditions in which each can be applied. The potential drawbacks of the uniformitarian method are highlighted by a review of the structure of oxygen deficient biofacies through time. With regard to carbon preservation the ongoing debate on whether or not a lack of oxygen actually affects microbial decay rate is reviewed. Some workers, for example, have suggested that an accumulation of carbon results in low oxygenation in sediments and

that carbon preservation in oxygen deficient sediments is merely a function of a high rate of supply (Henrichs & Reeburgh 1987).

The authors conclude with two case studies. The first is a local-scale study on the world-renowned Cambrian Burgess Shale of British Columbia, Canada. This study shows that the sediments were deposited under conditions of fluctuating oxygenation and that many of the fossils are para-autochthonous. Finally, the identification and effects of global anoxia are discussed with respect to the massive Permo-Triassic extinction event which supposedly led to the demise of 96% of all marine species.

Nutrients

Fossils are the main way in which biolimiting nutrients in ancient marine environments may be assessed. This relatively new field is reviewed in two contributions by Brasier (this volume). The first discusses the biological importance of phosphorus and nitrate in organisms and the interlinked carbon–nutrient cycles of the oceans. Potential fossil indicators of nitrate-limited, eutrophic ecosystems are high accumulation rates of biogenic silica, non-spinose smaller planktonic foraminifera, high Ba/Ca and Cd/Ca ratios in skeletal carbonate and increased differences between $\delta^{13}\text{C}$ in planktonic and benthic foraminiferal calcite. Such eutrophic indicators are shown to peak during glacial phases in the Quaternary suggesting that lower solar insolation may have influenced the availability of nutrients.

In his second contribution Brasier investigates foraminifera and the $\delta^{13}\text{C}$ values of their tests as proxies for oligotrophic ecosystems. He argues that photosymbiosis may be used as a proxy of oligotrophic waters and may be indicated in ancient forms by particular skeletal architectures, by the larger benthic foraminifera, and by certain planktonic foraminifera. A case history shows the expansion of presumed oligotrophic larger benthic foraminifera in the mid Eocene. These faunas are reduced by a mid to late Eocene cooling which results in increased oceanic circulation, and therefore nutrients, accompanied by expansion of biosiliceous sedimentation.

Substrate

Sedimentary rocks preserve primary sedimentary structures and sequences indicative of processes and environments of formation. They also record former biological substrates (Goldring this volume) which, with few exceptions,

have been modified by interacting bio-sedimentary processes (transporting, baffling, binding, ventilating and disturbing) and trophic processes (transforming and modifying). These processes affect substrate morphology, fabric, consistency, erodability, chemistry, sedimentation rate and colonization potential, creating opportunities to which other organisms, in turn, may respond. Body and trace fossils exhibit adaptations and responses to these processes, which occurred in life or during various taphonomic stages, that are significant in the interpretation of ancient environments.

Goldring discusses and illustrates three rapidly advancing areas within this field. He argues convincingly that ichnofabrics should replace ichnofacies as they are more objective, do not suffer so many nomenclatural and interpretational problems, and integrate better with sedimentology and sequence stratigraphy. The very large amount of palaeoenvironmental information encoded in hardgrounds and their biotas, and shell concentrations are illustrated and discussed.

Water depth

The establishment of ancient water depths or palaeobathymetry from palaeontological or sedimentological information is fundamental to most palaeoenvironmental analyses of marine sequences but is probably the hardest parameter to measure. This is because, with the exception of shorelines, there are few sedimentological criteria controlled precisely by water depth and most organisms which show a depth-related distribution, or onshore–offshore trend, are controlled by factors such as light, hydraulic energy, temperature, salinity, nutrients, oxygen, etc., rather than by water depth itself. The depth-related zonation of reef-building organisms is reviewed by Perrin *et al.* (this volume) using direct measurement of reef assemblages preserved *in situ* down ancient reef slopes. The data obtained from such analyses will enable the fine-scale determination of relative or quantitative water depths for different periods of time even though the exact controls may never be fully understood.

Ocean water masses

Whilst earlier works were concerned with the identification of deep-water facies and environments from micropalaeontological data, recent studies by Murray and his colleagues (Murray this volume) indicates that the finer scale distribution of preserved planktonic and benthic

oceanic organisms is related to ocean water masses. Therefore, their distribution in the fossil record can be used as a proxy of past water masses and their development through time. In addition, oxygen and carbon stable isotopes provide information on water temperature and nutrient levels. However, when using the modern oceans as a key to past oceans it is important to realize that modern conditions are by no way typical of former oceans.

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Palaeoecological models, non-uniformitarianism, and tracking the changing ecology of the past

DAVID J. BOTTJER,¹ KATHLEEN A. CAMPBELL,¹
JENNIFER K. SCHUBERT² & MARY L. DROSER³

¹ *Department of Earth Sciences, University of Southern California, Los Angeles, California 90089, USA*

² *Department of Geological Sciences, University of Miami, Miami, Florida 33124, USA*

³ *Department of Earth Sciences, University of California, Riverside, California 92521, USA*

Abstract Palaeoecological models are commonly used by palaeontologists and sedimentary geologists to reconstruct ancient palaeoenvironments. In order to illustrate the ways in which palaeoecological models develop as new information is discovered, four examples are discussed: (1) reefs and fossil cold seeps; (2) biofacies models for strata deposited in ancient oxygen-deficient environments; (3) palaeoenvironmental distributions of post-Ordovician stromatolites; and (4) onshore-offshore trends of trace fossils. The development of physical sedimentological and geochemical criteria that can independently be used for evaluating ancient depositional environments provides a base line with which to assess palaeoecological change through geological time. Thus, the possibility now exists to free palaeoecological models and the study of ancient ecology from traditional uniformitarianism and Lyell's dictum that the 'present is the key to the past', so that palaeoecological models may be developed which are useful for segments of time not anchored in the present. This approach will also be essential for evaluating the changing ecology of the past, which at present is only poorly understood. Future development and independent testing of such palaeoecological models will allow a more complete appreciation of the changing roles of environment, ecology and evolution in the history of life.

Palaeoecological models for palaeoenvironmental reconstruction proceed through a history of development that involves steady incorporation of new information, from modern and ancient environments and ecologies. All palaeoecological models for palaeoenvironmental reconstruction have sets of palaeontological, sedimentological, stratigraphic and sometimes geochemical criteria that are used, in some cases loosely, in others fairly strictly, for interpretative decisions. To a large extent the level of rigour with which a palaeoecological model is applied depends upon how formally it has been conceptualized, and how much agreement exists on the applicable features of the model to specific examples from the geological record. These models are usually designed to lead to a better understanding of depositional environments.

Through their history of use palaeoecological models have developed in a variety of ways. New discoveries can lead to splitting-away of a subset of the phenomena originally thought to be explained by the model. This partitioning then may lead to the development of new palaeoecological models for the newly delimited

phenomena. New discoveries can also lead to the reevaluation of specific palaeoecological criteria previously thought to indicate a particular environmental condition, leading to a refinement of the model. New discoveries may also demonstrate the need for a general reevaluation of the model, or possibly, even abandonment of the model. In these ways, palaeoecological models for palaeoenvironmental interpretations transform and evolve just like any other scientific approaches to solving problems.

Models for reconstructing the history of the natural world, whether they be a history of the Earth or a history of the universe, use uniformitarianism as one of their guiding principles. However, use of palaeoecological models in reconstructing Earth history differs from the use of immutable physical and chemical axioms. The reason for the difference is because biological features of Earth's environments, by their very nature, have changed through time due to organic evolution. It is generally agreed that the utility of body or trace fossils for palaeoenvironmental reconstruction is best

when environmental preferences of the fossils used are not thought to have varied significantly through time, so that taxonomic uniformitarianism can be applied.

Commonly, because of the need for useful approaches to palaeoenvironmental reconstruction, early usage of a new model or criterion is made over broad spans of geological time. However, as refinements are made to palaeoecological models, during their use in field and laboratory studies, it is usually determined that the length of geological time over which a particular feature can be used effectively usually diminishes.

Relatively little attention has been paid to the ecology and palaeoecology of organisms and associated biosedimentological features that have changed their environmental range through time because, under classic uniformitarian principles, these biotic elements would potentially be of less utility for palaeoenvironmental reconstruction. This view, however, has slowly changed as palaeontologists have come to realize that an understanding of ecological and environmental change will lead to a vast source of hitherto untapped information with which to test evolutionary processes, as well as a richer understanding of the history of life. This realization has led to the development of the field of evolutionary palaeoecology, where research is focused on changes in palaeoenvironmental patterns through the Phanerozoic for the varied components of the biosphere.

Many palaeoecological models have been extant in some form since the nineteenth century; other models are relatively new. In order to illustrate the ways in which palaeoecological models develop as new information is discovered four examples are discussed: (1) reefs and fossil cold seeps; (2) biofacies models for strata deposited in ancient oxygen-deficient environments; (3) palaeoenvironmental distributions of Phanerozoic stromatolites; and (4) onshore-offshore trends of trace fossils. In each of these examples we discuss how a particular widely used palaeoecological paradigm has evolved due to discoveries from modern and ancient environments of a more dynamic environmental history than had previously been understood to exist.

Fossil cold seeps

Sedimentary geologists have traditionally maintained a high level of interest in lens- to irregularly-shaped carbonate bodies which contain macrofossils. These fossiliferous carbonate bodies have commonly been interpreted to

indicate deposition in shallow-water marine environments such as reef settings. This interest has been generated both because reef carbonates are typical reservoir rocks for petroleum and because the geological history of reefs has attracted a significant amount of attention as diverse, dynamic communities that show spectacular trends in evolution and extinction (e.g. Fagerstrom 1987; Geldsetzer *et al.* 1988).

The study of fossiliferous carbonate bodies has been extensive, spawning new terms such as bioherm, biostrome and build-up, fuelling much debate about the meaning of the term 'reef' (e.g. Fagerstrom 1987). Because modern reef growth and development are linked directly to associated photosynthetic organisms, that require a photic zone habitat, the predilection to interpret such carbonate features as having been deposited in relatively shallow water has been compelling. Perhaps the best-known example of this problem is the occurrence of azooxanthellate scleractinian corals that produce mounds or build-ups with constructional frameworks in deep-water environments, which in the stratigraphic record are potentially confused with shallow-water reefs (e.g. Teichert 1958; Stanley & Cairns 1988).

Development of palaeoecological models used to determine palaeoenvironments of ancient reefs and associated strata has thus been complex, and no simple and widely-followed formalized approach is available. Furthermore, in the broad study of such deposits, recent investigations of modern environments have led to the realization that many carbonate bodies which were formerly interpreted as shallow-water deposits may in fact be the fossilized remains of deeper-water hydrocarbon cold seeps.

For example, near Pueblo, Colorado (USA) numerous 'limestone masses of peculiar character' (Gilbert & Gulliver 1895, p. 333) occur within the Upper Cretaceous (Campanian) Pierre Shale. These carbonates are more resistant than the shales so that in surface outcrops they tend to erode in a topographically characteristic conical shape, dubbed 'Tepee Buttes' (Gilbert & Gulliver 1895) (Fig. 1). A typical Tepee Butte consists of a cylindrical, vertical core with vuggy carbonates and abundant, articulated specimens of the lucinid bivalve *Nymphalucina occidentalis* (Figs 2 & 3). Gilbert & Gulliver (1895) interpreted the Tepee Buttes to have formed owing to concentrated biotic colonization by these bivalves in an offshore, open environment. Later, Petta & Gerhard (1977) and Bretsky (1978) suggested that the mounds accumulated beneath lagoonal grass



Fig. 1. Upper Cretaceous Tepee Buttes near Pueblo, Colorado (USA). Each butte is 6-8 m high.



Fig. 2. Cross section of Tepee Butte in road cut near Pueblo, Colorado (USA) showing carbonate masses deposited during cold seep activity.

beds, and they re-interpreted Pierre Shale deposition as a terrigenous shallow-marine setting. The model used for this interpretation included a modern analogue of marine grass

banks (which also contain lucinid bivalves) that currently exist along the north coast of St Croix, in the US Virgin Islands (Petta & Gerhard 1977; Bretsky 1978).



Fig. 3. Cross-sections of articulated *Nymphalucina occidentalis* from exposure of Tepee Butte shown in Fig. 2.

At the same time that the Cretaceous Tepee Buttes were being diagnosed as having a shallow-marine grass bank origin, the first stunning announcement was made of the discovery of modern hydrothermal vent faunas in the deep sea (Lonsdale 1977). Unexpectedly, large macroinvertebrates (molluscs, tube worms) were found flourishing at fluid venting sites along oceanic spreading centres, in marked contrast to the otherwise typical deep-sea faunas in the surrounding environment. Subsequently, invertebrate tissues were found to contain endosymbiotic bacteria (e.g. Cavanaugh 1985) that release the energy locked-up in the reduced, sulphide- or methane-rich vent fluids to generate metabolites for the larger hosts (review in Fisher 1990). Hence, with the discovery of chemosynthetically-based ecosystems at hydrothermal vents, and later at hydrocarbon cold seeps and elsewhere (e.g. Hovland & Judd 1988), a new mechanism could be invoked to explain dense, flourishing communities of benthic macroinvertebrates in various deeper water, non-photic zone modern and ancient marine settings. Moreover, hydrothermal vents and cold seeps by their nature also provide point sources of fluids to the overlying depositional environments. For example, closely associated with hydrocarbon seeps are isolated anomalous carbonates precipitated at the sea-floor when methane-rich fluids contact sea water (e.g. Ritger *et al.* 1987). Therefore, another

mechanism which leads to *in situ* precipitation of carbonate lenses and mounds in deep-water marine depositional settings is now available for application to ancient strata. This mechanism can be contrasted with that proposed by several workers for the origin of mud in many ancient mud mounds, such as those that developed during the Carboniferous in the Waulsortian. This mud, which forms the bulk of the mounds, has been attributed to precipitation caused by microbial organisms that lived in surface sediments of the mound (e.g. Monty *et al.* 1982; Bridges & Chapman 1988), without any active hydrocarbon-rich fluid source.

Although the evolutionary history of geochemically-based marine invertebrate communities is still relatively poorly known, examples from the fossil record are increasingly recognized. Uniformitarian principles have been applied to interpret as fossil seeps numerous Cenozoic and Jurassic–Cretaceous carbonate bodies in western North America that contain the fossils of organisms which are chemosymbiotic in modern environments, and that are surrounded by otherwise typically deep-water sedimentary deposits (e.g. Campbell & Bottjer 1993; Campbell *et al.* 1993). For example, subsequent palaeoecological and geochemical work on the Tepee Buttes, with their presumably chemosymbiotic lucinid bivalve fauna, has verified their origin as submarine springs deposited in a deeper-water (hundreds to

thousands of metres) terrigenous seaway (e.g. Kauffman 1977; Arthur *et al.* 1982; Kauffman & Howe 1991).

Continued study of both modern and ancient hot vent and cold seep sites has yielded characteristic patterns useful to their identification; namely, association with appropriate tectonic settings that generate the reduced fluids, enclosure within anomalous sedimentary deposits derived from fluid seepage (e.g. sulphide minerals or isotopically distinctive carbonates) and stratigraphically restricted occurrence of chemosynthetic taxa (e.g. Campbell & Bottjer, 1993; Campbell *et al.* 1993). Campbell & Bottjer (1993) have successfully used these geologic criteria to predict the occurrence of and to identify previously unknown ancient seep sites within deep-water sedimentary sequences that were deposited in convergent tectonic settings along western North America during the Mesozoic and Cenozoic. In earlier more traditional palaeoecological interpretations of these kinds of isolated fossiliferous carbonate bodies they were interpreted either as *in situ* shallow-water deposits (e.g. banks, reefs) or as displaced photosynthetic habitats that slid into deeper-water depositional settings.

For example, the Great Valley Group (Jurassic–Cretaceous) of California is one of the best studied examples of a thick marine siliciclastic sequence deposited within the forearc region of an arc–trench system (e.g. Ingersoll & Dickinson 1981). Preserved within dark coloured Great Valley slope and basinal turbidites along the western Sacramento Valley are isolated carbonate lenses and mounds, originally described by Stanton (1895) as fossiliferous ‘white limestones,’ and interpreted by subsequent workers as shelfal or shoaling reef deposits (e.g. Anderson 1945). Until recently, detailed studies of these anomalous carbonates have been lacking and their significance to the geologic history of western California has gone unrecognized. For Great Valley white limestones, of particular importance is that unusual fossil molluscs have long been known from these deposits, including the bivalves *Modiola major*, *Solemya occidentalis*, *Lucina ovalis* and *Lucina colusaensis* (Gabb 1869; Stanton 1895). In the last decade or so it has been documented that representatives of these same fossil bivalve genera are characteristic of many modern chemosynthetically-based marine invertebrate communities, including those found at methane seeps. Uniformitarian application of the new understanding of life habits of these modern bivalves to these fossil occurrences, as well as considering the presence of complex cement

stratigraphies and methane-derived carbon isotopic signatures from some of the carbonates, has led to the interpretation that many of the white limestones of the Great Valley Group represent ancient cold seeps (Campbell & Bottjer 1991, 1993; Campbell *et al.* 1993). These carbonate bodies mark the sites of ancient, compression-related fluid venting in the Mesozoic forearc and preserve the oldest fossil seeps yet found within subduction-influenced marine depositional environments.

Similar isolated carbonate lenses occur within subduction-related Cenozoic siliciclastic strata of coastal Oregon and Washington (USA). Limestones of variable size and morphologies contain fossils of organisms now recognized to have modern chemosymbiotic representatives. Many of these deposits were ignored by earlier workers or interpreted as shallow-water deposits. For example, Danner (1966) described the large Bear River limestone deposit as a reef or bank based on its exceptionally fossiliferous and misconstrued shallow-water aspect. Deep-water siliceous sponges (*Aphrocallistes*) were misidentified as dasycladacean algae and the bivalve *Solemya* was mistaken for the shallow-water razor clam *Solen* (Danner 1966). The Bear River and other isolated limestone deposits of Oregon and Washington have now also been determined to have had a cold seep origin using, among several criteria, a uniformitarian approach to interpret chemosynthetically (rather than photosynthetically) based fossil occurrences (Campbell 1989, 1992; Goedert & Squires 1990; Campbell & Bottjer, 1990, 1993).

The depositional environments of other carbonate bodies preserved worldwide have recently been reinterpreted utilizing a cold seep palaeoecological paradigm. For instance, Miocene-age carbonate blocks rich in lucinid bivalves (‘*Calcar* a *Lucina*’) from the northern Apennines (Italy) are found within strata deposited as foreland basin turbidites. The blocks were originally interpreted to have been transported from shelfal origins via slumping into deep basins (Aharon *et al.* 1993). Re-study of these carbonate blocks has confirmed their origin as *in situ* cold seep deposits (Aharon *et al.* 1993), and several other examples, from as old as Carboniferous in age, have similarly been reported (e.g. Gaillard *et al.* 1985; Clari *et al.* 1988; Beauchamp *et al.* 1989; Niitsuma *et al.* 1989; von Bitter *et al.* 1990). A problem arises in interpreting these older examples, as is true with so many palaeoecological models. The application of uniformitarianism becomes a much less fruitful avenue of investigation because many of these older deposits are dominated by fossils

which have no chemosymbiotic representatives in modern environments. However, this problem is resolvable if diagenesis has not been too severe and a methane-derived carbon isotopic signature can be recovered from the seep-suspect carbonates (e.g. Clari *et al.* 1988; Beauchamp & Savard 1992).

Thus, the cold seep paradigm has already passed through its first stage of development and application to examples from a broad swath of geological time; the second stage to determine the uniformitarian limitations of the model has begun. Geologists have begun to re-evaluate the origin and development of other carbonate bodies deposited in the spectrum of classically viewed reef and carbonate environments in light of the processes occurring at cold seeps in deeper water settings. For example, Hovland (1990) explores the possibility that hydrocarbons trapped in some ancient reef structures may have actually preceded and initiated reef development. Hovland (1990) also suggests that the seep paradigm might be applied to other palaeoenvironmental settings, such as some features typically interpreted as patch reefs, pinnacle reefs, stromatolitic deposits and even the enigmatic Waulsortian mud mounds. Thus, in the future, application of palaeoecological models for fossil seeps to carbonate bodies in the stratigraphic record may continue to add to the list of seep-related phenomena that were once considered to have been deposited in a spectrum of reef and shallow-water carbonate environments.

The exaerobic biofacies

Black shales are that subset of mudrocks which are laminated and/or fissile. Sedimentary geologists and palaeontologists have worked for decades refining palaeoecological and other models for interpreting the oxygen-deficient environments that lead to the deposition of black shales and the sometimes remarkably well-preserved fossil faunas that are found within them [e.g. see summary of early literature in Dunbar & Rogers (1957)]. These fossils typically exhibit a mixture of planktonic, pseudoplanktonic (organisms that attach to floating algae or logs, and hence are not truly planktonic), nektonic and benthic life habits. Earlier palaeoecological models for interpreting such faunas incorporated data on the stratified nature of the water column in many modern oxygen-deficient basins and utilized a general principle that large benthic animals should not be able to live on the presumably anoxic seafloors where black shales are being deposited. Thus, all fossils found in

black shales were classically interpreted to be planktonic, pseudoplanktonic or nektonic, even if certain of these fossils would typically be interpreted as benthic if they were found in other sedimentary rock types (e.g. Jefferies & Minton 1965). For the purposes of this discussion, fossils that would be interpreted as *in situ* and benthic in sedimentary rocks other than black shales are termed 'typically' benthic.

Rhoads & Morse (1971) synthesized data on modern oxygen-deficient basins in order to understand better the role that increasing oxygen concentrations (which they reported as mL L^{-1} at STP) may have had in the early Phanerozoic history of the metazoa. In a paper on black shales by Byers (1977) this synthesis was utilized to develop a palaeoecological model for recognizing three oxygen-related biofacies in the stratigraphic record. In the Rhoads–Morse–Byers (RMB) model, marine environments with $>1.0 \text{ mL L}^{-1}$ (STP) of dissolved oxygen typically produce a sedimentary record characterized by abundant bioturbation and calcareous body fossils; these conditions result in deposition of the aerobic biofacies. A somewhat oxygen-deficient seafloor environment, with oxygen concentrations between 1.0 and 0.1 mL L^{-1} (STP), is interpreted in the RMB model to lead to deposition of the dysaerobic biofacies, which they described as characterized by a partially bioturbated sedimentary fabric with poorly calcified benthic faunas dominated by deposit feeders. The concept of the dysaerobic biofacies has received wide acceptance in the study of ancient oxygen-deficient basins (e.g. Kammer *et al.* 1986).

The biofacies which represents the lowest oxygen concentrations, the anaerobic biofacies [oxygen concentrations $<0.1 \text{ mL L}^{-1}$ (STP)], is defined in the RMB model as undisturbed (laminated) sediment lacking all benthos. This definition for an anaerobic biofacies tended to reinforce older ideas that 'typically' benthic fossils associated with laminated black shale strata could not be *in situ* but must have been transported to their final place of deposition from an overlying, better-oxygenated water mass or by processes such as turbidity currents or debris flows. Further detailed investigations into the exact nature of biofacies defined by the RMB model have served to drive much of the recent palaeoecological work on black shale biofacies (e.g. Svrda *et al.* 1984).

Controversy over the nature of 'typically' benthic macroinvertebrate fossils found associated with laminated shales can be illustrated with occurrences in the Jurassic (Toarcian) Posidonienschiefer of southern Germany. Be-

cause this unit is generally characterized by laminated black shale, all 'typically' benthic fossils had been interpreted by earlier workers to be either nektonic or pseudoplanktonic [see Kauffman (1981) for a summary of this earlier work]. Later studies maintained that at least some of these 'typically' benthic faunas were truly benthic and that they had lived in 'weak to moderately oxygenated benthic environments' (Kauffman 1981, p. 311). The earlier studies were largely based upon inferences that were made of life habit based on an examination of functional morphology of skeletons of these fossils. However, as shown by the controversies

over determination of life habit that were generated, these examinations of functional morphology of fossil skeletons commonly lacked the resolving power to determine the mode of life, so that additional independent evidence was needed to solve this general black shale palaeoecological problem.

Additional evidence was provided in a study done by Savrda & Bottjer (1987a) on the late Miocene Canyon del Rey Member of the Monterey Formation, in Monterey County, California. Application of a trace fossil model for determining relative amounts of depositional palaeo-oxygenation (see Savrda & Bottjer 1986, 1987b, 1989, for an in-depth discussion of this model) to a 1 m thick *Anadara montereyana*-bearing interval revealed that this section had been deposited under oxygen-deficient conditions (Fig. 4). Furthermore, *Anadara montereyana* occurred only in bedding-plane accumulations at interfaces between laminated and bioturbated strata (Fig. 4) (Savrda & Bottjer 1987a). From an interpreted palaeo-oxygenation curve, made from independent sediment fabric and trace fossil evidence (Fig. 4), it was concluded that these bivalves had lived on the seafloor at the dysaerobic-anaerobic boundary, according to the RMB model (Savrda & Bottjer 1987a).

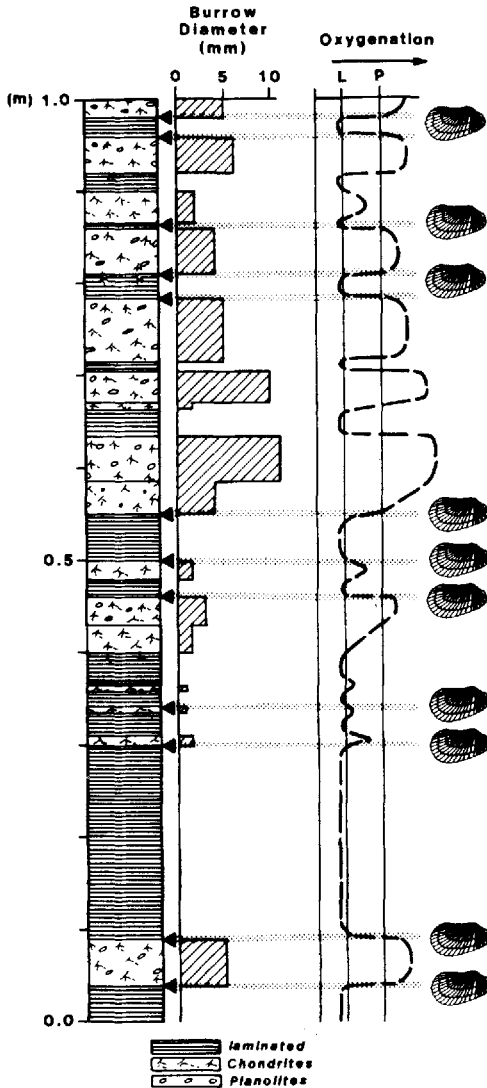


Fig. 4. Presentation of data from high-resolution vertical sequence analysis of section of the Monterey Formation located along Toro Road (locality described in Savrda & Bottjer, 1987a). General sedimentary rock fabric types and trace fossil assemblage composition, illustrated schematically in the column, have been used in conjunction with burrow size data to construct the interpreted relative oxygenation curve using the model described in Savrda & Bottjer (1986, 1987b, 1989). The oxygenation curve shows only relative increases and decreases; determination of specific oxygen concentrations is not possible using this model (Savrda & Bottjer, 1986, 1987b, 1989). Line L represents oxygen levels below which lamination is preserved and above which producers of *Chondrites* can survive. Line P represents oxygen levels below which producers of *Chondrites* can survive, and above which producers of both *Chondrites* and *Planolites* can survive (presence/absence of *Chondrites* and *Planolites* indicated in left-hand column). Arrows, stippled bars and schematic *Anadara montereyana* indicate locations of horizons characterized by dense accumulations of large specimens of this bivalve, all of which occur at transitions between anaerobic and more oxygenated strata. From Bottjer & Savrda (1993), modified from Savrda & Bottjer (1987a).

Thus, 'typical' benthic macroinvertebrates found in black shales were shown to have had a benthic life habit. Using the RMB model, Savrda & Bottjer (1987a) determined that this association of benthic macroinvertebrates, which occurs in bedding-plane accumulations at the dysaerobic-anaerobic biofacies boundary, was an oxygen-deficient biofacies that had great significance but which had not been formally defined for broad use. Therefore, Savrda & Bottjer (1987a) proposed the term 'exaerobic' biofacies for this association, and formally extended it also to include other occurrences of shelly benthic macroinvertebrates within laminated, organic-rich strata of Phanerozoic marine sequences. Earlier studies (e.g. Duff 1975; Morris 1979), like those of Kauffman (1981), had also concluded that fossils found within laminated shales were truly benthic. However, unlike Savrda & Bottjer (1987a), conclusions in these earlier studies were not based on evidence independent from that obtained from the presumed benthic body fossils, nor did these earlier studies place their conclusions within the framework of a general oxygen-deficient biofacies model (e.g. the RMB model), so that they could easily be used to analyse other similar occurrences in the stratigraphic record.

The question remained as to why benthic macroinvertebrates would live in such a presumably hostile oxygen-deficient habitat. Such low levels of oxygenation might provide a refuge for benthic macroinvertebrates from predators which require higher levels of oxygenation (Savrda & Bottjer, 1987a). Oschmann (1993) has hypothesized that the 'blood cockles' *Anadara* and *Scapharca* may have a blood circulatory system that is particularly tolerant of low-oxygen conditions; this may provide an explanation for occurrences of *Anadara montereyana* in the Monterey Formation. The relatively high levels of organic material deposited in oxygen-deficient environments may also have provided a powerful attractant as a food source. Macroinvertebrates found in the exaerobic biofacies may also be similar to already discussed faunas at modern cold seeps as well as hydrothermal vents and sewage outfalls (e.g. Savrda & Bottjer, 1987a; Savrda *et al.* 1991). Chemosymbiosis would enable these organisms to utilize energy from forms of sedimentary organic material that typically cannot be metabolized by macroinvertebrates.

In such settings oxygen levels would need to be sufficient for respiration by these metazoans. Indeed, given the nature of oxygenation gradients from the seafloor to the overlying water column, it is possible that oxygen levels in

water directly overlying the seafloor could have had dysaerobic concentrations. However, such periods of higher oxygen concentrations would probably have been brief, because if they had persisted for any length of time an infauna would have been expected to colonize the seafloor and to leave evidence of bioturbation. Because, by definition, evidence for bioturbation does not exist, oxygen levels must have been more typically at the lower end of dysaerobic concentrations. Thus, this is a biofacies in the black shale biofacies model that does not indicate a specific range of benthic sea-water oxygen concentration values. For example, Wignall & Meyers (1988) described from the Jurassic Kimmeridge Clay (UK) bedding planes covered with macroinvertebrate fossils within otherwise laminated deposits, which Bottjer & Savrda (1993) interpreted as representing the exaerobic biofacies. For these occurrences Wignall & Meyers (1988) postulated an episodically dysaerobic depositional environment where, during brief dysaerobic conditions, shelly macroinvertebrates colonized an otherwise anaerobic setting.

Since its definition from investigation of the Monterey Formation by Savrda & Bottjer (1987a), the exaerobic biofacies has been recognized in numerous studies on a variety of other ancient oxygen-deficient strata (e.g., Dimberline *et al.*, 1990; Baird & Brett, 1991; Doyle & Whitham, 1991; Bottjer & Savrda, 1993). Characterization to date of depositional conditions for the exaerobic biofacies has been made only from interpretations of ancient examples (e.g. Bottjer & Savrda, 1993). Thus, an understanding of the exaerobic biofacies, as a refinement to the general black shale biofacies model, is continually developing. For example, although the exaerobic biofacies has been recognized in stratigraphic units of varying ages, as old as the Palaeozoic (Dimberline *et al.* 1990; Baird & Brett, 1991), the geological time intervals and ranges for which a uniformitarian application of the exaerobic biofacies can be made are currently poorly understood. Similarly, detailed studies of modern analogues to understand the physical and biological dynamics of depositional conditions for this biofacies have not been attempted.

A possible site for occurrence of a modern analogue is the oxygen-deficient Santa Barbara Basin in the California Continental Borderland (Fig. 5). Although not directly comparable to the Miocene Monterey Basins, the basin centre has a general history of bottom-water low oxygenation that extends over much of the Holocene (Pisias 1978). From this basin Cary

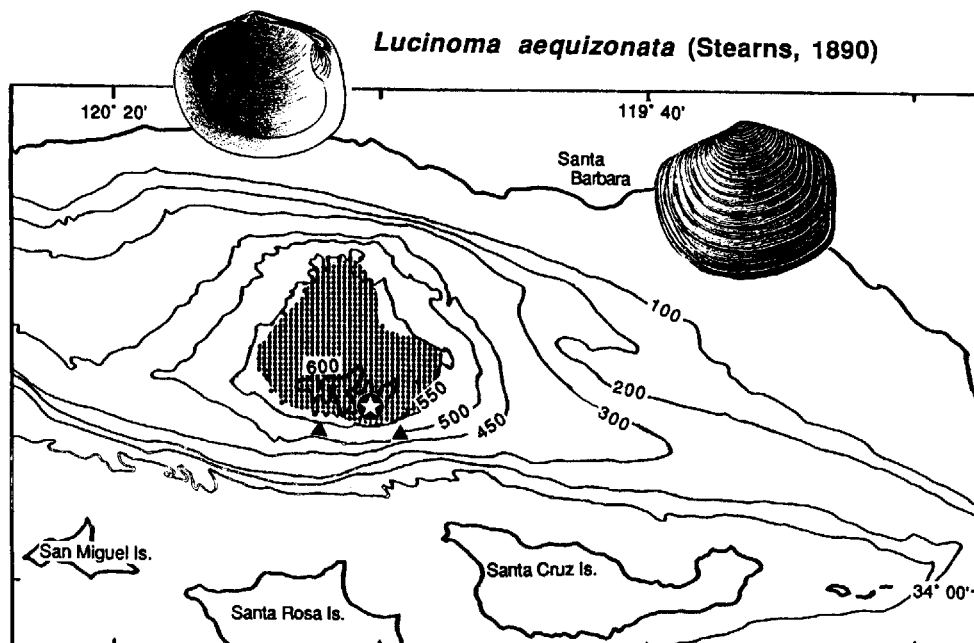


Fig. 5. Distribution of *Lucinoma aequizonata* in Santa Barbara Basin, California Continental Borderland (USA). Stippled portion generally within 550 m contour is the modern laminated non-bioturbated area as defined by Savrda *et al.* (1984), from study of bottom photographs. Locations marked by filled triangles are where samples of these lucinids studied by Cary *et al.* (1989) were collected. The location marked by an open star in a filled circle is where the box-core was taken from, and from which the X-radiograph (AHF 27744) shown in Fig. 6 was made.

et al. (1989) have reported that in bioturbated sediments just above the anaerobic-dysaerobic boundary lives a population of *Lucinoma aequizonata*, which are restricted to an approximate depth range of 490–510 m (Fig. 5). *Lucinoma aequizonata*, a chemosymbiotic lucinid bivalve, lives buried shallowly in the sediment and uses its foot to probe extensively below the shell, leaving burrows that in artificial habitats appeared to remain for 10–15 days (Cary *et al.* 1989). Hydrogen sulphide is necessary for maintenance of the bacterial endosymbionts of this bivalve. Cary *et al.* (1989) suggest that this hydrogen sulphide may come from pockets of black reduced mud that they found in grab samples, which may be discovered and exploited by the probing action of the foot. Production of such tunnels by the foot is typical of many lucinids, and in some taxa commonly exceeds 20 cm in depth (Cary *et al.* 1989; Savrda *et al.* 1991). These descriptions of the distribution and life habits of this modern lucinid by Cary *et al.* (1989) indicate many similarities to the depositional setting proposed for the exaerobic biofacies, particularly if the organisms in this biofacies were chemosymbiotic.

No detailed studies have been made to determine how such lucinids would be distributed as fossils, and whether they would be preserved in an exaerobic biofacies. However, one clue to answering this question can be found in an apparent fossil example of *Lucinoma aequizonata* from the Santa Barbara Basin. A large number of Santa Barbara Basin box-cores, from which X-radiographs have been made of vertical slabs, has been taken by the University of Southern California Marine Geology Laboratory over the past 20 years. A search of these X-radiographs was made for the presence of lucinids. None was found in the surficial parts of the cores, most likely because only a few of the cores were taken from the specific depth contours (490–510 m) where Cary *et al.* (1989) report that they now live. However, a specimen of *Lucinoma aequizonata*, in living position, was found 30 cm beneath the box-core top in an X-radiograph taken from 585 m water depth (Figs. 5 & 6). This is some 80 m deeper than their zone of current inhabitation and is a site where laminations are now being deposited. Because this specimen occurs in life position in the box-core (Fig. 6), below the known burrowing depth for the shell of *L. aequizonata*, the bivalve is

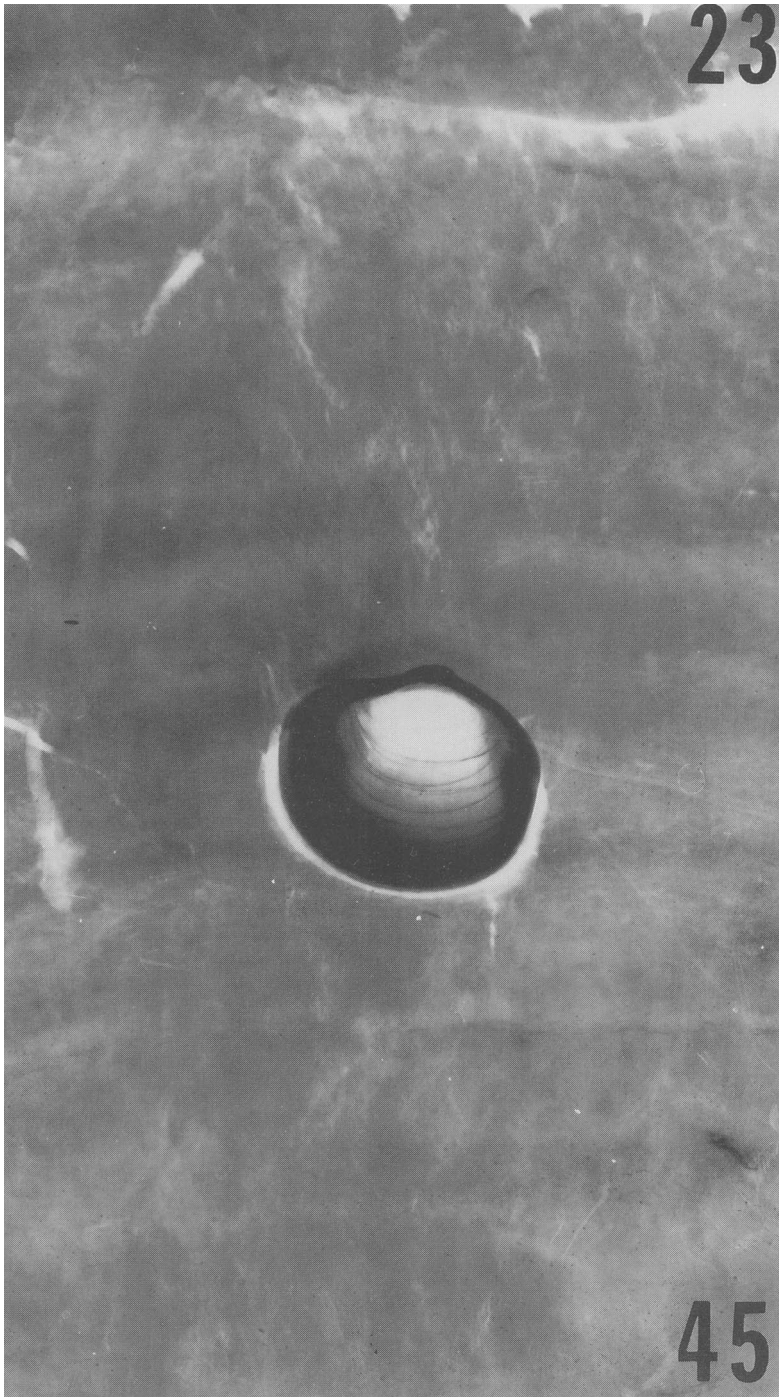


Fig. 6. Print of radiograph of lower part of box core (AHF 27744) containing a specimen of *Lucinoma aequizonata* in life position. Depth in core of the specimen is c. 35 cm, representing a time c. 200 years BP. Core generally shows a fabric of primary laminations that has been blurred and/or destroyed by secondary diffuse bioturbation. No burrows that could have been made by the probing foot of the lucinid are apparent, although possible faint inhalent and exhalent burrows of this bivalve exist. Possibly, because this lucinid existed in organic-rich laminated sediment, little or no probing of the foot was needed to obtain adequate amounts of hydrogen sulphide. Location of core is shown in Fig. 5. Numbers indicate core depth in centimetres.

most likely a fossil. Similarly, because the specimen is oriented vertically in the X-radiograph in life position (Allen 1958), there is no possibility that it was transported to the box core site from some other area.

Sediment surrounding this lucinid is crudely laminated but contains an overprint of diffuse bioturbation, which has caused the laminations to become either blurred or destroyed (Fig. 6). This sediment fabric most likely indicates fluctuating periods of bottom-water oxygenation between anaerobic and dysaerobic conditions, indicating that in the past periods of greater bottom-water oxygenation existed at this site than are found today. This lucinid probably lived at the site during one of the periods of dysaerobic bottom-water oxygenation. The sedimentologic context of this lucinid is therefore one of occurrence in sediment with primary laminations that have a diffuse secondary overprint of bioturbation.

Thus, although bearing many similarities to the depositional setting proposed by Savrda & Bottjer (1987a) for the exaerobic biofacies, presence of bioturbation in this one example indicates that *Lucinoma aequizonata* in the Santa Barbara Basin probably does not represent a direct modern analogue. This is not surprising because, although *Lucinoma aequizonata* appears to have all the appropriate characteristics for a chemosymbiotic exaerobic biofacies organism, its burrowing behaviour is not characteristic. Not only does this allow the lucinid the capability of bioturbating sediments, but it also allows it to live in bioturbated sediments at the anaerobic margin of the dysaerobic biofacies (Fig. 5). Here, as described by Cary *et al.* (1989), the lucinid burrow system links reducing sediment, deposited during some previous interval of anaerobic bottom-water conditions, and usually at some depth below the shell, with somewhat oxygenated bottom water circulated from above, through the inhalent and exhalent siphons. Thus, because all ancient examples of the exaerobic biofacies include only epifaunal and/or semi-infaunal taxa, the search for a direct modern analogue should include settings that only have organisms with these life habits.

Because black shales contain relatively few sedimentary and palaeoecological components, and because they are commonly well-bedded, with abundant laminated intervals, microstratigraphic investigations ('lamina by lamina') of black shale depositional environments are typically done (e.g. Fig. 4). Thus, due to the nature of these sedimentary deposits, definition and understanding of each black shale biofacies, in comparison with broader palaeoecological

models, such as those developed for reefs and associated carbonate strata, is particularly crucial for precise palaeoenvironmental analysis. This is reflected in a variety of other important contributions recently published on definition and understanding of black shale biofacies (e.g., Sageman *et al.* 1991; Oschmann 1991, 1993; Wignall & Hallam 1991; Allison *et al.* this volume), which have produced a lively debate in the literature. Therefore, it can be predicted that there will continue to be fairly intense investigations on the nature of the exaerobic biofacies and on the general phenomenon of benthic fossils found within laminated sedimentary rocks.

Stromatolites

Stromatolites have a long history of study by palaeontologists and sedimentary geologists [for a summary of early studies see, for example, Bathurst (1975), Awramik (1990), Golubic (1991)]. Studies of modern and ancient stromatolites over the past few decades have led to development of a palaeoecological model whereby the presence of stromatolites in post-Ordovician sedimentary sequences has typically been interpreted as indicating extreme, commonly marginal marine, depositional conditions (e.g. Golubic 1991). Much of this has been due to a uniformitarian application to the fossil record of the perceived restriction of modern stromatolites to stressed intertidal environments, such as was concluded in early studies of modern stromatolites at Shark Bay (Australia) (e.g. Golubic 1991). Part of this model was based on the concept that abundant benthic marine metazoans in subtidal environments restrict stromatolite growth (e.g., Garrett 1970; Awramik 1971, 1990; Golubic 1991).

These palaeoecological interpretations have led to the development of a well-known Proterozoic and Phanerozoic palaeoenvironmental history for stromatolites (e.g. Awramik, 1990). During the Proterozoic stromatolites were at their acme of abundance and diversity, and developed in many marine habitats, including level-bottom subtidal and intertidal areas where they formed thick and extensive accumulations (e.g. Awramik 1990). However, in level-bottom subtidal settings they underwent a series of reductions in diversity of form, overall abundance and environmental range in the early Cambrian and middle Ordovician (e.g. Awramik 1971, 1990), when they apparently retreated to environments characterized by hyper- or hypersalinity (e.g. Anadon & Zamarreno 1981) and strong currents or wave action (e.g. Dill *et al.*

1986), which typically cause reduced activity of epifaunal, grazing and/or burrowing animals (e.g. Awramik 1990). This post-Ordovician general exclusion of stromatolites from many normal-marine soft-bottom habitats has been specifically related to the early Palaeozoic diversification of metazoans (e.g. Garrett 1970; Awramik 1971, 1990) that (1) consumed and disrupted stromatolite accumulations by increased predation and bioturbation, (2) increased space competition for substrates favourable for colonization, and (3) accelerated generation and deposition of carbonate sediment (in the form of skeletal debris and silt- and sand-sized bioclasts and pellets) that would bury microbial mats (Pratt 1982). Similarly, the role of stromatolites as the principal or only reef builders during the Proterozoic and in the Cambrian–early Ordovician (along with archaeocyathids and thrombolites) (Kennard & James 1986; West 1988) is thought to have been drastically reduced by stresses associated with the early Palaeozoic metazoan radiation. Although interpretations of the early Phanerozoic decline of the stromatolites as a direct or indirect consequence of metazoan evolution have gained wide acceptance, some workers have sought to understand stromatolite history in terms of major changes in atmospheric oxygen content or sea-water carbonate content (e.g. Grotzinger 1990).

In light of this widely-known palaeoenvironmental history for stromatolites, the occurrence of two beds of stromatolite mounds in the Lower Triassic Virgin Limestone Member of the Moenkopi Formation (Spring Mountains, Nevada, USA), interpreted by Schubert & Bottjer (1992) to have been deposited in level-bottom normal-marine settings, is noteworthy. The upper bed (0.5–1.0 m thick) was removed by erosion from most of the outcrop area, but the lower bed (1.0–1.5 m thick) may be continuous over a distance of 29 km (Schubert & Bottjer, 1992). Columnar digitate forms, laterally-linked hemispheroids and isolated hemispheroids in a micrite matrix make up these mounds (Schubert & Bottjer 1992). A clotted or thrombolitic fabric is common and may be gradational with any of the stromatolitic structures (Schubert & Bottjer 1992). Fossils of organisms considered to be strictly stenohaline, including crinoids, rare ammonoids and an ophiuroid, have been found in the mounds; gastropods and bivalves are also present (Schubert & Bottjer 1992). These palaeoecological data on palaeosalinity, association with adjacent limestones interpreted by sedimentological analysis to have been deposited in subtidal normal marine environments, and lack

of any sedimentological evidence for development of marginal marine conditions or emergence of the mounds (such as erosion surfaces, vugs, evaporite layers or desiccation cracks) leads to the conclusion that the stromatolites accumulated in a normal marine, subtidal, level-bottom environment (Schubert & Bottjer 1992). This interpretation is strengthened when considered in the larger framework of regional palaeoenvironmental interpretations of previous workers, who regard this area of Virgin deposition to represent shelf to ‘basin’ conditions (e.g. Poborski 1954; Bissell 1970).

To evaluate better the significance of these Lower Triassic stromatolites in Nevada, an extensive literature search has shown that stro-

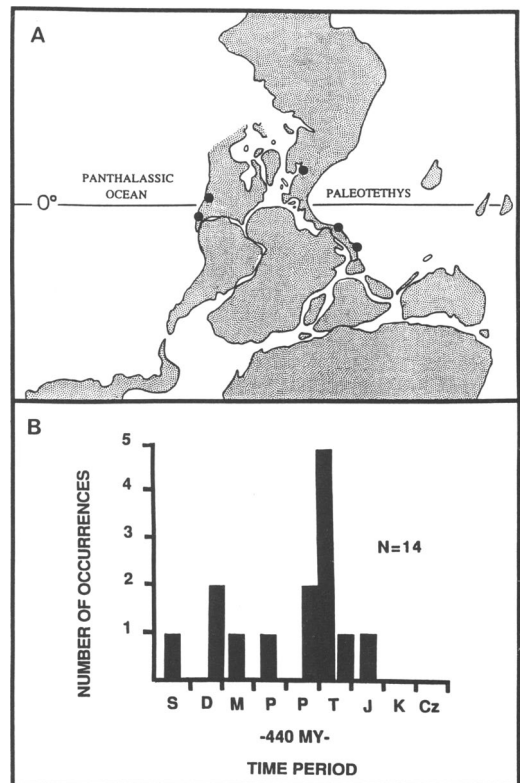


Fig. 7. (A) Map of Early Triassic palaeogeography (after Baud *et al.* 1989) showing locations (black dots, clockwise from left) of normal-marine level-bottom stromatolites in Mexico, western United States (Virgin Limestone), Poland, Transcaucasia and Iran. (B) Histogram of normal-marine level-bottom stromatolites (left to right) in Silurian, Late Devonian, Mississippian, Pennsylvanian, Late Permian, Early Triassic, Late Triassic and Jurassic (K is Cretaceous, Cz is Cenozoic). After Schubert & Bottjer (1992).

matolites, with evidence that they were deposited in normal-marine subtidal level-bottom environments, have been described from four other Lower Triassic localities in North America, Europe and Asia (Fig. 7A) (Schubert & Bottjer 1992). An equivalent literature search was conducted for normal-marine level-bottom stromatolites from strata ranging in age from Silurian through the Cenozoic, and only nine other occurrences were found (making a total of 14 occurrences in the post-Ordovician, including this occurrence) (Fig. 7B). Although the number of occurrences of normal-marine stromatolites documented from the literature is clearly too small to be statistically meaningful, their relative prominence in the Early Triassic (Fig. 7), exemplified by this Virgin Limestone occurrence, is suggestive of a real phenomenon. These Early Triassic stromatolites thus represent an exception to the predictions of the typically accepted palaeoecological model for post-Ordovician stromatolites and palaeoenvironments.

This phenomenon is intriguing because: (1) the post-Ordovician restriction of stromatolites from normal-marine level-bottom subtidal environments is postulated to have been caused by the Early Palaeozoic evolution of the metazoans; and (2) the Early Triassic follows the Permian/Triassic mass extinction, which was the largest of all the Phanerozoic mass extinctions (Raup 1979; Sepkoski 1984). Due to biotic devastation, post-mass extinction aftermath and recovery periods may be a time when metazoan-imposed barriers to the nearshore normal marine environments previously dominated by stromatolites are removed, so that opportunities for stromatolites to thrive in such settings might increase (Schubert & Bottjer 1992). This window of relatively low invertebrate abundance and species richness would be largest following a mass extinction, such as the end-Permian event, which involved a drastic disruption of the benthic invertebrate community, and a slow protracted rebound that was as long as 5 Ma (Hallam 1991).

Thus, these Early Triassic stromatolites may have acted as 'disaster forms' (Schubert & Bottjer 1992). Disaster forms are generalists, commonly of long stratigraphic range which are known primarily from stressful settings between mass extinction events but become abundant and environmentally widespread during times of biotic crisis. The term was first coined by Fischer & Arthur (1977) in reference to species that exhibit episodic blooms and achieve extensive distribution during intervals marked by environmental disruption and drastically reduced mar-

ine diversity. Occurrence of stromatolites, and potentially other disaster forms, might be characteristic of post-mass extinction times which may be marked by a period of ecological relaxation caused by a diminution of natural selective pressures such as predation or competition (Vermeij 1987).

This suggestion that stromatolites may have acted as disaster forms, particularly after the Permian/Triassic mass extinction, adds a refinement to the palaeoecological model of post-Ordovician stromatolite palaeoenvironmental distribution. It also indicates that palaeoecological models for determining palaeoenvironments may be less useful for mass extinction aftermaths, and other periods of environmental and ecological stress, when normal ecological conditions may have experienced a breakdown.

Trace fossil onshore-offshore patterns.

Perhaps the best known palaeoecological application of trace fossils is their use as broad palaeoenvironmental indicators. Seilacher (1967) demonstrated that certain suites of trace fossils, characterized by similar trace morphology and hence tracemaker behaviour, typically occur in strata deposited under similar depositional conditions. Each characteristic suite is termed an ichnofacies and each ichnofacies is named for a typical component trace fossil. These generally include the *Trypanites* (hard substrata), *Glossifungites* (firm substrata), *Skolithos* (nearshore shifting substrata), *Cruziana* (shelf above storm wave base), *Zoophycos* (outer continental shelf and slope) and *Nereites* (deep sea) marine ichnofacies. As a palaeoecological model, ichnofacies have typically been defined on observations made from the fossil and stratigraphic record, and not from modern environments (e.g. Seilacher 1967; Bromley 1990). The use of ichnofacies has been widespread for over two decades, with the definition of a few new but minor ichnofacies as the only major changes (e.g. Bromley 1990).

Increasing knowledge of the body fossil record has slowly led to the realization that fossils of many marine invertebrate taxa first appear in sedimentary rocks deposited in one environment, but through geological time they can migrate into other environments or retreat from environments in which they once occurred. Although earlier studies had given some indication that such patterns of change exist, they were initially recognized to be very significant for benthic invertebrates at the palaeocommunity level in the Palaeozoic (e.g. Sepkoski & Sheehan 1983; Sepkoski & Miller 1985) and the

Mesozoic (Jablonski & Bottjer 1983). These patterns of palaeoenvironmental change for body fossils have been investigated using time–environment diagrams, which are depicted with time on the vertical axis and environment on the horizontal axis. Subsequent investigations have shown that such patterns can also be recognized for individual higher taxa of benthic macro-invertebrates (e.g. Bottjer & Jablonski 1988; Jablonski & Bottjer 1991).

As for body fossils, earlier studies have demonstrated that several trace fossil genera did not have a static environmental distribution through time. For example, irregular echinoid burrows (*Scolicia*) were shown by Frey & Seilacher (1980) to follow a palaeoenvironmental pattern through time that, as would be expected, parallels that of the irregular echinoids. This pattern shows an origin in Jurassic shelf environments and migration into the deep sea in the Cretaceous (Frey & Seilacher 1980).

Moreover, studies of trace fossils in an ichnofacies context began to indicate that several other traces with distinctive morphologies probably had not had a static palaeoenvironmental distribution through time. In particular, *Zoophycos* and *Ophiomorpha*, which had been described as characteristic trace fossils of specific ichnofacies, were reported by a number of studies from anomalous environmental settings (e.g. Osgood & Szmuc 1972; Kern and Warme 1974). Bottjer *et al.* (1988) expanded upon these earlier reports of palaeoenvironmental variability in *Zoophycos* and *Ophiomorpha* distribution to produce time–environment diagrams for each of these ichnogenera (Figs 8 & 9).

Zoophycos, a complex spreiten structure with two basic forms (helical and planar; Hantzschel 1975) occurs throughout most of the Phanerozoic (Fig. 8). The oldest data point for *Zoophycos* (480–490 Ma), reported by Bottjer *et al.* (1988), is from Lower Ordovician strata deposited in inner shelf environments (Fig. 8) (Droser, 1987). Because data are sparse for this time interval, this apparent environment of first occurrence should be viewed with caution. By the Early Silurian (430–440 Ma) *Zoophycos* was present in slope and deep-basin environments, and was present in nearshore environments by the Early Devonian (390–400 Ma) (Fig. 8). *Zoophycos* was fairly common in nearshore habitats through the remainder of the Palaeozoic, after which time it is unknown from these environments (Fig. 8). The youngest inner- and middle-shelf occurrences (80–90 Ma) are Late Cretaceous in age and the youngest outer shelf occurrence (20–30 Ma) dates from the Oligocene

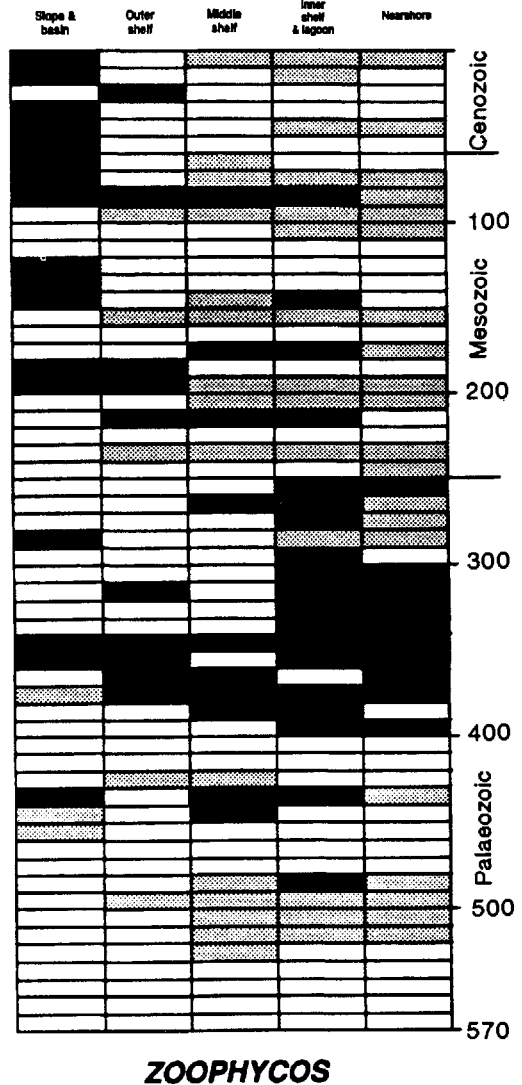
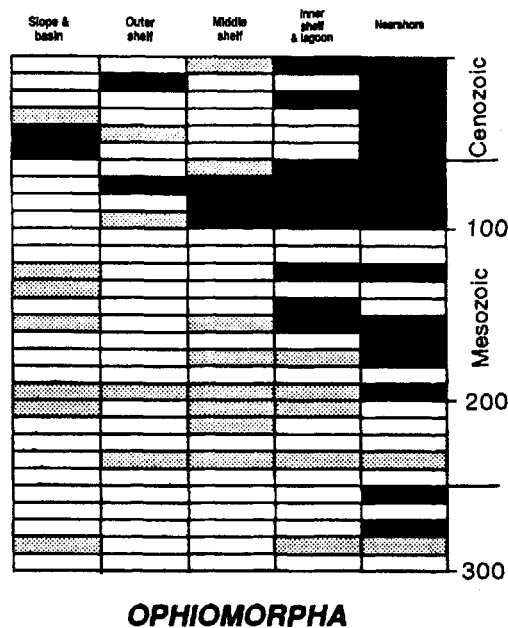


Fig. 8. *Zoophycos* time–environment diagram. Vertical axis is in millions of years; each box has a duration of 10 Ma. Horizontal axis shows palaeoenvironmental categories. Presence of *Zoophycos* indicated by a black box, absence indicated by a box with stippling; white boxes = no data available. Database the same as in Bottjer *et al.* (1988); modified from Bottjer & Droser (1992).

(Fig. 8). *Zoophycos* has remained common in slope and deep-basin environments since its first Palaeozoic occurrence in that setting (Fig. 8). This palaeoenvironmental pattern for *Zoophycos* shows at least a 150 Ma history of common occurrence in all environments examined by Bottjer *et al.* (1988), until its disappearance from



OPHIOMORPHA

Fig. 9. *Ophiomorpha* time-environment diagram. Vertical axis is in millions of years; each box has a duration of 10 Ma. Horizontal axis shows palaeoenvironmental categories. Presence of *Ophiomorpha* indicated by a black box, absence indicated by a box with stippling; white boxes = no data available. Database the same as in Bottjer *et al.* (1988); modified from Bottjer & Droser (1992).

nearshore environments at the end of the Palaeozoic, followed by subsequent retreat from shelf environments in the Cretaceous and Cenozoic. The Neogene to present-day occurrence of *Zoophycos* in slope and deep-basin settings (Fig. 8) conforms to the environmental conditions classically defined for the *Zoophycos* ichnofacies. The study by Bottjer *et al.* (1988) confirmed indications in the literature that such an onshore-offshore pattern existed for *Zoophycos* (Frey & Pemberton 1985; Seilacher 1986).

Ophiomorpha, a three-dimensional branching burrow system with pelleted linings (Hantzschel 1975), occurs primarily in the Mesozoic and Cenozoic (Fig. 9). The oldest known occurrence, however, is in Lower Permian strata (270–280 Ma) deposited in nearshore environments (Chamberlain & Baer 1973). By the Late Jurassic (150–160 Ma) *Ophiomorpha* was present in inner shelf environments, and by the mid-Cretaceous (90–100 Ma) this trace fossil was present in middle-shelf to slope and deep-basin environ-

ments (Fig. 9). Since then it generally has occurred in all the environments studied by Bottjer *et al.* (1988), although it has remained most common in its original nearshore habitat (Fig. 9)

Over a period of 170 Ma *Ophiomorpha* progressively appeared in more offshore environments, from the oldest known occurrence in the Early Permian nearshore to its mid-Cretaceous appearance in slope and deep-basin settings. Therefore, *Ophiomorpha*, typically thought to be a common component of the *Skolithos* ichnofacies, was restricted to environments with bathymetric characteristics of this classical ichnofacies only during the first two-thirds (120 Ma) of its history (Fig. 9). All *Ophiomorpha* occurrences considered by Bottjer *et al.* (1988) occurred in sandstone, indicating that the organisms making the traces had widened the range of sandy substrata that they could colonize through time, from nearshore to shelf sands and then offshore to submarine canyon and deep-sea fan sands.

Since the development of the ichnofacies model it has become apparent that onshore-offshore trends such as those described above are particularly common for a variety of Early Palaeozoic trace fossils. The meandering, patterned and spiral traces that are typically thought to be characteristic of the classic deep water *Nereites* ichnofacies apparently first originated in the late Precambrian and Cambrian in strata deposited in shallow water environments (e.g. Fedonkin 1980; Crimes & Anderson 1985; Paczesna 1986; Hoffman & Patel 1989; Sokolov & Iwanowski 1990; Crimes & Droser 1992). These ichnogenera subsequently appear in strata truly deposited in deep water environments during the Ordovician and Silurian (Crimes *et al.* 1992). Such migration of Early Palaeozoic trace fossil assemblages into deeper-water environments seemingly parallels patterns for Early Palaeozoic body fossil assemblages documented by Sepkoski & Sheehan (1983) and Sepkoski & Miller (1985). These patterns of migration for Early Palaeozoic trace fossils indicate that the development of characteristic trace morphologies in specific environments, or ichnofacies, was perhaps only realized by the Silurian or Devonian. Thereafter, although the observations underlying the ichnofacies concept generally remain undisputed, a number of middle Palaeozoic to Recent ichnogenera show a more dynamic historical pattern.

Therefore, although the broad behavioural trends reflected in morphological characteristics of trace fossil suites can generally be used for determinations of environment of deposition,

integration of onshore-offshore trends of trace fossils with the ichnofacies model requires the recognition that particular ichnogenera could have a Phanerozoic history independent of that predicted by study of ichnofacies (for further discussion see Goldring, this volume). An understanding of such onshore-offshore trends has thus produced a potential refinement of the ichnofacies model.

Conclusions

As demonstrated by these examples, palaeoecological models for reconstruction of palaeoenvironments come in all shapes and sizes, and can undergo change in a variety of ways. The cold seep palaeoecological model has appeared and evolved due to discoveries of a new ecological system in modern environments, the chemosynthetically-based community, thus causing a re-evaluation of the origins of some of the stratigraphic phenomena formerly interpreted through utilization of a reef and shallow-water carbonate palaeoecological model. In contrast, the exaerobic biofacies was defined through examination of phenomena found in rocks, thus leading to refinements in the black shale biofacies model, which was initially founded on study of modern environments; attempts to study modern depositional settings of the exaerobic biofacies have only just begun. Similarly, changes in the palaeoenvironmental significance of post-Ordovician stromatolites, which was also initially based on their study in modern environments, have come from increased study of the stratigraphic record. The early development of the ichnofacies model, however, was based on observations from the stratigraphic record and refinements of this model, through study of onshore-offshore trends in trace fossils, continue to be made through study of trace fossils in ancient sedimentary rocks.

The early history of development of palaeoecological models, exemplified by the taxonomic uniformitarianism approach, tended towards pure uniformitarianism, in the sense of 'the present is the key to the past'. The development of the cold seep model to date has proceeded in this traditional sense. However, many of the recent additions and refinements to palaeoecological models have come from studies of ancient settings. These modifications to palaeoecological models have been coupled with the development of geochemical and sedimentological criteria that can be used independently for evaluating ancient depositional environments. In this way,

because it is believed that these sedimentological and geochemical criteria can be used in a uniformitarian sense, at least through the Phanerozoic, they provide a base line with which to assess palaeoecological change.

Thus, the possibility now exists to free palaeoecological models and the study of ancient ecology from traditional uniformitarianism and 'the present is the key to the past', where what is learned from modern environments is then applied to the geological record as far back in time as is possible. One may develop palaeoecological models which are useful for a segment of geological time not anchored in the present. For example, *Ophiomorpha* appears to be an excellent indicator for nearshore palaeoenvironments during the first 120 Ma of its history (Fig. 9), from the Early Permian to the Late Jurassic. Similarly, the palaeoecological model for pre-Ordovician stromatolites and palaeoenvironments is, to a large extent, distinct from modern environmental distributions.

Such an approach is not only useful for palaeoenvironmental analysis but is essential for an understanding of the changing ecology of the past. In a large sense, in our past efforts to recognize changing ecological patterns from study of the fossil record we have been blinded by our reliance on traditional uniformitarianism and 'the present is the key to the past'. For example, over the past decade we have learned to understand the importance of mass extinctions. However, we have not paid sufficient attention to the possibility that aftermaths of mass extinctions may have had dramatically different ecological structures and roles, which would then alter the way palaeoecological models can be applied to these intervals, as compared with 'normal' ecological times between intervals of mass extinction.

Thus, the door is open for a surge in palaeoecological studies as the discipline is freed from some of the strictures of traditional uniformitarianism. In a modified uniformitarian approach, palaeoecological models should be dynamic, as has been the evolutionary process, with similar biotic features playing varying ecological roles and occupying different environments at different spans of geological time. Palaeoecologists have caught a glimpse of this dazzling aspect of life's history, but have only just begun to reconsider the verity of many of the static aspects of currently-used palaeoecological models. A more complete appreciation of the changing roles of environment, ecology and evolution in life's history will come with further development of what has come to be known as evolutionary palaeoecology.

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An introduction to the techniques, limitations and landmarks of carbonate oxygen isotope palaeothermometry

RICHARD M. CORFIELD

Department of Earth Sciences, University of Oxford, Parks Road, Oxford OX1 3PR, UK

Abstract: The fractionation of oxygen isotopes is temperature dependent. The ratio of the two commonest isotopes (^{16}O and ^{18}O) in carbonate fossils can, in principle, be used to reconstruct the temperature of ancient oceans. Fossil foraminifera are commonly analysed in the Cenozoic and late Mesozoic and, when appropriately identified and separated, sea-surface, deeper-water and bottom-water temperatures can be inferred. More ancient carbonate precipitating macrofossils (e.g. molluscs, brachiopods) have also been used, as well as inorganically precipitated carbonate cements. Drawbacks to the oxygen isotope method of palaeotemperature determination are the uncertainties in the isotopic composition of the water of ancient oceans, the occurrence of non-equilibrium fractionation in organically precipitated calcites (especially in macrofossils) and diagenetic alteration to the $\delta^{18}\text{O}$ values of carbonate fossils.

Notwithstanding these limitations, trends in palaeotemperature and/or the $\delta^{18}\text{O}$ of seawater, such as the Palaeozoic ^{18}O enrichment, the long-term Cretaceous and Tertiary climatic cooling, the middle Miocene ^{18}O enrichment, as well as the Pleistocene succession of glaciations, are discernible from appropriate studies of fossil carbonates.

The oxygen isotope method of palaeotemperature determination is integral to the science of palaeoceanography. No other single method is so widely quoted as a proxy for determining temperature fluctuations in the geological past, and, perhaps because of this, the method has been the subject of several previous reviews since its inception in the 1940s and 1950s (e.g. Bowen 1966; Shackleton 1982; Hudson & Anderson 1989; Anderson 1990). The explicitly quantitative nature of the method has made it attractive to a wide variety of earth scientists, although historically there has been an uneasy balance within the community between those whose confidence in oxygen isotope palaeothermometry is perhaps optimistic, and those who mistrust the method because of quasi-mystical misgivings about its reliance on high-technology (e.g. Ericson & Wollin 1966).

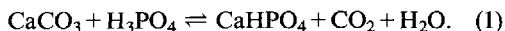
The temperature dependence of the fractionation of the oxygen isotopes $^{16}\text{O}/^{18}\text{O}$ was first calculated by Urey (1947). His computations were supported by the work of the Chicago group (Epstein *et al.* 1951, 1953), who demonstrated empirically the relationship between temperature and ^{18}O abundance in marine shells. The subsequent story of the development of stable isotope palaeothermometry is most effectively told by the problems that it has been used to investigate. These landmarks of oxygen isotope palaeothermometry are discussed below.

This contribution is divided as follows: (1) the procedures necessary to produce high-quality oxygen isotope ratio measurements; (2) the

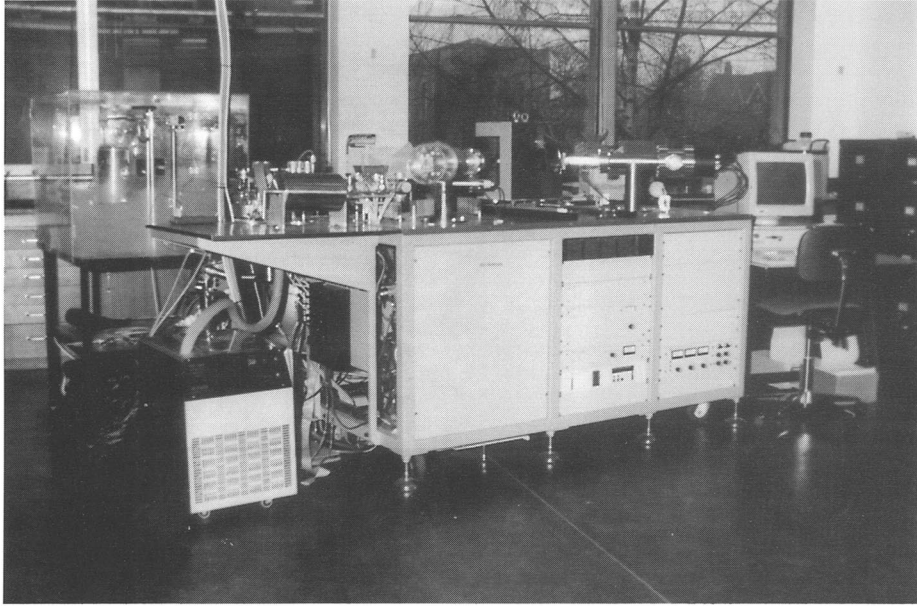
limitations of the technique; and (3) the major features of Earth history that have been highlighted by oxygen isotope measurements.

The techniques of oxygen isotope palaeothermometry

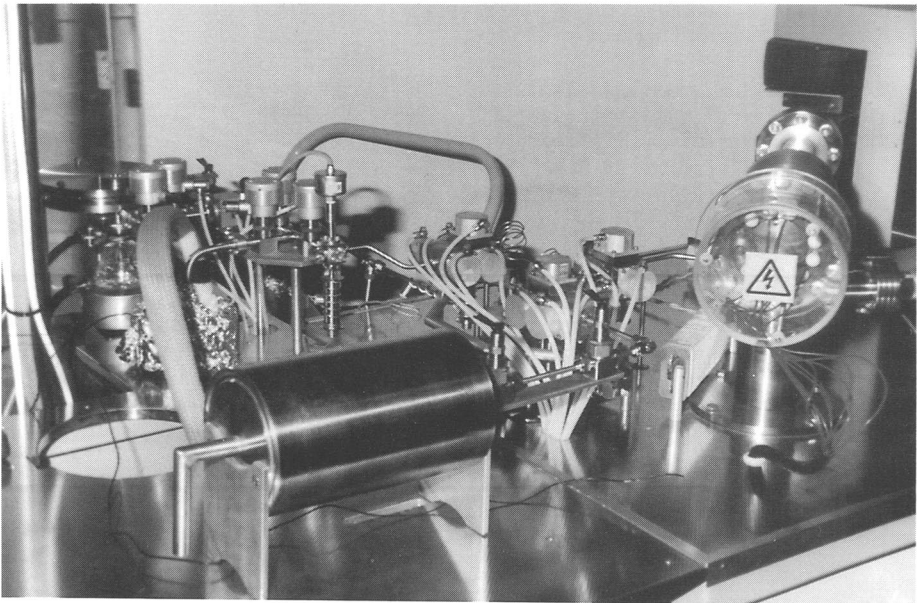
The instrument used to produce oxygen and carbon isotope ratio measurements is the stable isotope ratio mass spectrometer (Fig. 1). This type of mass spectrometer was originally devised by Nier (1947) and modified by others. The material to be analysed (in the case of this discussion some form of carbonate) is converted to CO_2 , typically by acidification in dehydrated orthophosphoric acid, following essentially the same techniques as those pioneered by McCrea (1950). The reaction is as follows:



The CO_2 and H_2O are drawn off from the reaction and the gas mixture typically passed through a cryogenic trap at -100°C to remove water and other impurities. The CO_2 gas is then admitted to the sample side of the mass spectrometer inlet. The gas is ionized within the source of the mass spectrometer and after balancing the ion beam pressures against a gas of known isotope composition (the reference gas) a comparison of the molecular isotopic abundances is made and the ratio calculated. To measure small samples where the ion beam pressure is low (i.e. when using small numbers



(A)



(B)

Fig. 1. PRISM stable isotope ratio mass spectrometer in the Oxford Laboratory; (A) detail of on-line automatic carbonate digestion device (B).

of foraminifera) liquid nitrogen is used to condense the CO_2 into a smaller volume which is then isolated. Subsequent sublimation of the CO_2 yields proportionally higher ion beam pressures. Today, instruments with three Fara-

day collectors are typically used, so capturing ion beams in the mass range 44–46. The ratio of mass 46:44 yields the oxygen isotope ratio after appropriate corrections ($\delta^{18}\text{O}$) while the ratio of mass 45:44 yields the carbon isotope ratio

($\delta^{13}\text{C}$) after appropriate corrections.

Stable isotope ratio results are reported using the conventional δ notation to indicate deviation (in parts per thousand or ‰) from the arbitrary PDB (Pee Dee Formation, Belemnite) standard of zero using the following equation:

$$\delta^{18}\text{O} = \frac{[(^{18}\text{O}/^{16}\text{O})_{\text{sample}} - (^{18}\text{O}/^{16}\text{O})_{\text{standard}}]1000}{(^{18}\text{O}/^{16}\text{O})_{\text{standard}}} \quad (2)$$

In addition, a correction for the contribution to the ion beams from rare molecular isotopic species of CO_2 (e.g. $^{17}\text{O}^{18}\text{O}^{13}\text{C}$) must be made (Craig 1953).

Today, the machinery necessary to produce an oxygen isotope ratio determination is widely available and the above calculations are performed automatically. Carbonate digestion, water stripping and gas capture are often also performed automatically, using on-line systems which are commercially available [e.g. the VG OPTIMA or PRISM with the ISOCARB I (common acid-bath) or ISOCARB II individual acid-bath devices]. In many respects the mass spectrometers and ancillary carbonate digestion devices required to turn a carbonate precipitate into gas (CO_2) and measure it are automated to such a degree that some users of stable isotope data suggest that the role of the analyst is merely that of an attendant. The truth is that automatic procedures allow unattended running, but because of this the data screening between runs must be more rigorous than in manual systems where screening is performed as the measurement is made. Automatic instruments must have standards run routinely to check for minor errors which might remain undetected, and which might therefore imperceptibly degrade the quality of the sample data. The situation remains now as it always has, namely that interactive control by the analyst breeds accurate, precise and reproducible data. Automation cannot change this, or, to put it another way, as Scott (1984) has observed, 'the more they overtake the plumbing, the easier it is to stop up the drains'.

The limitations of oxygen isotope palaeothermometry

Variations in the isotopic composition of seawater

Analyses of oxygen isotope ratios can provide information about palaeotemperature change in

the geological past subject to certain qualifications. Chief among these is the fact that absolute palaeotemperature calculations rely on a knowledge of the isotopic composition of the water (δ_w) from which the carbonate was precipitated. The various palaeotemperature equations used to convert delta values to $^\circ\text{C}$ reflect the importance of the δ_w term.

Although several palaeotemperature equations exist for the purpose of converting δ values to temperatures (e.g. Epstein *et al.* 1953; O'Neil 1969; Anderson & Arthur 1983), the author prefers the version of Shackleton (1974) who rewrote the O'Neil *et al.* (1969) relationship as:

$$T = 16.9 - 4.4\Delta + 0.10\Delta^2, \quad (3)$$

where Δ is $\delta_c - \delta_w$. The advantage of this version for foraminiferal analyses is that O'Neil (1969) obtained calibration data close to 0°C , which is supposedly close to average deep-ocean temperatures (Shackleton 1984).

One of the most common causes of variation in the $\delta^{18}\text{O}$ of seawater during geological time is the frequent intervals of glaciation that characterize the Earth's climatic history. Polar ice is formed from precipitation of waters which were evaporated at low latitudes. Water vapour formed by evaporation is enriched in ^{16}O and the remaining ocean water is therefore enriched in ^{18}O . Hence, during periods of glaciation (e.g. the last glacial maximum) seawater and, by implication, carbonates precipitated from it, will have a more positive $\delta^{18}\text{O}$. The fact that this effect has the same polarity as the temperature-dependent fractionation of $^{16}\text{O}/^{18}\text{O}$ means that some effort must be invested in estimating the δ_w of ancient seawater before palaeotemperature calculations can be attempted. This limitation was originally recognized by Shackleton (1967) while investigating the causes of $\delta^{18}\text{O}$ variability during the Pleistocene. His hypothesis was that deep waters were of stable temperature and, consequently, that any variability in benthic foraminiferal $\delta^{18}\text{O}$ would be due to ice-volume fluctuations alone. The fact that similarly large $\delta^{18}\text{O}$ variations are found in benthonic foraminifera as are found in planktonic foraminifera was used by Shackleton as the basis for inferring that ice-volume fluctuations were the dominant control on $\delta^{18}\text{O}$ fluctuations during the Quaternary. Formerly, Emiliani (1955) had suggested that the total range of $\delta^{18}\text{O}$ variability during the Pleistocene was solely attributable to temperature change. The perception of ice volume as the predominant control on Quaternary $\delta^{18}\text{O}$ fluctuations in the deep sea persisted

throughout the 1970s and early 1980s; for instance, Shackleton (1982) reaffirmed that subsequent to the onset of northern hemisphere glaciation, *c.* 3 Ma ago, variations in the $\delta^{18}\text{O}$ composition of the ocean swamp was in effect attributable to temperature change. However, more recently, Chappell & Shackleton (1986), by comparing $\delta^{18}\text{O}$ variations in a late Pleistocene Pacific core with the height of sea-level terraces in New Guinea, have suggested that a cooling effect of *c.* 1.5°C (*c.* 0.4‰) in the deep ocean may contribute to the observed $\delta^{18}\text{O}$ variability after all. What is clear from these maturing hypotheses is that, even in the relatively recent past, assumptions about the δ_w of ancient oceans are not straightforward.

To facilitate estimates of palaeotemperature from more ancient sediments Shackleton & Kennett (1975) estimated that the $\delta^{18}\text{O}$ composition of pre-middle Miocene ocean was *c.* 0.9‰ more negative than the present day. Their estimate is based on the current size of the Antarctic ice sheet and its presumed much smaller volume prior to the middle Miocene. Hence, in their interpretation scheme, any calculations of absolute temperatures prior to the middle Miocene must use a different estimate of δ_w , ideally from independent data.

A radically different interpretation of the history of Cenozoic oxygen isotope change is that of Matthews & Poore (1980) and Prentice & Matthews (1988), who asserted that modifying the δ_w term on the basis of estimates of polar ice-volume leads to unrealistically cool tropical sea-surface temperatures (SST) in sediments older than the middle Miocene. They suggest that there is no compelling evidence on which to base ice-volume estimates, and that tropical SST have stayed constant through time at a theoretical maximum of 28°C. Any increase in insolation merely leads to energy loss from the ocean surface by evaporative flux rather than by further SST increase. In their interpretation scheme, by assuming that tropical SST in the thermally stable western equatorial regions of the Indian and, particularly, Pacific Oceans have remained constant through time, they assert the probable presence of significant volumes of ice on the poles at least as far back as the early Eocene and possibly also during the Cretaceous.

Even more radically, Prentice & Matthews (1991) have proposed the 'snow gun hypothesis'. In this they reassert that ocean deep water $\delta^{18}\text{O}$ fluctuations predominantly reflect thermal variability, and furthermore suggest that deep-ocean warming during the Tertiary drove ice-volume increases. Their proposed mechanism is through the formation of variable quantities of warm

saline deep water in the low latitudes, which they suggest forced episodic increase in southern ocean SST and hence increased moisture flux to the Antarctic continent, thereby stimulating ice-sheet growth.

It is clear that these two groups of hypotheses, one based on assumptions about deep-ocean temperature variability and the other based on assumptions about SST variability, lead to fundamentally conflicting interpretations of the history of Cenozoic $\delta^{18}\text{O}$ change. As yet there is no clear consensus as to which is correct, or whether the oxygen isotope community should embrace some form of compromise scheme.

On a smaller scale, both temporally and spatially local fluctuations in δ_w occur due to variations in the ratio of evaporation : precipitation. The range in $\delta^{18}\text{O}$ in today's ocean is 2‰ (Hudson & Anderson 1989), which corresponds to a temperature change of *c.* 8°C. In nearshore areas marine waters register more negative $\delta^{18}\text{O}$ due to dilution with fresh waters (Craig & Gordon 1965), while in enclosed basins, such as the Mediterranean, evaporation results in more positive $\delta^{18}\text{O}$ (Thunell *et al.* 1987). Clearly, for these reasons $\delta^{18}\text{O}$ and salinity in marine waters are correlated and it is common in the literature to see $\delta^{18}\text{O}$ used as a proxy for salinity variations. Note, however, that salinity does not affect the fractionation of oxygen isotopes in a manner analogous to that of temperature.

Diagenetic alteration of $\delta^{18}\text{O}$ values

In his excellent review of the subject, Marshall (1992) has discussed the diagenetic limitations on the retrieval of original stable isotope ratios from carbonates. He differentiates four factors that control the post-depositional chemical alteration of a carbonate: (1) the diagenetic potential of the carbonate; (2) the proportion of cementation; (3) the proportion of recrystallization; and (4) the diagenetic environment. The following brief discussion on diagenetic alteration of oxygen isotope ratios is substantially based on his review, to which the reader is referred.

Diagenetic potential The diagenetic potential of high-magnesium calcites and aragonite is higher than low-magnesium calcites. In addition, small particles have a higher diagenetic potential than large particles because of their greater surface area:volume ratio. Due to these differences mineralogically well-preserved low-magnesium calcites are common in the fossil record, but mineralogically well-preserved high-magnesium calcites and aragonite are rare. Because high-

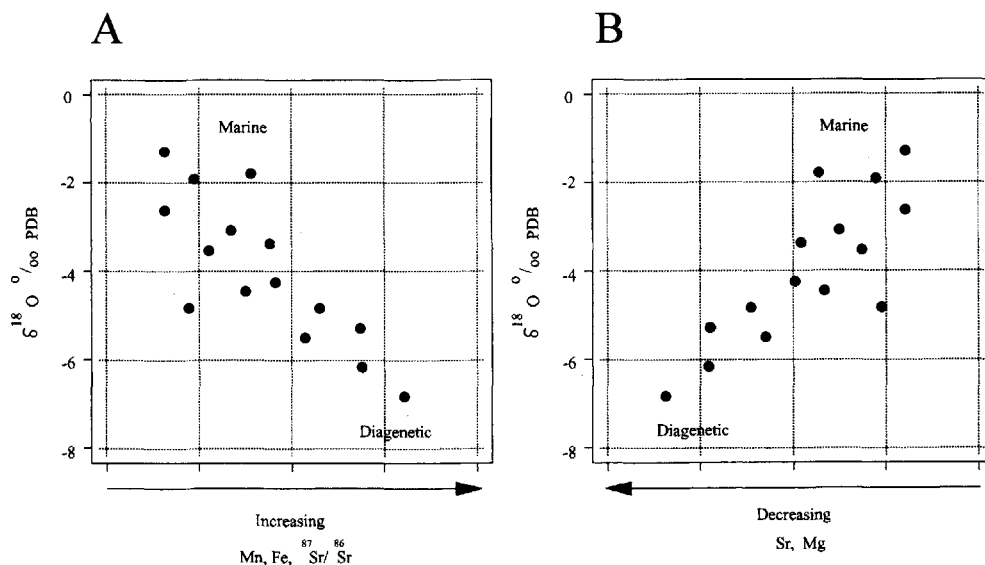


Fig. 2. The recognition of diagenesis by the backstripping technique of Marshall (1992). (A) Increase in Mn, Fe and $^{87}\text{Sr}/^{86}\text{Sr}$ are often correlated with a diagenetic decrease in $\delta^{18}\text{O}$; (B) decrease in Sr and Mg are often correlated with a decrease in $\delta^{18}\text{O}$.

magnesium carbonates and aragonites are metastable, the preservation of primary mineralogy is a good indication that $\delta^{18}\text{O}$ analyses are likely to yield original values.

Cementation Cementation is the precipitation of a mineral in the pore spaces of a rock and is one of the most common diagenetic processes leading to an alteration in isotopic composition of a carbonate sample. Cementation can proceed uniformly in a fluid of uniform post-depositional isotopic composition or in stages in fluids of varying isotopic composition. In the former case estimation of the proportion of the two phases may allow evaluation of the original isotopic composition, while in the latter case the complexities of the rocks' cementation history may preclude the characterization of the original isotopic composition of the rock.

Recrystallization. Recrystallization in sedimentary systems is principally driven by dissolution and reprecipitation rather than by solid-state processes. Multiple recrystallization events are also a possibility (Land 1986; Marshall 1992). Where recrystallization occurs in pore waters of similar isotopic composition to the host rock (as occurs when the water:rock ratio is low because the system is closed, or nearly so) the newly precipitated phase is similar to that of the host rock, and consequently the post-depositional isotopic deviation from the primary composition

will be minor. In open systems with greater porosity and permeability the water:rock ratio is higher and the resulting diagenetic changes are accordingly of potentially greater magnitude.

Diagenetic environments Most Cenozoic and late Mesozoic $\delta^{18}\text{O}$ measurements made for the purposes of palaeotemperature reconstruction are from material recovered from the ocean basins (generally planktonic and benthonic foraminifera). Analyses from older sediments are generally from terrestrial exposures of continental shelf deposits using either macrofossils or limestone cements.

The deep-ocean environment, from which most Deep Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) material is recovered, is often of low diagenetic potential, at least at relatively shallow burial depths. However, if the sediment is more deeply buried than *c.* 400 m and especially if temperatures are elevated, cementation and recrystallization processes act to lighten $\delta^{18}\text{O}$ values (Elderfield *et al.* 1982; Miller & Curry 1982; Marshall 1992). For example, in the heavily cemented K-T boundary transition at ODP Hole 807C $\delta^{18}\text{O}$ ratios are significantly more negative than in other, shallower K-T boundary sections (Corfield & Cartlidge 1993a).

Nearly all Palaeozoic limestones were deposited in water depths shallower than *c.* 20 m. Hence, their potential for sub-aerial exposure,

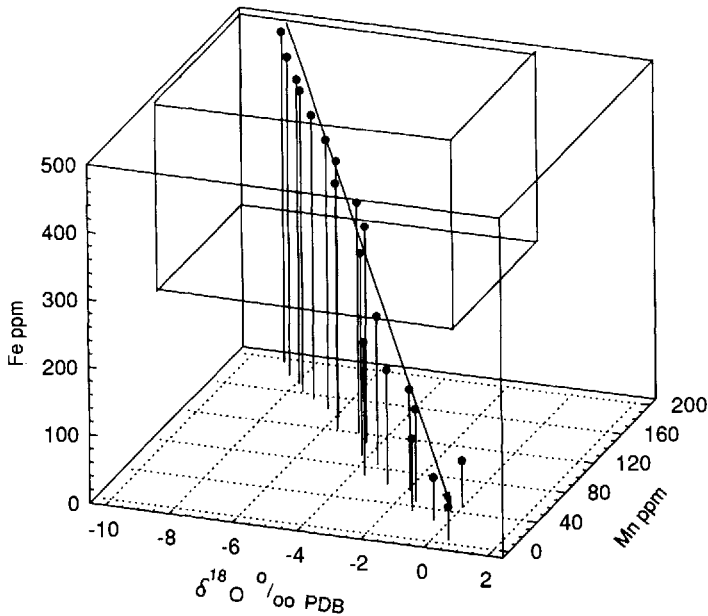


Fig. 3. Multiple regression showing relationship between $\delta^{18}\text{O}$ and Mn and Fe concentration both within and between carbonate rock samples during diagenetic alteration. The backstripping trajectory is shown, and the inner cube shows the volume of $\delta^{18}\text{O}/\text{Mn}/\text{Fe}$ space in which diagenesis becomes overwhelmingly likely.

and consequent diagenetic alteration of $\delta^{18}\text{O}$ values by isotopically negative precipitation, is very high (Marshall 1992). Note, however, that in arid areas the upper part of the exposure may have enriched $\delta^{18}\text{O}$ values because of evaporative removal of ^{16}O .

A basic test for diagenetic alteration of utility in both deep sea core and meteoric diagenetic environments is correlation of (particularly) $\delta^{18}\text{O}$ variability with carbonate content. Carbonate content reflects the porosity and permeability of a rock fabric. Samples with high CaCO_3 tend to have more and larger pores between the calcite rhombs and are thus more susceptible to diagenetic alteration by interaction with pore fluids than rocks with, for example, a more clayey content (Zachos *et al.* 1989).

Notwithstanding the capacity for diagenetic complications in carbonate fossils and cements, it is possible to identify diagenetic alteration both within and between samples (intrasample vs. intersample testing). In some cases of intrasample diagenetic alteration it is possible to identify the likely isotopic composition of the water from which the carbonate was originally precipitated, by tracing trajectories of post-depositional alteration through multiple $\delta^{18}\text{O}$ and elemental abundance measurements. This

technique has been termed 'backstripping' by Marshall (1992) and is fundamentally an analysis of relative concentrations of diagenetically sensitive indicators which span the spectrum of a sample's post-depositional history. It is based on the observation that certain elemental concentrations increase (e.g. Fe, Mn or $^{87}\text{Sr}/^{86}\text{Sr}$) or decrease (e.g. Sr or Mg) with increasing alteration from their marine values, and hence can be correlated with $\delta^{18}\text{O}$ or $\delta^{13}\text{C}$, which also tend to change systematically with progressive diagenesis. Figure 2 illustrates a plot of $\delta^{18}\text{O}$ against some of the primary geochemical tracers of diagenesis. Using multiple correlations of diagenetically sensitive elements against $\delta^{18}\text{O}$ or $\delta^{13}\text{C}$ it is possible to identify, in some cases, the likely primary isotopic composition of the fossil or whole-rock sample.

In addition to tracing trajectories of diagenetic transformation, absolute elemental concentrations can be useful in warning of likely diagenetic alteration. Figure 3 illustrates a hypothetical example of $\delta^{18}\text{O}$ vs. Mn and Fe concentration. As well as illustrating the potential through multiple backstripping for identifying likely primary $\delta^{18}\text{O}$ values, the inner cube shows the volume of $\delta^{18}\text{O}/\text{Mn}/\text{Fe}$ space where diagenesis in Cenozoic and the Mesozoic rocks

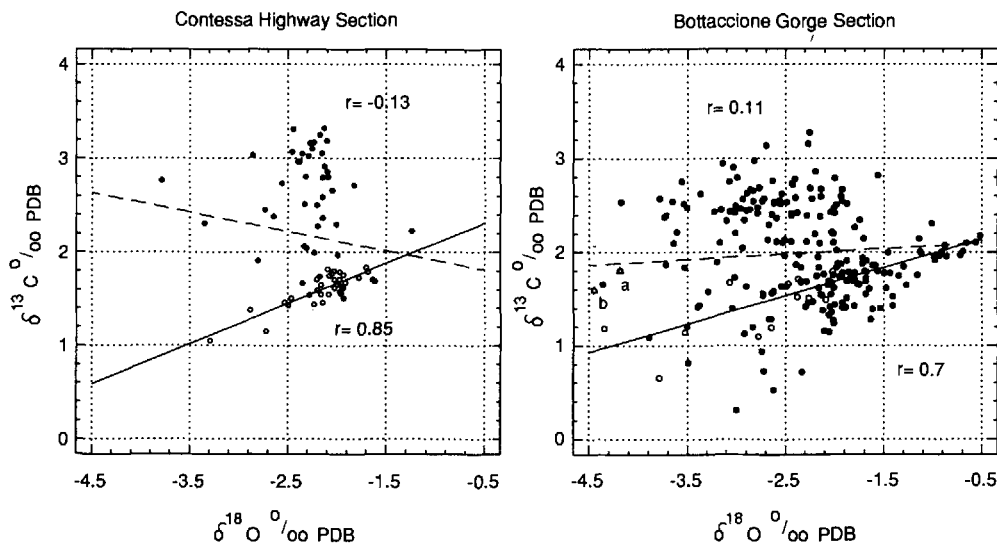


Fig. 4. $\delta^{18}\text{O}$ vs $\delta^{13}\text{C}$ cross-plots of Bottaccione Gorge and Contessa Highway data. Note that each data set as a whole is uncorrelated ($r = -0.13$ and 0.11) but that adjacent samples above the K-T boundary (open circles) show a much higher correlation ($r = 0.85$ and 0.7), suggesting that the signal in these samples is probably dominated by diagenetic alteration rather than marine $\delta^{18}\text{O}$ values. Redrawn from Corfield *et al.* (1991).

may be assumed to swamp the primary signal. This is based on the observation that Fe concentrations > 300 ppm and Mn concentrations > 75 ppm may suggest diagenetic alteration (fig. 3 in Anderson 1990), while $\delta^{18}\text{O}$ values much in excess of $c. -2.5\%$ (in the Cenozoic and the Mesozoic, although not the Palaeozoic) suggest re-equilibration with isotopically negative fluids. In Palaeozoic rocks, which are commonly depleted in ^{18}O , the $\delta^{18}\text{O}$ value at which diagenesis becomes the likely cause of the isotopic composition is correspondingly more negative.

Cathodoluminescence (CL) microscopy and X-ray diffraction can also be useful in highlighting areas within fossils and whole-rock samples which have been altered by diagenesis (Marshall 1992). Luminescence is caused by activator ions from diagenetically sensitive elements (especially Mn^{2+}) within the rock fabric. Hence CL may indicate, qualitatively, the presence of diagenetic alteration.

Although multiple geochemical and isotopic measurements on single fossil or whole-rock samples comprises the most rigorous test for diagenetic alteration (Veizer 1992), intersample correlations (i.e. comparisons of single measurements on different samples throughout a stratigraphic sequence) can also be instructive in showing the spread of values throughout a

measured section and highlighting likely areas of diagenetic alteration. The most simple intersample test for diagenetic alteration is to plot $\delta^{18}\text{O}$ vs. $\delta^{13}\text{C}$ and search for areas of correlation in adjacent samples, although in certain cases, as Marshall (1992) pointed out, $\delta^{13}\text{C}/\delta^{18}\text{O}$ covariance may reflect primary signals. Corfield *et al.* (1991) used this technique to suggest that the reason for an anomalously protracted $\delta^{13}\text{C}$ minimum in the earliest Palaeocene of the Bottaccione Gorge and the Contessa Highway was diagenetic rather than primary (Fig. 4).

There is no general, encompassing rule for the recognition of diagenetic alteration in ancient carbonate fossils or cements. Each case must be judged within the context of its diagenetic potential and likely post-depositional history. However, as a rough guide, Table 1 shows a key which may be of some use in identifying carbonate fossils or cements which have undergone post-depositional alteration.

The landmarks of oxygen isotope palaeothermometry

This section examines some of the major palaeoceanographic and palaeoclimatic features

of Earth history that have been illuminated by the use of $\delta^{18}\text{O}$ measurements.

Table 1. Key for the recognition of diagenetic alteration in carbonate fossils and cements

-
1. Sample from deep sea cores (go to 2).
 1. Sample from land exposure (go to 3).
 2. SEM check reveals presence of calcite overgrowths (go to 4).
 2. SEM check does not reveal presence of calcite overgrowths (go to 5).
 3. Significant cementation, i.e. hard chalk or limestone (go to 6).
 3. Friable sample i.e. little cementation (go to 7).
 4. Probable dissolution of carbonates and cementation in saturated pore waters, diagenesis likely, especially if $\delta^{18}\text{O}$ lighter than c. 0‰ in Cenozoic samples. Correlate carbonate contents with $\delta^{18}\text{O}$ to corroborate this. Note that in Cretaceous samples the uncertainty of potential $\delta^{18}\text{O}$ values is greater, essential to correlate carbonate contents with $\delta^{18}\text{O}$.
 5. No calcite overgrowths and $\delta^{18}\text{O} > 0\%$ in Cenozoic deep-sea samples. Sample probably minimally altered.
 6. Cathodoluminescence scan of selected samples. If completely luminescent then pervasive diagenetic alteration likely. If not, or luminescent in patches (go to 8).
 7. SEM check reveals presence of calcite overgrowths (go to 4).
 7. SEM check does not reveal presence of calcite overgrowths (go to 5).
 8. $\delta^{18}\text{O}$ analysis of non-luminescent samples, correlate with carbonate content and trace element abundances (e.g. Mg, Mn, Sr, Fe). If no correlation than diagenesis not likely.
-

The Pleistocene

Since its inception, oxygen isotope palaeothermometry has, to a large extent, focused on the Pleistocene principally because of the availability of deep-sea material from conventional ocean coring techniques, and also because the deep-ocean environment was perceived as one of stability where a sedimentary record could be retrieved which did not contain the interruptions and complications common in outcrop sections of shallower-water carbonates. In palaeoceanographic terms the special significance of the Pleistocene was the large variation in global temperatures that had accompanied the late Cenozoic glacial ages.

Ice volume vs. temperature change. This topic has been discussed above. Essentially, the consensus

now is that δ_w and temperature fluctuations together control the $\delta^{18}\text{O}$ composition of carbonates precipitated from ancient seawater. The remaining argument concerns what proportion of the $\delta^{18}\text{O}$ signal can be attributed to each of these two effects.

Milankovitch cyclicity Hudson & Anderson (1989) have referred to the 'heroic age of Pleistocene oceanic geology'. They allude to the activities of the CLIMAP project that set out to map the temperature of the Earth's surface at 18 000 Ka using a combination of factor analysis of foraminiferal distributions (Imbrie & Kipp 1971) and $\delta^{18}\text{O}$ analysis of foraminiferal calcite. This attempt culminated in the mid-1970s when Hays *et al.* (1976) demonstrated that systematic variations in the Earth's orbital geometry were indeed responsible for the succession of glaciations in the late Cenozoic. Subsequently, Shackleton *et al.* (1983), using subtle variations in vertical carbon isotope gradients ($\Delta\delta^{13}\text{C}$), further demonstrated that a CO_2 decrease in the atmosphere preceded ice-volume increase (onset of glacial periods) and a CO_2 increase in the atmosphere preceded ice-volume decrease (onset of interglacial periods).

Time-scale calibration. An important inference resulting from the discovery of a linkage between the near-metronomic variations in the Earth's orbital geometry and the $\delta^{18}\text{O}$ cycles, identified and labelled (Emiliani 1955; Shackleton & Opdyke 1973; Ruddiman *et al.* 1986) in Pleistocene marine sequences, is that it should, in theory, be possible to use the former to date the latter accurately, provided that all the oxygen isotope stages are present, i.e. the section is continuous. Imbrie *et al.* (1984) produced a stacked $\delta^{18}\text{O}$ record for the past 800 Ka and used astronomical data to fine-tune the time-scale that the record was plotted against. However, the data set generated by Imbrie *et al.* (1984) and a newer data set generated by Prell *et al.* (1986) showed discrepancies in the interval before 620 Ka that led to problems in developing a time-scale that was tuned against astronomical forcing. Shackleton *et al.* (1990) re-examined the interval between 620 and 800 Ka using data from the eastern equatorial Pacific sites DSDP 677 and 677B. They concluded that the currently adopted radiometric dates for the Matuyama–Brunhes boundary, the Jaramillo and Olduvai Subchrons and the Gauss–Matuyama boundary underestimate their true astronomical ages by between 5 and 7%. Hence time-scales tuned against astronomical variations probably represent the

most precise method yet developed of determining the date of events in the late Neogene and the Quaternary.

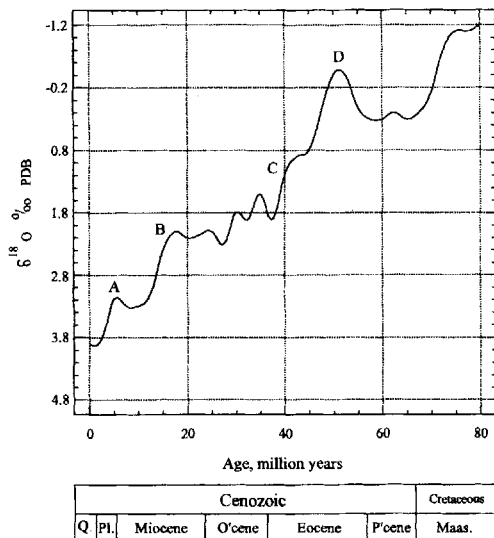


Fig. 5. Generalized oxygen isotope curve for the Cenozoic showing the major isotopic features discussed in this paper. Redrawn from Crowley & North (1990).

The Cenozoic: greenhouse termination and the onset of glaciation

The Cenozoic $\delta^{18}\text{O}$ record (Fig. 5), generated by the analysis of both benthic and planktonic foraminifera from DSDP and ODP drilling sites over the past two decades (e.g. data in Douglas & Savin 1975; Shackleton & Kennett 1975), is one of general ^{18}O enrichment with decreasing age. Superimposed on this long-term change [actually beginning around the Cenomanian/Turonian boundary; see Corfield *et al.* (1991), Jenkyns *et al.* (1994) and below] are several higher frequency fluctuations. These are predominantly enrichments (i.e. associated with cooling or glacial expansion), with the exception of a pronounced negative excursion (D on Fig. 5) in the early Eocene that is widely interpreted as a climatic optimum (e.g. Crowley & North, 1990; Plaziat, this volume). This climatic optimum is associated with reduced latitudinal thermal gradients (Shackleton & Boersma 1981; Zachos *et al.* 1993) and may be similar to the situation that prevailed in the Cretaceous. It is, however, important not to confuse the broad climatic optimum of the early

Eocene (lasting between 50 and 55 Ma) with the short-term $\delta^{18}\text{O}$ (and $\delta^{13}\text{C}$) event associated with the Palaeocene/Eocene boundary (Kennett & Stott 1991) at c. 57 Ma.

The first substantial ^{18}O enrichment in the Cenozoic (c. 1‰; see C in Fig. 5) occurs between 37 and 40 Ma at the Eocene/Oligocene boundary (Savin *et al.* 1975; Shackleton & Kennett 1975; Miller *et al.* 1991). Comparison of benthic $\delta^{18}\text{O}$ data and planktonic $\delta^{18}\text{O}$ data from the equatorial Pacific (Keigwin 1980; Keigwin & Corliss 1986) showed that a significant component (30–40%) of this change could be attributed to ice-volume increase (perhaps one-half of the volume of the East Antarctic Ice Sheet) while the rest of the change could be attributed to a cooling of the deep waters by c. 3°C. However, Zachos *et al.* (1992) have recently presented a compelling case for most of this $\delta^{18}\text{O}$ increase being attributable to ice-volume enlargement, to almost Pleistocene levels.

Another major threshold in the Cenozoic $\delta^{18}\text{O}$ record (B in Fig. 5) is the middle Miocene $\delta^{18}\text{O}$ increase associated with the Neogene expansion of the East Antarctic Ice Sheet. Initially this profound $\delta^{18}\text{O}$ increase in benthic foraminifera was thought to be associated with the onset of Antarctic glaciation (Shackleton & Kennett 1975; Savin *et al.* 1975, 1985; Woodruff *et al.* 1981), although the relative contributions to the $\delta^{18}\text{O}$ increase of ice volume vs. temperature remains obscure (Matthews & Poore 1980; see discussion in Miller *et al.* 1991 and above). More recently, several authors (e.g. Barrera *et al.* 1985; Savin *et al.* 1985; Vincent *et al.* 1985; Miller *et al.* 1989, 1991; Wright *et al.* 1992) have identified this mid-Miocene ^{18}O enrichment in deep waters at a number of sites in the Atlantic, Indian and Pacific Oceans. However, estimates of the precise timing of this cooling episode vary.

An important aspect of this event is the disparity between the magnitude of the ^{18}O enrichment in planktonic and benthic foraminifera. Miller *et al.* (pers. comm.) estimate that this enrichment was 0.8‰ in benthic foraminifera while only 0.4‰ in planktonic foraminifera. This discrepancy has been ascribed to either: (1) a cooling of deep waters superimposed on the ^{18}O enrichment of seawater due to the growth of the East Antarctic Ice Sheet (Matthews & Poore 1980; Prentice & Matthews 1988); or alternatively (2) a warming of sea-surface waters coincident with the ^{18}O enrichment caused by this phase of Antarctic ice growth (Shackleton & Kennett 1975), the net effect of which would be to decrease the apparent amplitude of the ^{18}O enrichment in sea-surface waters.

Prior to the recovery of well-preserved middle

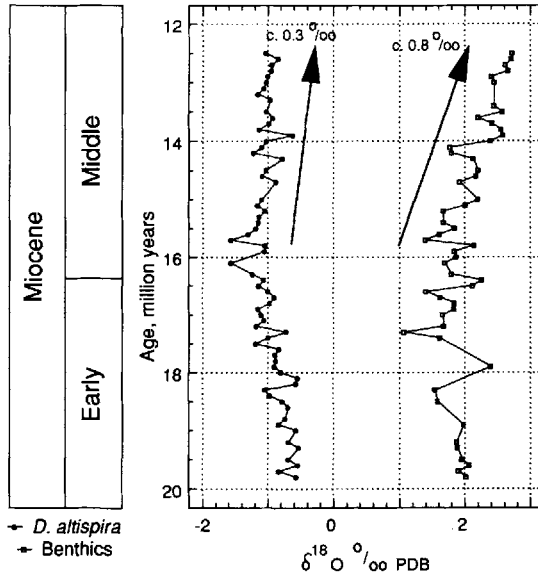


Fig. 6. $\delta^{18}\text{O}$ data from ODP Hole 806B (western equatorial Pacific). Note that the amplitude of the Middle Miocene enrichment in planktonic (*Dentoglobigerina altispira*) and benthonic foraminifera in sediments younger than c. 15.5 Ma is different in the two groups. The increase in $\delta^{18}\text{O}$ in planktonic foraminifera is c. 0.3‰ while in benthonic foraminifera the increase is 0.8‰. Redrawn from Corfield & Cartlidge (1993b).

Miocene sediments during Leg 130 of the Ocean Drilling Program, estimates of the magnitude of the planktonic and benthic ^{18}O enrichment during the middle Miocene $\delta^{18}\text{O}$ shift had not been made at the same location. Corfield & Cartlidge (1993b), by comparing benthic and planktonic $\delta^{18}\text{O}$ data from the same core in the western equatorial Pacific (Fig. 6), were able to confirm that the magnitude of the ^{18}O enrichment in benthic foraminifera was 0.8‰ while the magnitude of the ^{18}O enrichment in planktonic foraminifera was 0.3‰, very similar estimates to those put forward by Miller *et al.* (pers. comm.).

The most recent significant ^{18}O enrichment in the Cenozoic $\delta^{18}\text{O}$ record occurs in the Pliocene and is associated with the initiation of Northern Hemisphere glaciation (particularly the expansion of the mid-latitude northern ice-sheets). This feature is shown at A in Fig. 5 and, as discussed below, comprises several phases of ice growth and cooling.

The onset of the ^{18}O enrichment dates from c. 3.2 Ma and may be associated with the most recent phase of North Atlantic deep-water formation (Shackleton *et al.* 1984; Hodell *et al.* 1986; Crowley & North 1990). Between 3.2 and 2.4 Ma ^{18}O enrichment continued with higher frequency variability superimposed on this overall trend (Raymo *et al.* 1989), suggesting

ice-sheet fluctuations of between one-quarter and one-half of late Pleistocene ice volumes. The next phase of cooling occurred between c. 2.8–2.6 Ma (Jansen *et al.* 1988), together with significant cooling in the southern hemisphere (Cieselski & Grinstead 1986), while at 2.4 Ma ice rafting in the North Atlantic intensified in tandem with a further increase in $\delta^{18}\text{O}$ (Shackleton *et al.* 1984; Raymo *et al.* 1989).

The Mesozoic: the essential 'greenhouse' Earth

In general terms, sediments older than the K–T boundary which are suitable for $\delta^{18}\text{O}$ analyses become progressively scarcer. $\delta^{18}\text{O}$ measurements have been made successfully on late Cretaceous oozes (e.g. Douglas & Savin 1975, 1978; Barrera *et al.* 1987) but below the Cenomanian/Turonian boundary progressively greater emphasis is placed on the analysis of various carbonate cements or unaltered macrofossil calcite for palaeotemperature reconstruction using the oxygen isotope method. The well documented broad cooling trend through the Cenozoic has its origins at the Cenomanian/Turonian boundary (Fig. 7). The reasons for this are currently unclear, although there may have been some kind of climatic threshold reached

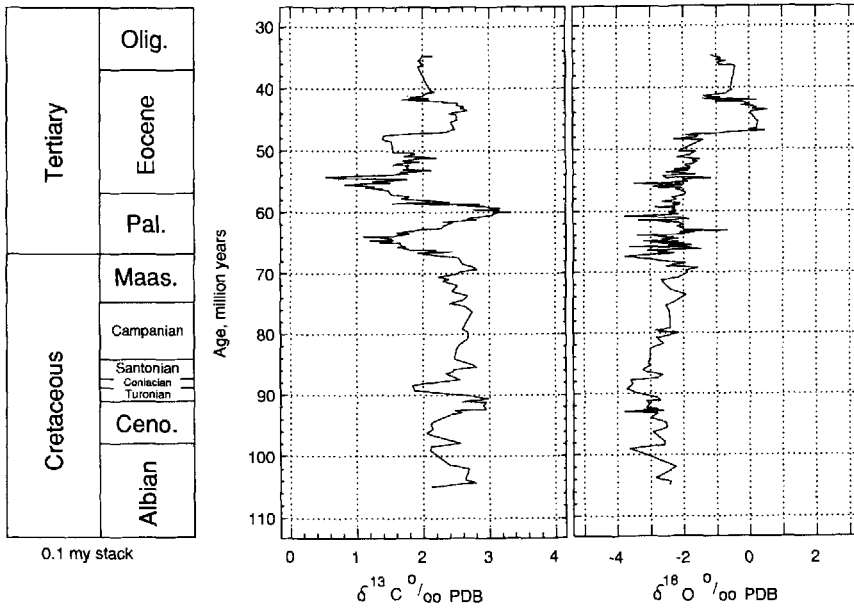


Fig. 7. Whole-rock isotope stratigraphy from the Bottaccione Gorge and the Contessa Highway showing the long-term enrichment through the late Cretaceous and the Cenozoic, together with the climatic threshold at the Cenomanian/Turonian boundary. Data are averaged into 0.1 Ma increments of modelled time. Redrawn from Corfield *et al.* (1991).

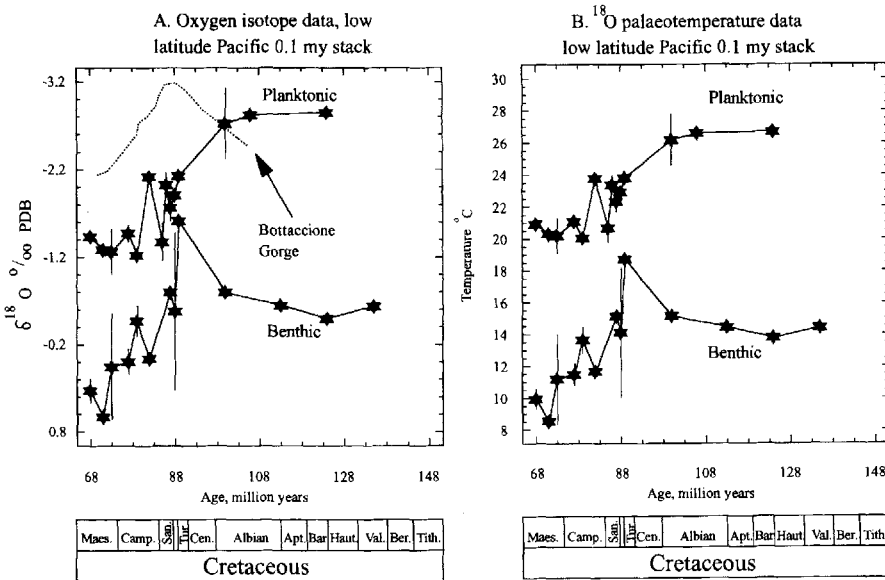


Fig. 8. Oxygen isotope curve for the Cretaceous based on planktonic and benthonic foraminifera from the equatorial Pacific. Also shown for comparison is the Cretaceous portion of the Bottaccione Gorge curve (dotted line). Redrawn from Spicer & Corfield (1992).

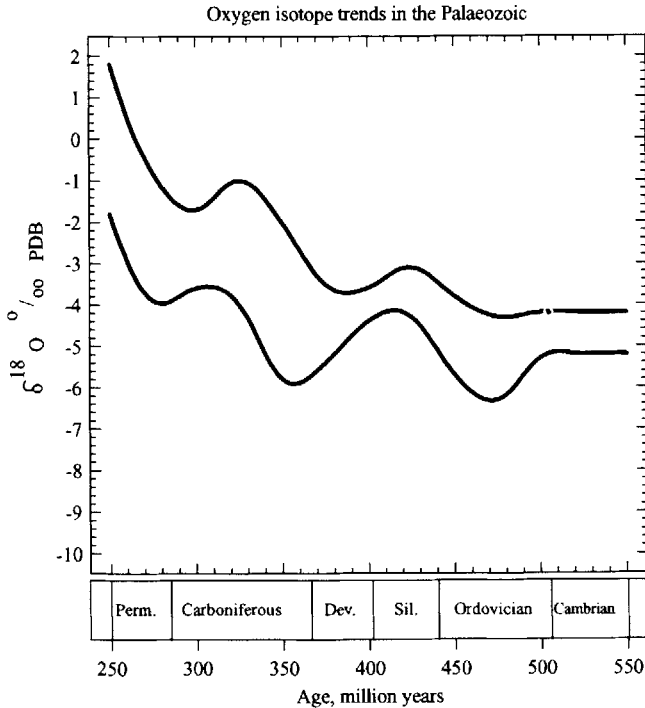


Fig. 9. Oxygen isotope profile for the Palaeozoic. Redrawn from Anderson (1990). The two curves reflect the upper and lower estimates of $\delta^{18}\text{O}$ composition of seawater.

during the Cenomanian/Turonian Oceanic Anoxic Event. Arthur *et al.* (1988) have suggested that the excess burial of organic carbon, which is a sedimentological feature of this boundary interval, stripped CO_2 from the atmosphere and thereby resulted in short-term climatic cooling. The $\delta^{18}\text{O}$ record of whole-rock carbonate retrieved from the Bottaccione Gorge in Umbria (Corfield *et al.* 1991; Jenkyns *et al.* 1994; Fig. 7), as well as the record recently recovered from the English Chalk (Jenkyns *et al.* 1994) shows that the temperatures never recovered to pre-Cenomanian/Turonian boundary levels and indeed declined steadily thereafter. As Fig. 8 shows, benthic foraminiferal $\delta^{18}\text{O}$ data from equatorial Pacific sites show the same trend (Spicer & Corfield 1992) supporting the contention that the Cenomanian/Turonian boundary threshold was of global significance.

In their recent review, Hudson & Anderson (1989) compiled $\delta^{18}\text{O}$ data from the entire Mesozoic using predominantly microfossil data from mid and northern Europe (Cretaceous and Jurassic) and from the European Tethys (Triassic). Their emphasis was on the use of material that independent testing suggested had been unaltered or only minimally altered by post-depositional effects. They showed that there

was large variability (of up to 3‰) even within one ammonite zone, which they attributed to seasonal or ecological variation. Within this large spectrum of variability they were unable to identify any clear time trend in the early Cretaceous and Jurassic intervals (note that 3‰ is approximately 75% of the total oxygen isotopic change characteristic of the entire Cenozoic) and concluded that, although there was probably little temperature variability during this interval, data were too sparse to make any but the most general inferences.

Data from the Triassic are rarer still and merely suggest higher temperatures consistent with the more southerly depositional location of the sediments analysed (Hudson & Anderson 1989).

The Palaeozoic: ocean δ_w or temperature change?

A paradox of oxygen isotope palaeothermometry is that despite the paucity of data in the earlier part of the Mesozoic, the data set assembled for the Palaeozoic is more extensive. The essential feature of $\delta^{18}\text{O}$ change during the Palaeozoic is a general enrichment in ^{18}O particularly from the Devonian to the end of

the Permian (Fig. 9). This change is considered to have become particularly abrupt at the end of the Devonian (Veizer *et al.* 1986; Kump 1989; Crowley & North 1990). In pre-Ordovician times the data suggest no systematic change in $\delta^{18}\text{O}$, although clearly more data are required.

The reason for the very negative isotopic compositions so characteristic of Palaeozoic oceans together with the cause of the increase in $\delta^{18}\text{O}$ with time are unclear. Suggestions include: (1) that the early Phanerozoic was characterized by anomalously warm ocean temperatures (Knauth & Epstein 1976; Kolodny & Epstein 1976; Knauth & Lowe 1978; Shemesh *et al.* 1983; Luz *et al.* 1984); (2) post-depositional alteration with meteoric waters of negative $\delta^{18}\text{O}$ composition, the degree of equilibration increasing with antiquity (Degens & Epstein 1962; Killingley 1983); (3) change in the $\delta^{18}\text{O}$ composition of ocean waters through time (Weber 1965; Perry 1967; Perry & Tan 1972; Perry *et al.* 1978; Veizer *et al.* 1986); and (4) partitioning of ^{16}O and ^{18}O between deep and surface waters (Railsback 1990), with surface waters (the depositional environment from which most of the carbonates available for analysis were deposited) being significantly depleted in ^{18}O .

The combination of rigorous criteria for the identification of diagenetic alteration, the correspondence in the trend towards heavier $\delta^{18}\text{O}$ values between fossil material and cements, plus the similarity of the trend to that derived from studies of cherts and phosphates, suggest (Popp *et al.* 1986*a, b*; Hudson & Anderson 1989) that the trend in Palaeozoic $\delta^{18}\text{O}$ is not the result of diagenetic alteration.

It follows, therefore, that the enrichment in ^{18}O during the Palaeozoic may be attributed to: (1) a decrease in the $\delta^{18}\text{O}$ content of seawater by 4‰; (2) a decrease in temperature by up to 16°C; or (3) the sequestration of ^{18}O into deeper waters. Note, however, that all of these explanations have complications which are outlined below.

Anomalously negative δ_w and secular δ_w increase

It has been suggested that the gross oxygen isotopic composition of the ocean throughout its history would have been buffered at values close to those that characterize the present day (Gregory & Taylor 1981; Muehlenbachs 1986; Hoffman *et al.* 1986), by the interaction of mid-ocean ridges and seawater. Hence, any change in seawater composition, particularly rapid changes such as those associated with the end of the Devonian, may be unlikely.

High temperatures and secular thermal decrease

The temperatures suggested by the very negative $\delta^{18}\text{O}$ values characteristic of the Palaeozoic may have exceeded, at least occasionally, the lethal limits for marine invertebrates based on neontological data (Kinne 1970; Railsback 1990) and yet there is, of course, a rich palaeontological record from the Palaeozoic. However, Valentine (1985) has suggested that modern thermal constraints would not necessarily have affected Phanerozoic evolutionary patterns.

^{18}O partitioning between deep and shelf waters

The hypothesis of Railsback (1990), while intriguing, is essentially based on the postulated occurrence of warm saline deep waters during the Phanerozoic. While there has been much speculation about high salinity deep waters forming at low latitudes by evaporative processes (e.g. Chamberlin 1906; Brass *et al.* 1982; Kennett & Stott 1990) there is still no consensus that this occurred. Railsback's hypothesis requires that warm saline deep water production was virtually ubiquitous during the Palaeozoic with the consequence that ^{18}O was concentrated by salinity stratification in the deeper parts of the ocean basins. This cannot be tested because these areas of ancient seafloor have long been subducted with the necessary consequence that our picture of climate change in the Palaeozoic (at least insofar as it is based on $\delta^{18}\text{O}$ analyses) is all from carbonate shelf facies.

Hence, at present the data are insufficient to distinguish between these various possibilities (see Hudson & Anderson 1989; Veizer *et al.* 1986 for fuller discussion), but it is reasonable to suppose that some combination of these and perhaps other hypotheses will eventually be invoked to explain the very negative $\delta^{18}\text{O}$ so tantalizingly characteristic of the Palaeozoic.

I thank Dan Bosence and Peter Allison for the opportunity to write this review. As always, thanks to Julie Cartlidge for her expert operation of the mass spectrometers in the stable isotope laboratory in Oxford. Thanks also to Peter Allison, Tim Astin, Mike Prentice and Leon Clarke for reviewing earlier versions of this paper.

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Organic carbon as a palaeoenvironmental indicator in the marine realm

J. W. DE LEEUW,¹ N. L. FREWIN,^{1,2} P. F. VAN BERGEN,^{1,2}
J. S. SINNINGHE DAMSTÉ¹ & M. E. COLLINSON²

¹*NIOZ Division of Marine Biogeochemistry, Netherlands Institute for Sea Research
(NIOZ), PO Box 59, 1790 AB, den Burg, Texel, The Netherlands*

²*Department of Geology, Royal Holloway, University of London, Egham, Surrey
TW20 0EX, UK*

Abstract: Recent developments in biogeochemistry have made accessible all information currently known to be present in sedimentary organic compounds, i.e. the carbon skeleton structure, the positions of functional groups and stable carbon isotope ratios. This combined information has strengthened the applications of sedimentary organic compounds as biomarkers and palaeoenvironmental indicators. This review summarizes the most important biomarkers and their applications in reconstructing marine palaeoenvironments and processes. The marine environment is characterized by the combined presence of specific compounds, such as organic sulphur compounds, dinosteroids, 24-*n*-propylsteroids (even in trace amounts), high amounts of C₂₅ HBI hydrocarbons and the absence of long chain *n*-alkanes with odd over even predominance, bicadinanes and specific higher-plant triterpenoids (e.g. oleanane). Furthermore, palaeoenvironmental conditions, such as photic zone anoxia, hypersalinity, microbial sulphate-reducing activity, algal blooming, palaeo-upwelling and palaeo-surface seawater temperature are indicated by molecular and/or isotopic characteristics. Biomarkers from terrestrial sources are included because land-derived organic matter is an important contributor to coastal and shallow-marine environments. A short case study, within a Holocene terrestrial/marine setting (Florida Bay, USA), is also presented to illustrate the reconstruction of transgressive-regressive trends using selected organic compounds.

Depending on the conditions in the original depositional environment, e.g. production, preservation, 0.1–1% of biologically derived organic matter is not recycled in the biosphere or biogeosphere and ‘escapes’ into the geosphere (Fig. 1). The composition of this sedimentary organic matter is substantially different from that of living organisms because major differences exist in the degree of biodegradation of biochemicals. For example, polysaccharides and proteins, representing the bulk of the biomass in most organisms, are very efficiently mineralized by bacteria and are thus selectively removed during transport through the water column or in the top layers of sediments. As a consequence, other biochemicals, such as certain low- and high-molecular weight compounds occurring in cell walls and membranes, and aromatic biomacromolecules, such as lignin, are selectively preserved and thus enhanced in sedimentary organic matter. In fact, series of novel highly aliphatic, highly resistant biomacromolecules in cell walls of algae and plant structures (i.e. cuticles, periderm, seed coats) were discovered by detailed analyses of microscopically recogniz-

able fossilized organic matter before they were identified as relatively minor constituents in their living counterparts (Nip *et al.* 1986; Tegelaar *et al.* 1993; Van Bergen *et al.* 1994a). In depositional environments where sulphate reduction prevails, lipids, which otherwise would be biodegraded, are preserved through reactions with inorganic sulphur species (H₂S and HS_x⁻) as low- or high-molecular weight organic sulphur compounds (OSC; Sinninghe Damsté & De Leeuw 1990 and references therein).

Despite the above mentioned processes, whereby only a minute, highly biased, fraction of the original biochemicals is preserved as such, partly altered or as sulphur derivatives, sedimentary organic compounds can still be considered as highly specific information carriers or molecular fossils, applicable in palaeoenvironmental reconstruction, biochemical evolution and as maturity indicators (Fig. 2). This is because many organisms or groups of organisms biosynthesize numerous highly specific biomolecules. Furthermore, analytical chemical tools have been developed to such an extent that all the information known to be present in sedi-

mentary organic molecules can, in principle, be retrieved.

Three modes of information are present in biochemicals: (1) the structure of the carbon skeleton (including its stereochemistry); (2) the position(s) and nature of functional groups; and (3) the stable carbon isotope ($^{13}\text{C}/^{12}\text{C}$) composition.

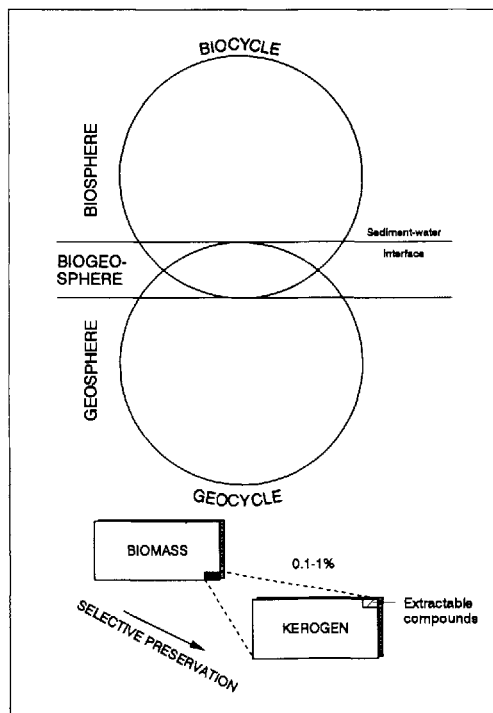


Fig. 1. Schematic diagrams showing the relationship between the biocycle and the geocycle and the selective preservation of the kerogen fraction.

The carbon skeleton structures and the position(s) and nature of functional groups are determined by species-specific biosynthetic pathways, whilst stable carbon isotope ratios in biochemicals are determined by biosynthesis and carbon source. Because the stable carbon isotope ratio of the carbon source is dependent on its nature, and on its position in the food web, stable carbon isotope ratios of biochemicals give clues to the niche of the organisms which biosynthesized these biochemicals. As already mentioned, retrieval of all three modes of information present in sedimentary organic compounds is now possible because of recently developed methods and technologies which are reviewed below.

How to obtain information from sedimentary organic molecules

Isolation and fractionation of solvent soluble organic compounds (loosely termed lipids) from fossils or whole sediments is generally performed by ultrasonic or Soxhlet extractions with common organic solvents, followed by column or thin-layer chromatography to obtain separation of classes of compounds according to their relative polarity (Fig. 3). These fractions are analysed using gas chromatography-mass spectrometry (GC-MS) or, if the compounds present in the fractions are thermolabile or too polar, by liquid chromatography-mass spectrometry (LC-MS). The residue after extraction generally contains the bulk of the organic matter which is macromolecular in nature. This residual insoluble organic matter, kerogen (Fig. 1), is analysed by spectroscopic methods (e.g. NMR and IR) and/or by chemolytic or pyrolytic methods. The latter analyses are indirect

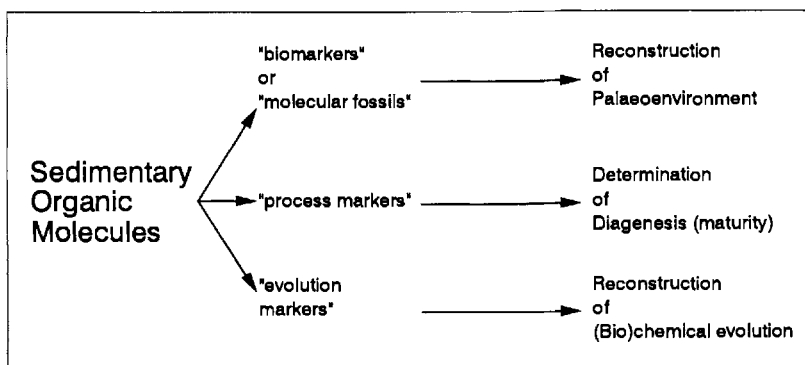


Fig. 2. Applications of sedimentary organic molecules.

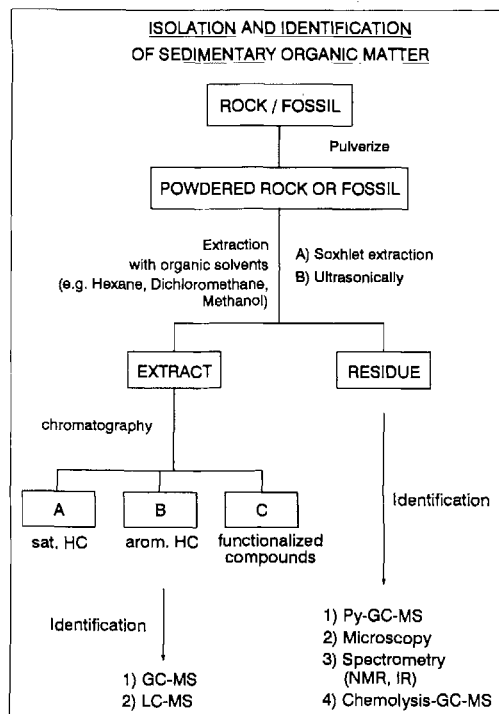


Fig. 3. A laboratory procedure for isolation and identification of sedimentary organic matter. Sat. HC, saturated hydrocarbons; arom. HC, aromatic hydrocarbons.

because characteristic moieties of the kerogen are released by specific chemical reagents (chemolysis) or by heating in an inert atmosphere (pyrolysis; Py). The compounds thus released are separated and identified by GC-MS or LC-MS. Reconstruction of the molecular structure of the macromolecular organic matter is a mental exercise based on the qualitative and quantitative analysis of the pyrolytic or chemolytic products obtained and on knowledge of chemolytic and pyrolytic mechanisms (Boon 1992; Hedges 1991 and references therein; Schouten *et al.* 1993a and references therein). Ultimately, the carbon skeletons as well as the position(s) of functional groups in sedimentary organic compounds are established in this way. It should be emphasized that in many cases the original functional groups, in particular double bonds and carbonyl groups in ketones and aldehydes, have reacted with hydrogen sulphides, intra- or intermolecularly, resulting in low- or high-molecular weight OSC. However, it should be stressed that the position(s) of the sulphurized carbon(s) in the carbon skeletons are the same as the position(s) of the original

functional group(s) (Kohnen *et al.* 1992, 1993).

The determination of stable carbon isotope ratios in individual organic compounds present in complex mixtures is performed by isotope ratio monitoring-GC-MS (irm-GC-MS), a technique which has only recently become commercially available (Freeman *et al.* 1990). The compound mixture to be analysed is injected on to a gas chromatograph (Fig. 4) and separated, individual compounds eluting from the gas chromatograph are combusted on-line to CO₂ and H₂O in a combustion reactor coupled to the gas chromatograph. After removal of the water (by a water separator) the CO₂ peaks are introduced into an isotope mass spectrometer where ¹³C/¹²C ratios can be measured reliably if the compounds are separated well during GC. In this way ¹³C/¹²C ratios of GC amenable sedimentary organic compounds are determined. The optimal interpretation of these carbon isotope data requires some prerequisite knowledge of isotope fractionation in organisms. An overview of δ¹³C fractionations, based on a recent paper by Hayes (1993), is given in Fig. 5. Different families of primary producers on land fix atmospheric CO₂ via different enzymatic pathways (C3, C4, CAM) resulting in clearly distinct ¹³C/¹²C values. Photosynthetic organisms in aqueous environments also differ in the pathway of CO₂ fixation using, for example, HCO₃⁻ pumping, the enzyme ribulose biphosphate carboxylase (RuBisCo) or the reverse tricarboxylic acid cycle (TCA), again leading to major differences in ¹³C/¹²C ratios in their biomass. Methanogenic bacteria discriminate against ¹³C even more significantly, leading to heavily depleted biomass and extremely negative ¹³C/¹²C values of CH₄. If methanotrophic bacteria, using this light CH₄, are present in the depositional environment further discrimination against ¹³C occurs so that biomass of these bacteria may have δ¹³C values of -80‰ or less. Apart from these biosynthetically induced isotope variations, the CO₂ concentration and its ¹³C contents (which usually varies with water depth), the water temperature, the salinity, as well as many other physical and (bio)chemical parameters, ultimately determine the ¹³C/¹²C value of a biochemical. Furthermore, δ¹³C values of different classes of compounds within an organism vary due to different biosynthetic pathways. Compared with the total biomass of an organism, polysaccharides and proteins are somewhat enriched in ¹³C, leading to less negative values, whilst *n*-alkyl lipids and isoprenoid lipids are 4.5 and 3.5‰ lighter (more negative), respectively (Hayes 1993 and references therein).

Compound Specific Carbon Isotopic Analysis

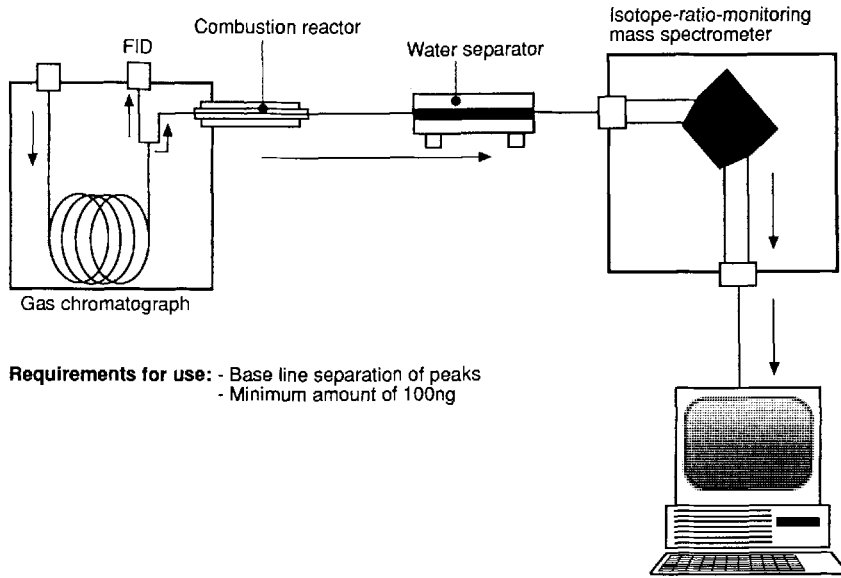


Fig. 4. Schematic diagram for isotope ratio monitoring-GC-MS set-up (after Hayes 1993).

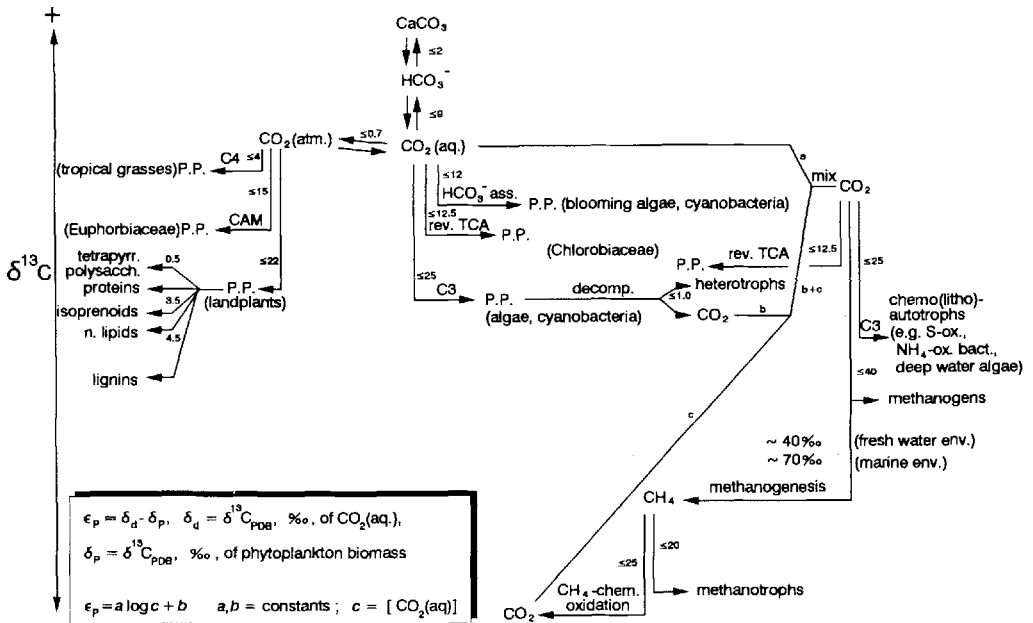


Fig. 5. Overview of $\delta^{13}C$ fractionation in the biosphere. P.P., primary producers; tetrapyr, tetrapyrrols; polysacch, polysaccharides; n. lipids, normal linear lipids; decomp, decomposition; CH_4 -chem. oxidation, CH_4 chemical oxidation; env., environment; S-ox, S-oxidation; NH_4 -ox, NH_4 oxidation; atm, atmosphere; aq., aqueous. For additional information see Hayes (1993).

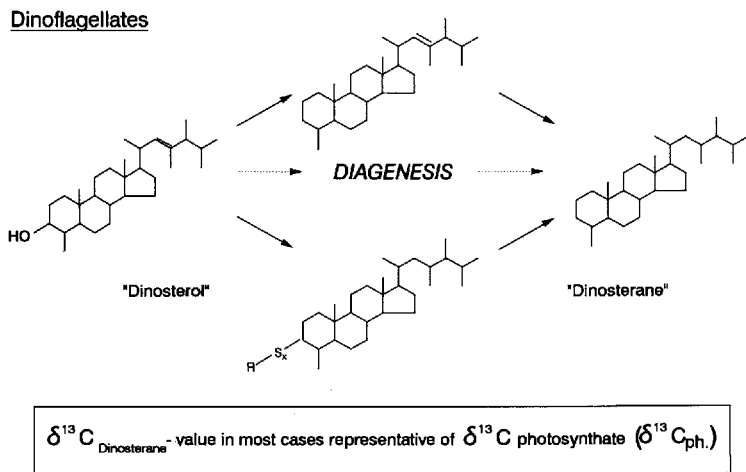


Fig. 6. Palaeoenvironmental indicators for dinoflagellates.

In the following section a number of examples of biochemicals specific for certain organisms have been selected to show the scope and limitations of this molecular palaeontological or molecular biogeochemical approach at its present stage; Appendix A provides some insight into the sometimes specialized nomenclature. Although the paper addresses palaeoenvironmental indicators in the marine realm a significant number of examples dealing with (palaeo)biochemicals derived from terrestrial higher plants are given. This is justified by the fact that terrestrially derived organic matter ending up in the seas and the oceans by riverine or aeolian transport mechanisms can contribute very significantly to sedimentary organic matter in marine sediments (Hedges 1992) and is important in the recognition of shoreline environments. Primary producers in the marine realm, the algae, are presented first, followed by the bacteria and finally the higher land plants.

Organic material derived from eukaryotic algae and higher plants (e.g. dinoflagellate cysts, cuticles, wood fragments, pollen and spores), as well as from certain animal sources, is often recognized in preparations of palynological organic matter from marine sediments. Coverage of these microscopically recognizable entities is outside the scope of this paper. The interested reader should consult Tappan (1980), Traverse (1988), Lipps (1993) and Jansonius & McGregor (in press) for an introduction to these topics.

Examples of palaeoenvironmental indicators

Dinoflagellates

The relatively stable saturated cyclic hydrocarbon 4,23,24-trimethylcholestane or 'dinosterane' (Fig. 6) is frequently encountered in crude oils or extracts of Late Triassic, or younger, relatively mature sediments (e.g. Summons *et al.* 1987; Thomas *et al.* 1993). It is thought to represent the diagenetic product of the biochemical 'dinosterol' or 4,23,24-trimethylcholesterol, a steroid present in relatively high amounts in many dinoflagellate algae (Nes & McKean 1977) and recently also encountered in the carnivorous fresh water plant *Utricularia neglecta* (Klink *et al.* 1992), and in very small amounts in a diatom (*Navicula* sp.; Volkman *et al.* 1993). It is, however, assumed that the presence of dinosterol in the carnivorous plant is of dietary dinoflagellate origin. To date, it is believed that dinosterol is mainly biosynthesized by dinoflagellate algae. Hence, the presence of dinosterol, dinosterane or intermediate diagenetic products in sediments, even in the absence of dinoflagellate cysts, is a strong palaeoindicator of dinoflagellate algae in the depositional environment (e.g. Boon *et al.* 1979). In some cases the dinosterane skeleton is only present as a sulphur bound moiety (carbon atom 3 is mostly involved in the C—S bond, indicating the original position of the hydroxy- or carboxy-group; see Appendix A for carbon numbering) in high-

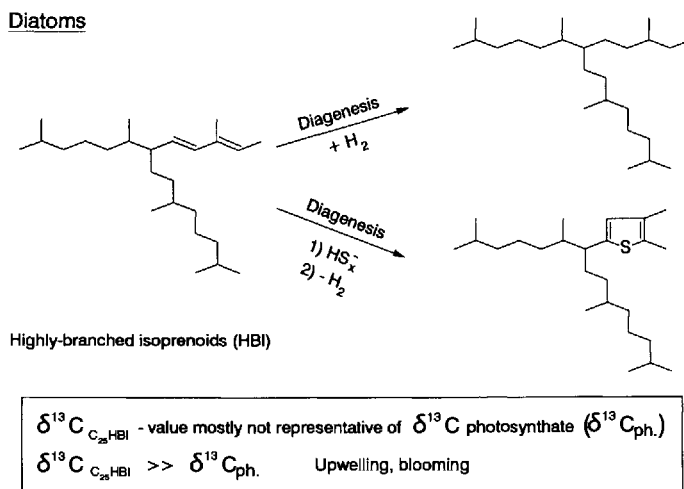


Fig. 7. Palaeoenvironmental indicators for diatoms.

molecular weight fractions of sediment extracts (Fig. 6). However, chemolysis of such a high-molecular weight fraction using Raney nickel releases dinosterane through selective cleavage of the C—S bond and the molecular fossil is retrieved (Kohnen *et al.* 1992). $\delta^{13}\text{C}$ values of dinosterol or its diagenetic products measured so far are in agreement with an origin from photosynthetic algae fixing CO_2 via the RuBis-Co pathway (Kohnen *et al.* 1992).

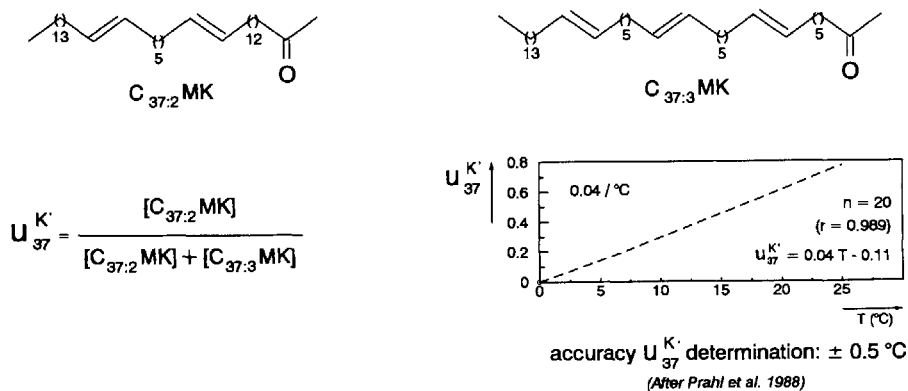
Diatoms

Highly branched C_{25} and C_{30} isoprenoid (HBI) alkanes, alkenes and thiophenes (Fig. 7) have been encountered for some time in crude oils and sediment extracts (e.g. Robson & Rowland 1986; Sinninghe Damsté *et al.* 1989a). Only recently has firm proof emerged that these specific compounds are biosynthesized by several species of diatoms (Nichols *et al.* 1988; Volkman *et al.* 1992). In sediment of the Black Sea it was noticed by Kohnen *et al.* (1990a) that the HBI thiolanes contain two double bonds less than their C_{30} polyunsaturated HBI precursors, indicating that these biochemicals readily react with hydrogen sulphides in the top layers of sediments. These sulphurized C_{25} HBI compounds, as well as their fully hydrogenated counterparts, are thus considered to be diagenetic products of the corresponding unsaturated biochemicals with the HBI skeleton. They strongly indicate the presence of diatoms in the depositional environment. It should be mentioned that these HBI compounds play an

important role as molecular fossils in sediments where the silica frustules of diatoms are absent, presumably through solution of the silica. $\delta^{13}\text{C}$ values have been measured for these compounds in several sediments (e.g. Kohnen *et al.* 1992; Summons *et al.* 1993; Freeman *et al.* 1994; Schouten *et al.* 1994). These values are less negative in comparison with those from compounds from other algal primary producers. This is usually due to seasonal blooming, triggered by upwelling, of certain diatoms biosynthesizing these HBI compounds. Less negative $\delta^{13}\text{C}$ values during blooming are caused by low CO_2 -dissolved concentrations so that ^{13}C cannot be discriminated substantially (Deuser 1970). It should be noted, however, that there is evidence that non-blooming diatoms also use relatively enriched CO_2 , probably by bicarbonate pumping (Summons *et al.* 1993). The phenomenon of less negative $\delta^{13}\text{C}$ values due to blooming may also apply to other algae.

Prymnesiophyte algae

Long chain di- and triunsaturated methyl- and ethylketones with 37, 38 and 39 carbon atoms (Fig. 8) are biosynthesized by the coccolithophorid (Prymnesiophyta) *Emiliania huxleyi* (Volkman *et al.* 1980) and some other present-day prymnesiophytes, like *Gephyrocapsa* sp. (Volkman *et al.* 1994). Although *E. huxleyi* is only present in the geological record for the last 150 000 years, these ketones have been encountered in sediments deposited since the Cretaceous (Marlowe *et al.* 1990). To date, it is believed

Prymnesiophytes (e.g. *E. huxleyi*)

$U_{37}^{K'}$ correlates with:

- $\delta^{18}\text{O}$ of carbonate tests of planktonic forams
- Milankovitch cycles
- Glacials / Interglacials

Surface Seawater Temperature (SST)

Fig. 8. Palaeoenvironmental indicators for prymnesiophytes. MK, methylketones.

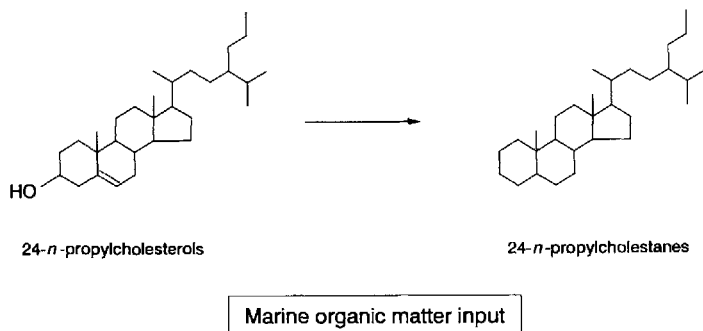
Chrysophytes (Sarcinochrysidales)

Fig. 9. Palaeoenvironmental indicators for chrysophytes.

that these long-chain ketones are exclusively biosynthesized by species belonging to the Prymnesiophyta (Jasper & Gagosian 1993). The importance of these compounds lies in the fact that they remain present in the sediments even though the carbonate remains of the coccoliths may be absent.

It is now well established that these ketones, when present in Recent sediments, can be used as palaeo-surface seawater temperature indicators (e.g. Brassell *et al.* 1986; Prahl *et al.* 1988)

with an accuracy of 0.5°C . A relatively simple analysis of sediment extracts enables the determination of the so-called $U_{37}^{K'}$, a ratio of the C_{37} ketones with two and three double bonds. Calibration of this ratio using cultures of *E. huxleyi* grown under well-controlled temperature conditions enables the recognition of natural climatic changes in the past. The $U_{37}^{K'}$ is also correlated with other temperature or climate indicators, such as $\delta^{18}\text{O}$ values in carbonate tests of planktonic forams and/or

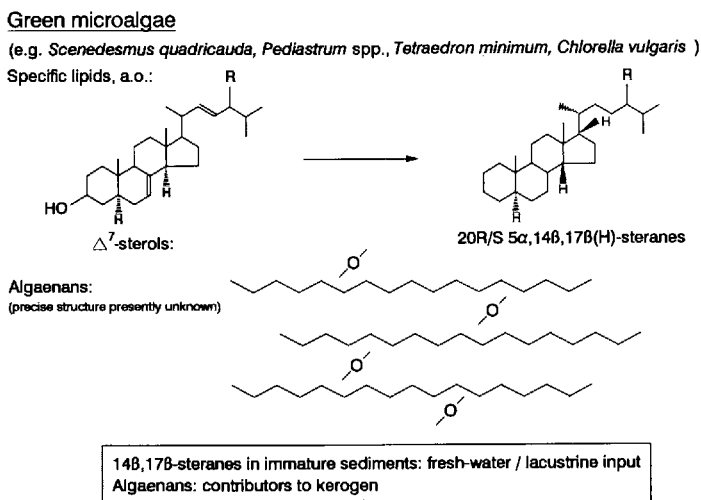


Fig. 10. Palaeoenvironmental indicators for green microalgae.

the Milankovitch cycles (Brassell *et al.* 1986). It is now well documented that these ketones can react with inorganic sulphur species during early diagenesis (Sinninghe Damsté *et al.* 1988, 1989*b*, 1990*b*). Reactions of carbonyl groups and double bonds in the original molecule with inorganic hydrogen polysulphides lead to the formation of (poly)sulphide bonds, in this case yielding sulphurized C₃₇–C₃₉ carbon skeletons. Upon Raney nickel desulphurization of high-molecular weight fractions of sediment extracts these carbon skeletons are released as saturated hydrocarbons with 37–39 carbon atoms (Sinninghe Damsté *et al.* 1988, 1990*a*; Schouten *et al.* 1993*b*). Summarizing, it can be stated that these compounds fulfil two functions: (1) ketones or their diagenetic counterparts (e.g. sulphur bonded) reveal the presence of prymnesiophytes in the depositional environment; and (2) the ketones, when present unaltered, function as a palaeothermometer.

Chrysophyte algae

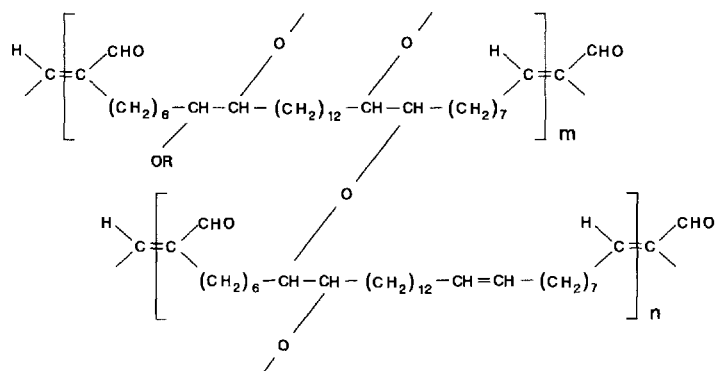
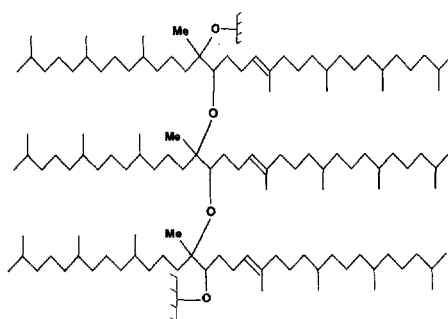
Recently, it has been shown by Moldowan *et al.* (1990) that the presence of 24-*n*-propylcholesterols or their diagenetically derived counterparts, 24-*n*-propylcholestanes (Fig. 9), in sediment extracts and oils can be considered as the most powerful indicators for the input of marine organic matter in the depositional environment. The sterols with this highly specific 24-*n*-propyl

group are biosynthesized by the Sarcinochrysidales, a group of marine Chrysophyte algae.

Green microalgae

A number of very common freshwater, green microalgae (e.g. *Scenedesmus* spp., *Pediastrum* spp., *Tetraedron minimum* and *Chlorella vulgaris*) biosynthesize Δ^7 sterols (Fig. 10) instead of Δ^5 sterols (Nes & McKean 1977; De Leeuw *et al.* unpublished results). The diagenetic pathways of these compounds are different from Δ^5 sterols (which are produced by most eukaryotic plants) and, as a result of this, 5 α ,14 β ,17 β (H) steranes with 20R and 20S stereochemistries are already present in relatively immature sediments (De Leeuw *et al.* 1989; Peakman *et al.* 1989). When present in more mature sediments, or crude oils, the 5 α ,14 β ,17 β (H) steranes cannot be used as indicators of freshwater, green microalgae because these steranes may also be derived from Δ^5 sterols in later stages of maturation (Peters & Moldowan 1993).

The above mentioned algae, as well as the three races of *Botryococcus braunii* and a few marine microalgae (e.g. *Nannochlorum eucaryotum*), biosynthesize highly aliphatic, non-saponifiable biomacromolecules called algaenans (Largeau *et al.* 1986; Derenne *et al.* 1992; Fig. 10). These substances make up a substantial part of algal cell walls and have been recognized recently by spectroscopic and pyrolytic analysis

(a) Green microalgae *Botryococcus braunii* race A(b) Green microalgae *Botryococcus braunii* race L

Algaenans	- Highly resistant aliphatic biomacromolecules
	- Major contributors to kerogen

Fig. 11. Palaeoenvironmental indicators for *Botryococcus braunii*: (a) race A (modified after Metzger *et al.* 1991); (b) race L. Me, methyl (after Gelin *et al.* 1994b).

methods (Goth *et al.* 1988; De Leeuw *et al.* 1991; Gelin *et al.* 1994b). Although algaenans of different algae are all highly resistant, non-saponifiable and aliphatic in nature, very precise structures are not known except for *B. braunii* races A and L (Fig. 11 a & b; Derenne *et al.* 1989; Metzger *et al.* 1991; Gelin *et al.* 1993, in press). Detailed analyses of flash pyrolysates of algaenans of these different algae indicate quite substantial differences in their chemical structures although they are thought, with one exception, to possess a backbone of *n*-alkyl chains linked via ether bridges (Gelin *et al.* 1993). The exception is the algaenan of *B. braunii* race L, which consists of ether-linked isoprenoidal lycopadiene units (Fig. 11b; Derenne *et al.* 1990; Gelin *et al.* 1994b).

Because of their apparent resistance against

(bio)degradation these algaenans are the major constituents of many kerogens and important precursors of *n*-alkanes in crude oils. For example, the widely studied kerogen of the Messel oil shale (Eocene, Germany) consists almost exclusively of algaenan of *T. minimum* (Goth *et al.* 1988), whilst many so-called torbanites and coorongites are made up almost exclusively of algaenans or comparable high-molecular weight substances originating from *B. braunii* species (Largeau *et al.* 1986). Hence, the presence of highly aliphatic macromolecules in kerogens indicate the selective preservation of green microalgae of terrestrial and/or marine origin. However, it should be noted that similar types of resistant insoluble highly aliphatic macromolecules also occur in a variety of tissues of higher plant (see below). Stable

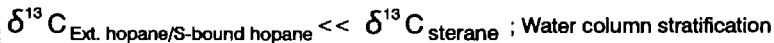
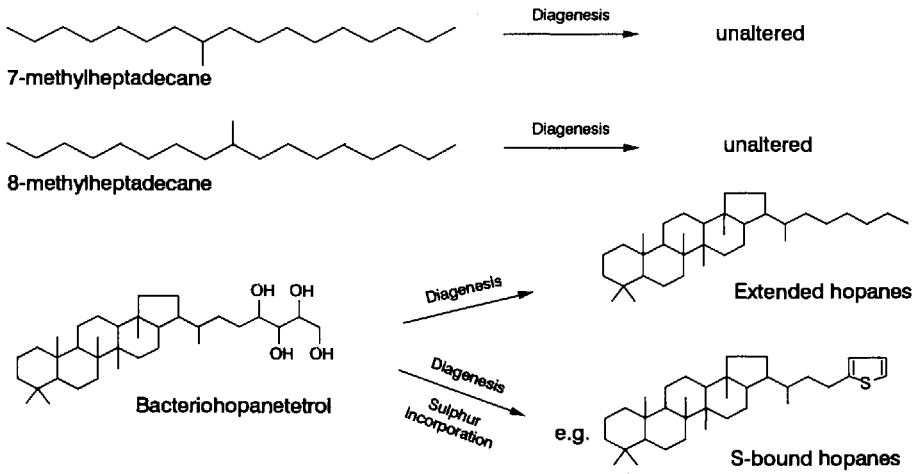
Cyanobacteria

Fig. 12. Palaeoenvironmental indicators for cyanobacteria.

carbon isotope measurements of homologous series of *n*-alkanes and *n*-alk-1-enes released from kerogens upon pyrolysis are in accordance with an origin from primary producers (Eglinton *et al.* 1993).

Cyanobacteria

A number of monomethyl branched alkanes, in particular 7-methylheptadecane and 8-methylheptadecane (Fig. 12), have been encountered in several cyanobacteria (Sheia *et al.* 1990). Because these two compounds virtually coelute during GC and co-occur in about equal amounts their first identification in cyanobacteria was not straightforward (Han & Calvin 1970). These branched hydrocarbons, as well as many others encountered in cyanobacteria (Sheia *et al.* 1990), can survive unaltered and thus are considered specific biomarkers for cyanobacteria when encountered in sediments (Han 1970).

Like many other bacteria, several cyanobacteria use the pentacyclic isoprenoid bacteriohopanetetrol derivatives (Fig. 12) to rigidify their cell membranes (Rohmer *et al.* 1989). These hopane derivatives occur exclusively in bacteria and can be considered as the bacterial counterparts of steroids in the cell membranes of algae. Depending on depositional and burial conditions a large variety of extended (i.e. containing

more than 30 carbon atoms) hopanes and functionalized hopanoids can be encountered in sediments (e.g. Peters & Moldowan 1993; Ourisson *et al.* 1979, 1984). In anaerobic marine sediments with an active population of sulphate-reducing bacteria a considerable part of the extended hopanoids is preserved as their sulphurized counterparts. In particular, C₃₅ hopanoid thiophenes (Valisolalao *et al.* 1984), like the one indicated in Fig. 12, as well as macromolecularly sulphur-bound hopanoids, sometimes represent an important contribution to the extractable organic matter in sediments (Kohnen *et al.* 1990b; Köster *et al.* 1993). Although these hopanetetrols are not exclusively biosynthesized by cyanobacteria, circumstantial evidence is building up that in many cases, in particular if their concentrations are relatively high, extended hopanoids in sediments are predominantly derived from cyanobacteria and much less from heterotrophic bacteria (Schoell *et al.* 1994). At present, we therefore consider them as relatively unique indicators of cyanobacterial activity in the depositional environment and not as indicators of bacterial reworking. $\delta^{13}\text{C}$ values of extended hopanoids in sediments have been measured on a few occasions (Kohnen *et al.* 1992; Schoell *et al.* 1994; Schouten *et al.* 1994). These isotope data confirm an origin from cyanobacteria (Kohnen

Unknown algae or cyanobacteria

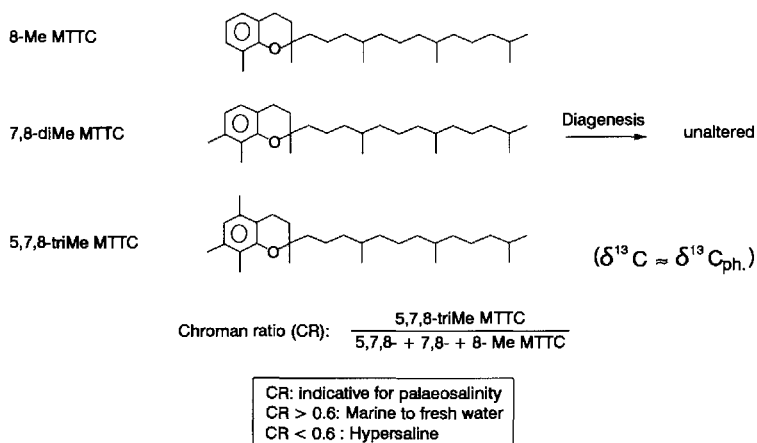


Fig. 13. Palaeoenvironmental indicators for palaeosalinity of unknown origin.

et al. 1992). In a recent paper Schoell *et al.* (1994) use differences between stable carbon isotopes of extended hopanes and steranes as a strong indication of water-column stratification, assuming that cyanobacteria live at a greater depth in the water column than eukaryotic algae. The underlying reason for this is that water stratification is normally associated with temperature change (deeper water being colder), CO_2 concentrations are higher in colder water leading to more discrimination against ^{13}C during CO_2 fixation.

Algae/cyanobacteria?

Several years ago series of so-called methylated chromans (Fig. 13) were unambiguously identified in aromatic hydrocarbon fractions of a variety of sediment extracts (Sinninghe Damsté *et al.* 1987). The relative amounts of the different methylated chromans can vary substantially. Based on circumstantial evidence it was assumed that changes in their relative amounts, as expressed by the chroman ratio (CR; Fig. 13), indicate salinity changes, between normal marine and hypersaline, in the depositional environment (Sinninghe Damsté *et al.* 1987). Recent investigations of organic matter in the Mulhouse Basin further supports this idea (Sinninghe Damsté *et al.* 1993a). From this latter study, it also became clear that these highly specific compounds are probably biosynthesized by algae or cyanobacteria because their distribution reflected the salinity (normal marine or hypersaline) of the upper part of the water

column of Lake Mulhouse. In addition, their stable carbon isotope values were similar to those of molecules related to photosynthetic organisms living in the upper part of the water column. It is interesting to note that these chromans can thus be used as palaeosalinity indicators despite the fact that their biological origin is not (yet) known.

Photosynthetic sulphur bacteria

Another group of bacteria, the photosynthetic sulphur bacteria, belonging to the family Chlorobiaceae, biosynthesize a number of very specific diaromatic carotenoids, e.g. isorenieratene (Fig. 14) and chlorobactene. These carotenoids are preserved in many sediments varying in their mode of occurrence from: (1) unaltered (Repeta, 1993); (2) to diaryl isoprenoids in which the isoprenoid chain between the benzene moieties has been fully reduced (Schaeffle *et al.* 1977; Requejo *et al.* 1992; Hartgers *et al.* 1994); (3) to macromolecularly bound sulphur moieties when hydrogen polysulphides were available in the anaerobic depositional environment (Kohonen *et al.* 1992; Sinninghe Damsté *et al.* 1993b; Hartgers *et al.* 1994); and/or (4) incorporated in kerogen (Douglas *et al.* 1991; Hartgers *et al.* 1991, 1994). In more mature sediments and crude oils $\text{C}_{11}\text{--C}_{31}$ arylisoprenoids, with the characteristic aromatic substitution pattern of isorenieratene, have also been encountered (Summons & Powell 1987; Requejo *et al.* 1992; Hartgers *et al.* 1994). It is proposed that these arylisoprenoids are formed from macromolecu-

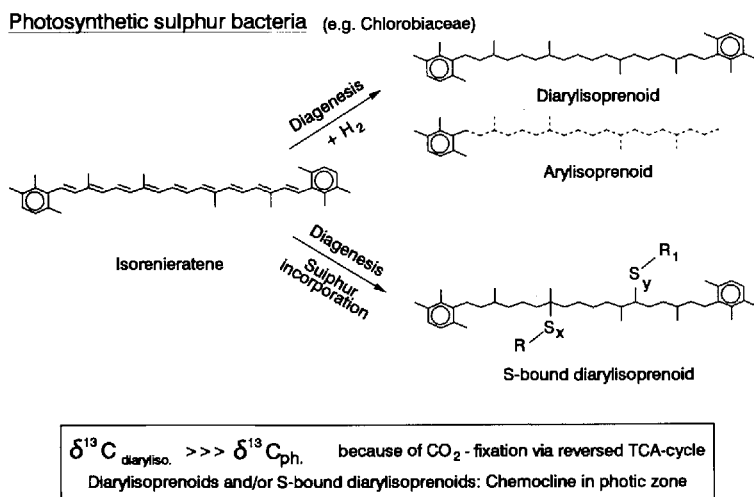


Fig. 14. Palaeoenvironmental indicators for photosynthetic sulphur bacteria.

larly bound diarylisoprenoids during diagenesis and catagenesis via carbon-carbon cleavages triggered by a sulphide- or ether-functionality at one of the carbon atoms (Hartgers *et al.* 1994). Because Chlorobiaceae fix CO₂ via the reversed TCA cycle (Quandt *et al.* 1977; Sirevag *et al.* 1977), isorenieratene, and hence their diagenetic products, are extremely enriched in ¹³C. $\delta^{13}\text{C}$ values of -8 to -18‰ have been recorded for diarylisoprenoids, sulphur-bound isorenieratene and the specific arylisoprenoids (Summons & Powell 1987; Kohnen *et al.* 1992; Sinninghe Damsté *et al.* 1993b; Hartgers *et al.* 1994). Such values make these compounds unambiguous biomarkers for Chlorobiaceae. These bacteria live at a chemocline which must be present in the photic zone, indicating a very specific niche in the depositional environment. Therefore, the presence of their specific carotenoids or carotenoid derivatives with the extremely high (less negative) $\delta^{13}\text{C}$ values clearly act as environmental indicators for a chemocline in the photic zone. In a recent paper the presence/absence of sulphurized isorenieratene in a 6000 year old sediment sequence of the Black Sea was used to reconstruct the depth variation of the chemocline during this period (Sinninghe Damsté *et al.* 1993b).

Gram-negative bacteria

Gram-negative bacteria are characterized by the presence of an extracellular substance called

lipopolysaccharides (LPS; Fig. 15; for a review see De Leeuw and Largeau 1993). LPS consists of a bacterium-specific polysaccharide moiety linked via phosphate groups and 2-keto-3-deoxyoctanoic acid (KDO) to the so-called lipid A part. This latter moiety contains esterified and amide bound normal, iso- and anteiso β -hydroxy acid moieties with chain lengths of C₁₂-C₁₈. In particular, the amide-bound β -hydroxy fatty acids are preserved to some extent in recent sediments and can be released from them after subsequent extraction, saponification and acid hydrolysis (Goossens *et al.* 1989a,b). Bacterial β -hydroxy fatty acids can occur in more mature sediments and are thought to result from natural cleavage during diagenesis of β -hydroxyacid moieties of LPS (Matsumoto & Nagashima 1984). To the best of our knowledge $\delta^{13}\text{C}$ values of sedimentary β -hydroxyacids have not yet been reported. The occurrence of bacterial β -hydroxyacids in sediments indicate the presence of bacterial activity or reworking in the depositional environment.

Sulphate reducing bacteria

Boon *et al.* (1977) have reported the presence of iso- and anteiso C₁₅ and C₁₇ monounsaturated fatty acids in cultures of sulphate-reducing bacteria as well as in a few very recent marine sediments. Although these acids are thought to be highly specific for some sulphate-reducing bacteria, their significance as biomarkers for

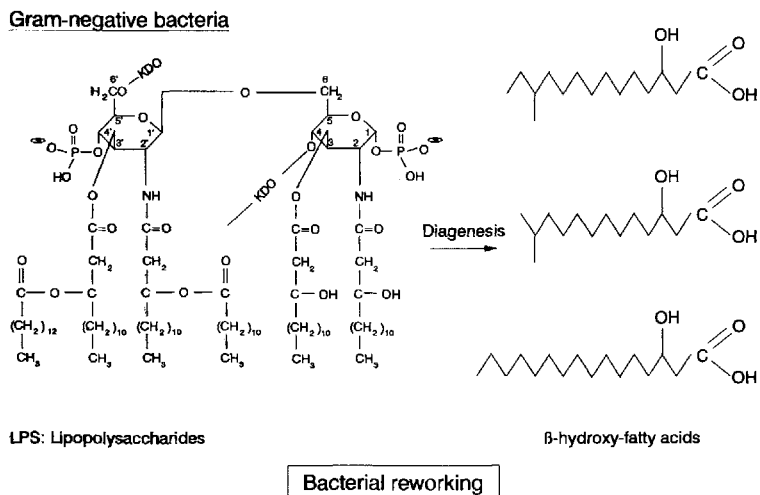


Fig. 15. Palaeoenvironmental indicators for gram-negative bacteria.

Sulphate reducing bacteria

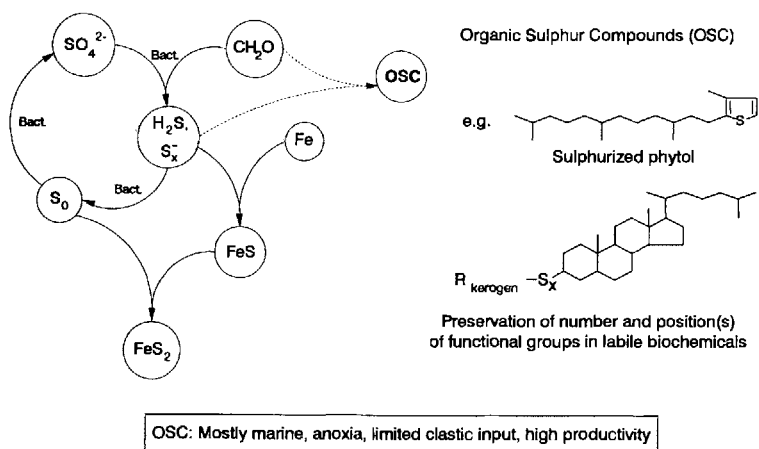


Fig. 16. Palaeoenvironmental indicators for sulphate-reducing bacteria. Bact, bacteria.

these organisms is limited because they are presumably mineralized at early stages of diagenesis. The presence of sulphate-reducing bacteria in anoxic, mostly marine, depositional environments can be deduced indirectly, but very clearly, from the presence of low- and high-molecular weight OSC in immature and mature sediments as well as in oils and coals. Over the last ten years it has become evident that organic compounds are sulphurized during the very early stages of diagenesis as a consequence of the reaction of inorganic polysulphides (H_2S and HS_x^-), produced by sulphate-reducing bacteria,

with double bond, ketone or aldehyde functionalities (Fig. 16) (for a recent review see Sinnighe Damsté & De Leeuw 1990; Schouten *et al.* 1993b). These sulphur constituents, often present as very complex mixtures, act as excellent biomarkers since they are not suitable substrates for bacteria so that biochemicals are preserved which would otherwise have been mineralized. Moreover, the position of the sulphur moiety in the carbon skeleton reveals the position of the original functional group. It is clear that the presence of OSC in sediments reveals sulphate-reducing activity. Therefore,

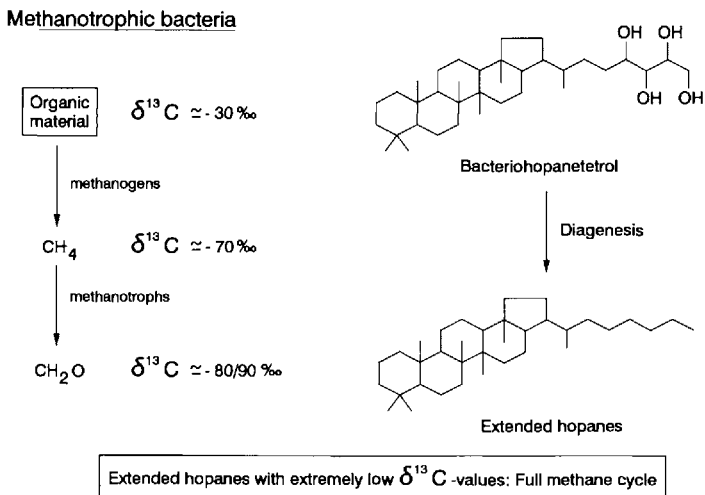


Fig. 17. Palaeoenvironmental indicators for methanotrophic bacteria.

Archaeobacteria: Halophiles, Thermoacidophiles, Methanogens

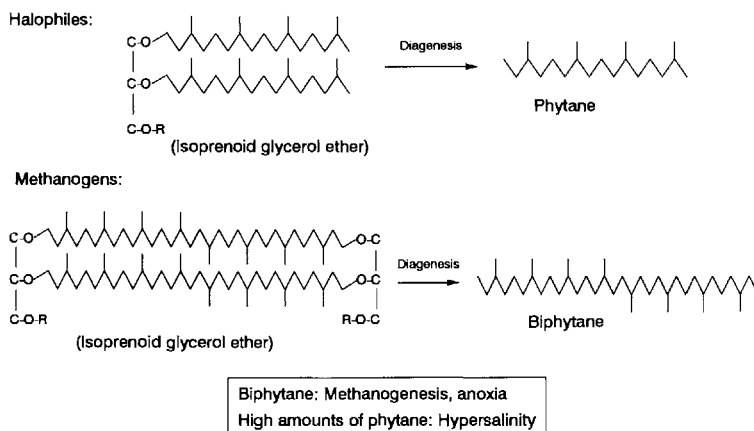


Fig. 18. Palaeoenvironmental indicators for archaeobacteria.

their presence points to anoxia in mostly marine sediments with a limited clastic input and presumably a relatively high production of organic matter in the water column, since the sulphate-reducing bacteria require relatively fresh organic matter as a substrate. From the above it is evident that $\delta^{13}\text{C}$ values of OSC can be highly variable because sulphurization can occur with molecules derived from all kinds of organisms living in different habitats in the depositional environment (e.g. Kohnen *et al.* 1992).

Methanotrophic bacteria

Methanotrophic bacteria (methanotrophs) oxidize methane to biosynthesize their cell constituents. The methane consumed is produced by methanogens which induce a major isotopic shift between their biomass and the methane released (cf. Fig. 17; Hayes 1993). The isotopically very light methane (very negative $\delta^{13}\text{C}$ values) is further fractionated during assimilation so that lipids of methanotrophic bacteria are extremely light ($\delta^{13}\text{C}$ c. -80 to -90‰). Amongst others,

bacterioplanan derivatives are biosynthesized by methanotrophs. These triterpenoids are diagenetically altered to hopanes with similarly highly negative $\delta^{13}\text{C}$ values. The presence of such hopanes and their methylated counterparts in sediments clearly indicate that a full methane cycle existed in the palaeoenvironment (Freeman *et al.* 1990; Collister *et al.* 1992).

Archaeobacteria

Archaeobacteria are well known for their specific membrane lipids which consist of series of isoprenoid glycerol ethers (Fig. 18). It has been suggested by Albaiges (1980) that these isoprenoid ethers yield the corresponding isoprenoid hydrocarbons upon diagenesis. In particular, biphytane represents a highly specific carbon skeleton biosynthesized predominantly by methanogenic archaeobacteria. The presence of this isoprenoid in oils or in sediments clearly indicates the presence of methanogens and, hence, anoxia in the depositional environment. Very high concentrations of phytane (or its sulphurized counterpart) may indicate palaeohypersalinity as a consequence of the presence of relatively high amounts of biphytanyl glycerol ethers in halophilic archaeobacteria (Volkman & Maxwell 1986). Methanogenic archaeobacteria do not significantly discriminate against ^{13}C in their organic substrate (Kohnen *et al.* 1992).

Vascular higher plants

As mentioned in the beginning, the contribution of vascular higher plants to sedimentary organic matter in the marine realm can be very significant (Hedges 1992). Vascular higher plants biosynthesize different suites of resistant bio(macro)molecules. Accumulation of terrestrial-derived material may be due to transportation of bio(macro)molecules by aeolian and/or riverine transport, or to the *in situ* development and senescence of specific aquatic higher-plant communities, such as seagrasses. As vascular higher plants do not occur throughout the marine realm, but only in shallow shelves or lagoons, all of the vascular higher plant derived macromolecules are indicative of input from relatively nearshore material. In several cases, e.g. lignin from woody material, spores, pollen and resins, these inputs must be derived from paralic or fully terrestrial settings.

The following account describes biomolecules found in both aquatic and terrestrial higher plant tissues, followed by the assignation of biomolecular signals to particular terrestrial and submarine higher plant groups. Finally, a brief

case study is presented where an attempt has been made to distinguish the depositional input of molecules from a terrestrial higher-plant source against molecules from a submarine higher-plant source.

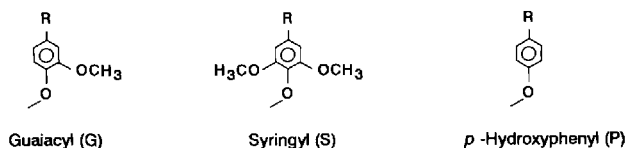
General bio(macro)molecules The most well-known low-molecular weight markers for higher-land plant input in sediments are long chain *n*-alkanes (C_{25} , C_{27} , C_{29} , C_{31}) with a strong odd over even predominance. These compounds are derived from epicuticular waxes on leaf surfaces (Eglinton & Hamilton 1967). The $\delta^{13}\text{C}$ values for these long-chain alkanes are *c.* -27‰ for C3 plants, whereas those from C4 plants are relatively enriched in ^{13}C (Hayes 1993). In addition to the alkanes, numerous other low-molecular weight compounds have been encountered indicating higher-plant input (see Mangroves and Case study). However, most higher-plant material contributing to the organic matter in the marine environment is macromolecular and consequently is resistant against biodegradation. In the following sections the macromolecular compounds present in or produced by higher plants will be discussed.

(a) Cutin and cutan. Chemical analyses of the insoluble matrix of higher-plant cuticles of leaf and stem surfaces have shown that they are composed of the biopolyester cutin, or of an insoluble, non-hydrolysable biomacromolecule, named cutan, or, most commonly, a mixture of both (Nip *et al.* 1986; Tegelaar *et al.* 1991). Cutins are composed of esterified fatty acids, hydroxy fatty acids and dicarboxylic acids of C_{16} and C_{18} carbon chain lengths. These acids often possess a mid-chain functional group (hydroxyl or epoxy) (Holloway 1984). The cutan is thought to be composed exclusively of *n*-alkyl moieties linked together via relatively stable ether bonds (De Leeuw *et al.* 1991). Although most cuticles are thought to be composed of these aliphatic macromolecules (cutin/cutan), a recent paper by Kögel-Knabner *et al.* (1994) reports the presence of lignin (see below) as the resistant biomacromolecule in *Picea abies* needle cuticles. The contribution of aliphatic cuticle constituents to marine sedimentary organic matter is difficult to prove since several marine green microalgae also contain resistant highly aliphatic macromolecules. However, cuticle fragments could easily be transported into the marine realm by wind or fluvial transport and Tegelaar *et al.* (1989b) have suggested that the cutans may contribute significantly to kerogen.

(b) Suberin and suberan. Aliphatic macro-

Vascular higher plants

Lignin units



Gymnosperms: only G units

Angiosperms (dicotyledon): G and S units

Angiosperms (monocotyledon + legumes): G, S and P units

Terrestrial input (fluvial/aeolian)

Fig. 19. Palaeoenvironmental indicators for vascular higher plants: lignins.

molecules, comparable with cutin and cutan, are also identified in periderm (bark of woody plants) tissues of fossil and extant higher plants (Holloway 1984; Collinson *et al.* 1994; Tegelaar *et al.* 1989a, 1994). These are named suberin and suberan, respectively. Suberin is a biopolyester similar to cutin, however, the main monomeric units are C₁₈ monomers (Holloway 1984; Tegelaar *et al.* 1989a). The molecular structure of suberan is thought to be mainly composed of *n*-alkyl moieties, similar to cutan (Collinson *et al.* 1994; Tegelaar *et al.* 1994). Bark fragments could also be transported into the marine organic matter by fluvial or aeolian means.

(c) Sporopollenin. One distinctive group of higher-plant structures which often provide microscopically observable proof of their long distance transport into the marine realm are spores and pollen (Traverse 1988). The recognizable entities are the spore or pollen walls of which the resistant insoluble constituent is named sporopollenin. The molecular structure of this compound is still not completely clear despite numerous studies (for a review see De Leeuw & Largeau 1993). However, recent papers imply the presence of both aromatic and aliphatic moieties (Van Bergen *et al.* 1993; Hemsley *et al.* 1993) of which the aromatic moieties can be altered quite drastically upon diagenesis (Collinson *et al.* 1994). Nonetheless, the presence of benzaldehyde, acetophenone and acetophenol in combination with phenol in pyrolysates of marine kerogens may be used to determine input from spores and/or pollen.

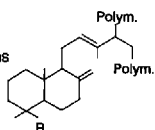
Being microscopically recognizable, and identifiable to parent plant groups, spores and pollen

in marine sediments provide evidence of the type of vegetation on the surrounding land and, hence, also some indication of regional climate. Furthermore, the overall proportions of land-derived spores and pollen vs. marine derived algal resting cysts (e.g. dinoflagellates) are indicative of distance from the land. Certain categories of spores and pollen are known to undergo very long distance transportation in air (e.g. bisaccate pollen of conifers such as *Pinus*) whilst others (e.g. certain fern spores) tend to undergo very little transport. Hence, a suite of pollen and spores not only documents terrestrial input but provides evidence for the proximity of source material as well as indicating climate and the vegetation from which it was derived. For further details consult Jansonius & McGregor (in press), Traverse (1988) and references therein (also see Plaziat, this volume).

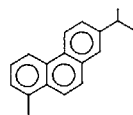
(d) Lignin. Despite the importance of the mainly aliphatic biomacromolecules mentioned above, because of their selective enrichment upon diagenesis, the most abundant biomacromolecules in extant vascular higher plants are lignins. Three different types of lignins are recognized (Fig. 19; Sarkanen & Ludwig 1971). Gymno-sperm lignin contains only monomethoxyphenol units (guaiacyl; G), whereas angiosperm lignin contains dimethoxy (syringyl; S) as well as monomethoxyphenol units (e.g. Sarkanen & Ludwig 1971; Saiz-Jimenez & De Leeuw 1986; Ralph & Hatfield 1991). Within the angiosperms the lignin of the monocotyledons and legumes are composed of both methoxyphenol units (S and G) and *p*-hydroxyphenyl units (P) (cf. Fig. 19; e.g. Ralph & Hatfield

Vascular higher plants

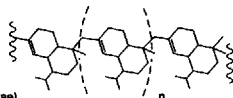
(A) Polyditerpenoids
Polycyclic acid type resins
(Gymnosperms)



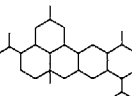
Late diagenesis/
catagenesis
→ a.o.



(B) Polysequiterpenes
Polycadinene resins
(Damar)
(Dipterocarpaceae + Mastidoideae)



Late diagenesis/
catagenesis
→ a.o.

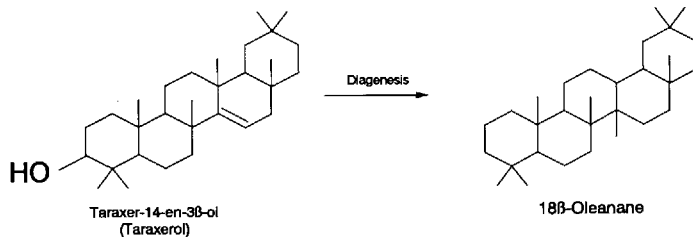


Terrestrial input (fluvial/aeolian)

Fig. 20. Palaeoenvironmental indicators for vascular higher plants: resins.

(a) **Vascular higher plants** (Transitional plants: e.g. Mangroves)

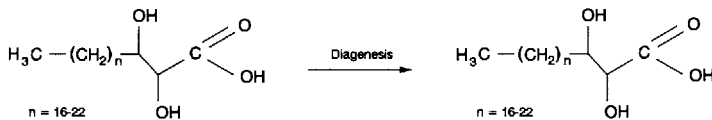
Triterpenoids



Taraxerol derivatives: Paralic environment

(b) **Vascular higher plants** (Seagrasses)

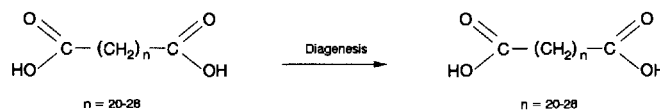
Zostera marina: α,β-dihydroxy fatty acids



Mode of occurrence: Amide- and/or glycosidically bound

"Free" ?

Thalassia testudinum: long chain α,ω-dicarboxylic acids



Mode of occurrence: Ester bound

"Free"

α,β-dihydroxy fatty acids and long chain α,ω-dicarboxylic acids: Lagoonal environment

Fig. 21. Palaeoenvironmental indicators for: (a) transitional higher plants – mangroves; (b) lagoonal aquatic higher plants – seagrasses.

1991). The presence of these different specific lignin units in marine sediments can be used to determine the relative contribution of terrestrial material into the marine realm (Hedges & Parker 1976; Goñi & Hedges 1992 and references therein). However, in more ancient sediments, lignin macromolecules can be altered considerably (Hatcher *et al.* 1989; Van Bergen *et al.* 1994b) depending on overburden and lithology (Van Bergen *et al.* 1994c). Nevertheless, if present, the specific methoxyphenol units can still be recognized. Variations in the $\delta^{13}\text{C}$ values, due to different fixation pathway of atmospheric CO_2 of the C3 (c. -28%) vs. C4 plants (c. -17%), are also reflected in the lignin building blocks (Benner *et al.* 1987; Goni *et al.* 1993).

(e) Resins. The macromolecular substances in resins and resinates can be subdivided into three major structural types (Anderson *et al.* 1992). Polyditerpenoids are macromolecules of which the basic structural unit has the diterpenoid labdane carbon skeleton (Fig. 20a; Carman *et al.* 1970); these polymers are present in gymnosperm resins. The second type are poly sesquiterpenes (Fig. 20b), recognized in resins from Dipterocarpaceae and Mastixioideae, which have as their basic structural unit a sesquiterpenoid cadinane skeleton (Van Aarssen *et al.* 1990, 1994). The third type is a natural polystyrene which is reported from *Liquidambar* (Grimaldi *et al.* 1989). During late diagenesis and catagenesis these macromolecules break down generating compounds which are frequently encountered in sediments and crude oils (e.g. Van Aarssen *et al.* 1990). Since, in most cases, these compounds still reveal some of their original structure they can be used to interpret the source plants and they indicate terrestrial input into the marine realm.

Mangroves One group of molecular markers commonly associated with higher-plant input in marginal marine sediments and oils are the non-hopanoid pentacyclic triterpenoids. Angiosperm input of oleananes and other pentacyclic triterpenoids (Fig. 21a) since the late Cretaceous (100 Ma) is well documented (Whitehead 1974; Ten Haven & Rullkötter 1988). For example, crude oils from the Tertiary Niger Delta have significant amounts of oleananes which are known to be sourced from terrestrial higher plants (Ekweozor & Udo 1988). In extant plant tissues the pentacyclic triterpenoids are secondary metabolites and have a major protective function within resins and waxes as they are secreted outside the cell or plant (Baas 1983).

The diagenetic transformation pathway from

biosynthesized pentacyclic triterpenols (e.g. α - or β -amyrin and taraxerol) within angiosperm tissues to saturated products (triterpanes, e.g. oleanane) has recently been determined in greater detail by Killups & Frewin (1994) (Fig. 22). Comparative diagenetic transformation of sterol precursors to steranes is known to occur through dehydration at the alcohol functionality with sterene intermediates (De Leeuw *et al.* 1989; De Leeuw & Baas 1986). Until recently, such intermediates were rarely found in sediments, despite the frequent alcohol functionality at C3. However, work by Ten Haven *et al.* (1992) has shown, from Recent sediments, that dehydration of triterpenols to Δ^2 -triterpenes does occur. Triterpadienes and A-ring contracted triterpadienes were identified in sediment extracts. The A-ring contracted homologues arise from 3β -OH alcohols, whilst Δ^2 -triterpenes are known to derive from 3α -functionalities. This led Ten Haven *et al.* (1992) to suggest a degradational pathway based on competing microbial and chemical transformations, whereby microbial action produces the triterpadienes and chemical action produces the A-ring contracted homologues. This suggestion was confirmed in work by Frewin *et al.* (1993) and Killups & Frewin (1994) where transformation products of pentacyclic triterpenols were isolated from the external membrane of the plant tissue itself, thus indicating that microbial degradation can occur at an even earlier stage than was at first speculated.

A study of leaf cuticular membranes from the mangrove *Rhizophora mangle* was performed using a methodology combining solvent extraction and elucidation of insoluble constituents using pyrolytic techniques (Frewin 1993). Cuticle extracts yielded quantities of triterpadienes which could be directly related to their triterpenol precursors in the higher-plant tissue. Pyrolysis of external tissues enabled direct thermal dehydration of most pentacyclic triterpenols and demonstrated the fractionated distribution of triterpenoids within the different functional tissues. For example, in *R. mangle*, β -amyrin was mostly located in solvent soluble wax fractions, whilst taraxeroid-type compounds were found as bonded/occluded moieties within the matrix of the cuticle and were not directly extractable. This provided compelling evidence for the preservation of selected triterpenoidal structures during sedimentary diagenesis. Similar extract and pyrolytic analyses to those conducted on plant tissue were undertaken for < 5000 years BP sediment samples from Florida Bay, southeastern USA (Frewin 1993). Solvent extracts yielded substan-

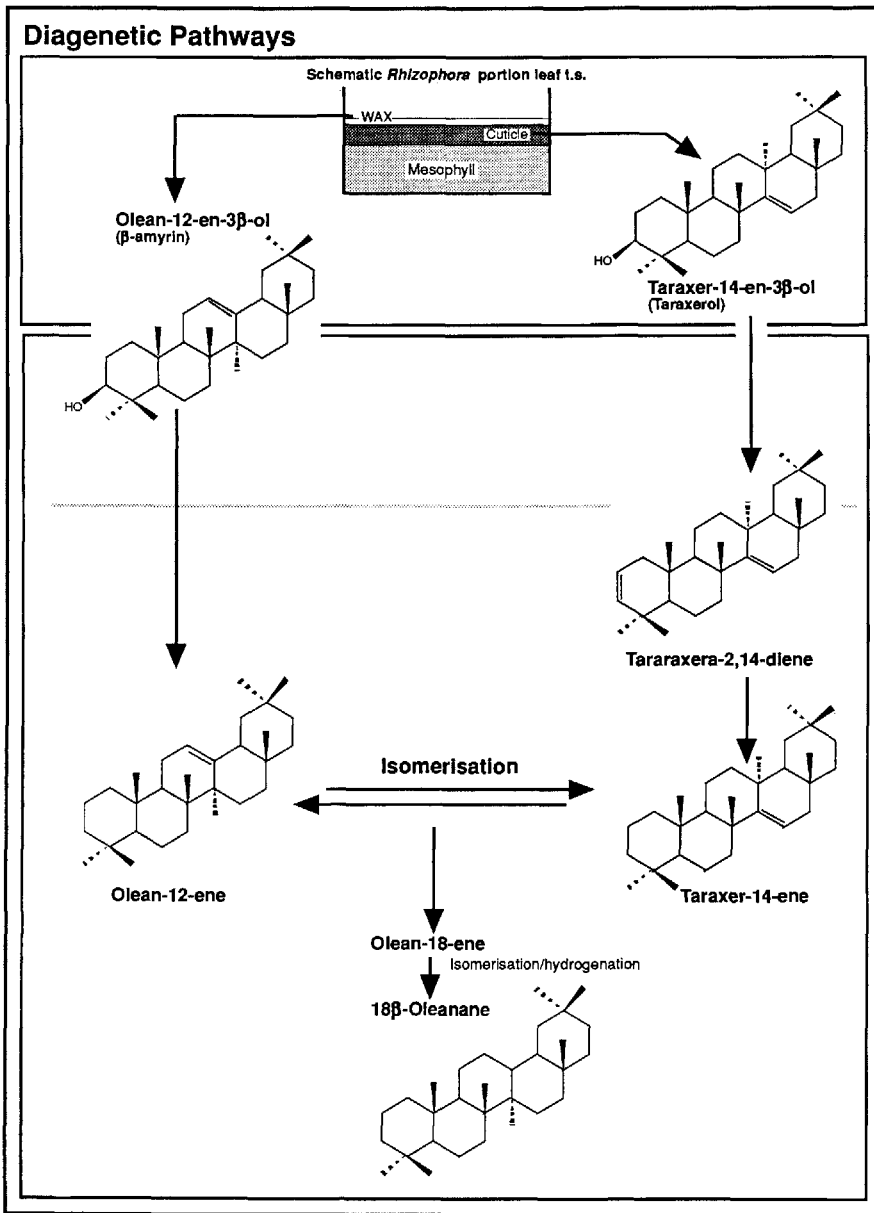


Fig. 22. Diagenetic pathway for pentacyclic triterpenoids from mangroves.

tial amounts of β -amyrin, whilst pyrolysis again demonstrated that taraxeroid structures were retained within the insoluble fraction. These data pointed to the selective release of taraxeroid structures into the geosphere and their rapid isomerization to oleanoid structures, thus joining the oleanoid degradational pathway, as was earlier speculated by Ten Haven & Rullkötter (1988).

Interestingly, these observations were true for the *Rhizophora* species and not for another mangrove species, *Avicennia germinans*. In the latter, all triterpenoids were directly extractable and none were retained in the pyrolysate (Frewin 1993).

The information presented above has several implications. Firstly, mangrove ecosystems have been described as one of the most productive

(Lugo & Snedaker 1974) and, in the case of Florida Bay, they are documented as producing 40% of the organic matter entering the marine system (Heald 1971). Amongst angiosperms, this places them in a position of particularly high preservation potential, with deposition of litter occurring directly at the water-sediment interface (compared with plants of the terrestrial hinterland which are deposited sub-aerially). Secondly, the unusual distribution of pentacyclic triterpenoids within some species of mangroves and not others means that the origin of these compounds within sediments and oils should be re-evaluated. For example, the high oleanane content of the southern Nigerian crude oils was not ascribed to mangrove vegetation (which has dominated the marine margins of the delta throughout Tertiary and Recent sediments; Ekweozor & Udo 1988). This reasoning was based on the observation that the endemic *Rhizophora* species did not contain amyirin constituents and that, therefore, fluvial transport of allochthonous organic matter from other sources was considered a more likely explanation (Ekweozor & Udo 1988). *Rhizophora mangle*, which was examined by Frewin (1993), contained an unusual distribution of triterpenoids, as described above, and this may well be reflected in the Nigerian species with all structures joining the oleanoid degradational pathway. High amounts of taraxerol were isolated from anoxic, semi-restricted, lacustrine sediments of Kau Bay in Indonesia (Middelburg *et al.* 1993). The abundant presence of taraxerol in these sediments is thought to reflect the surrounding mangrove vegetation and its survival is a result of anoxic conditions during sedimentation.

Thus, the presence of specific non-hopanoid pentacyclic triterpenoids in ancient sediments may be more indicative of shoreline proximity than previously thought and may corroborate other methods of recognition (see Plaziat this volume).

Aquatic higher plants Aquatic higher plants (freshwater as well as marine) require a different physiology with which they control the effects of their local environment and this may be reflected in their biomolecular composition. Freshwater plant remains which might be transported into the marine realm include resistant parts such as seed material. The biomacromolecular composition of such seeds and the preservation potential in the marginal marine realm have recently been studied by Van Bergen *et al.* (1991, 1994a, b, c). They showed that these seeds had seed coats which were composed of two layers. The outer

seed coat layer was composed of lignin which was dramatically altered during diagenesis (Van Bergen *et al.* 1994b), whereas the inner seed coat layer was composed of a cutan-like highly aliphatic macromolecule (Van Bergen *et al.* 1994a). The latter, in particular, could contribute to amorphous kerogen in marine sedimentary organic matter in a way similar to that of cutan (Van Bergen *et al.* 1994a).

One group of marine flowering plants are the seagrasses which occur in large areas of marginal shallow marine environments such as lagoons. This means that the blade material may form a large proportion of the photoautotrophically derived organic detritus. Pyrolysis-GC-MS of the thin external membrane covering the seagrass blade suggests that it is chemically different to that demonstrated in their terrestrial counterparts (Frewin 1993). The tissues are found to contain a high proportion of carbohydrates in association with a biopolymer which shows affinities to both the classical cutin chemistry and the suberin structure described by Holloway (1984). This may be a reflection of its submarine existence. The derivation of distinctive chemical markers for seagrass blade material is difficult to achieve as epibionts are generally found in close and inseparable association with blade tissues (Frewin 1993). However, extract analyses of a number of samples in different stages of senescence, from a number of different species, show that modified cutin-derived, long chain α,ω -dicarboxylic acids (C₂₆-C₂₈; Fig. 21b) are reliable markers for seagrass blade material within sediments (Nichols *et al.* 1982; Nichols & Johns 1985; Frewin 1993). Further acid treatment of temperate seagrass blades (*Zostera marina*) yields a distinctive series of α,β -dihydroxy fatty acids (Fig. 21b; De Leeuw *et al.* unpublished results). The high yields of these acids from extant tissues suggest that they are biosynthesized by the plants and incorporated by amide or glycosidic bonds and thus not directly extractable.

Estimation of shoreline proximity. - a case study The distinction between biomolecules derived from terrestrial higher plants and those derived from submarine higher plants has been addressed in a study of the lagoonal carbonate sediments of Florida Bay, southeastern USA (Fig. 23), by Frewin (1993) where there are two main floral types being actively incorporated into the sediments. The paralic margins of the bay are dominated by mangrove swamps, whilst the subtidal mud-banks of the bay have dense carpets of seagrass which extend 30-40 km from the nearest terrestrial higher plant input.

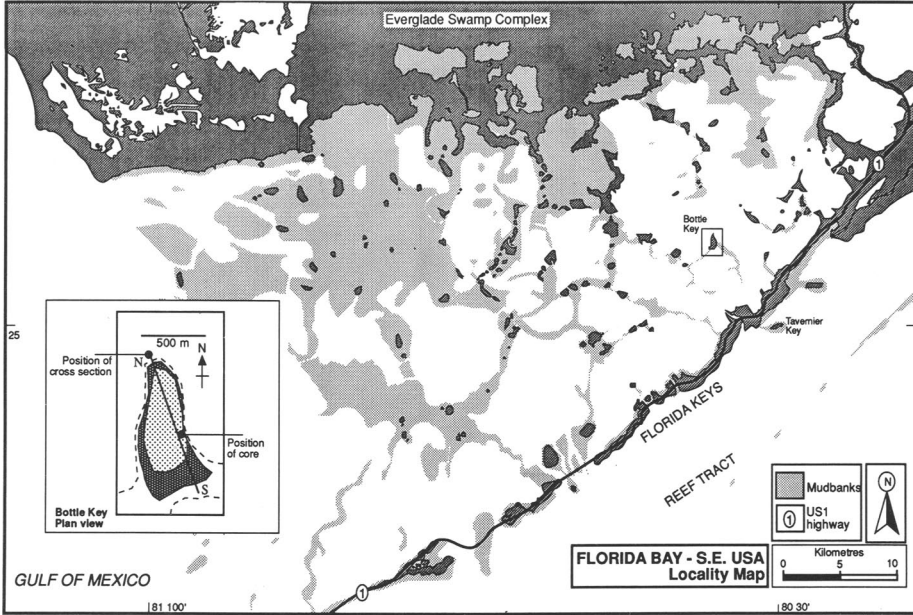


Fig. 23. Map of Florida Bay showing location of Bottle Key core.

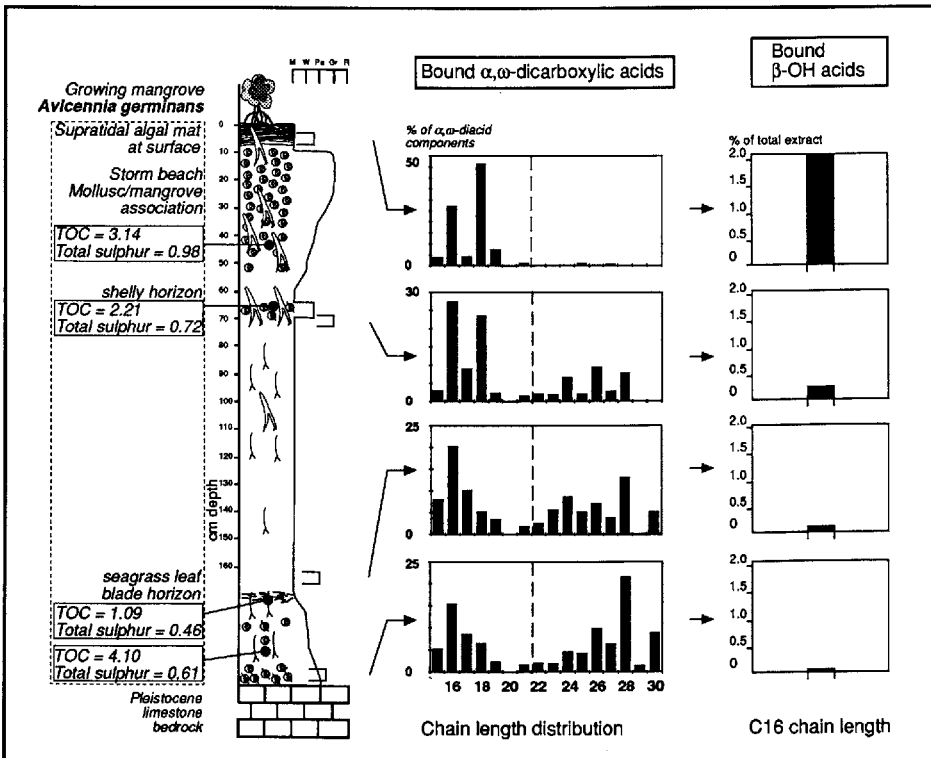


Fig. 24. Downcore distribution of two organic molecular components isolated from sediment extracts. Sediments taken from a core at Bottle Key, Florida Bay, southeast Florida. (Molluscs, half-filled circles; seagrass, thin roots; mangrove, thick roots.)

Table 1. Overview of the relationship between organism, biomolecule, molecular fossil and palaeoenvironment

Organisms	Biomolecule Biomacromolecule	Molecular fossil	Palaeoenvironmental parameter
PROKARYOTES			
Cyanobacteria	Mid-chain-methyl alkanes Bacteriohopanetetrol	Unaltered Extended hopanes, S-bound hopane	Water-column stratification
Archaeobacteria (especially methanogens)	Isoprenoid ether lipids Bound isoprenoid ether lipids	Specific isoprenoid alkanes Bound isoprenoid moieties	Anoxia
Sulphate reducing bacteria	Functionalized compounds	Organic Sulphur Compounds (OSC)	Anoxia
Photosynthetic sulphur bacteria	Specific carotenoids	Diaryl isoprenoids S-bound diaryl isoprenoids	Chemocline in photic zone
Methanotrophic bacteria	Bacteriohopanetetrol	'Isotopic light' extended hopanes	Methane cycling
Gram-negative bacteria	LPS	β -OH fatty acids	Bacterial reworking
EUKARYOTES			
Dinoflagellates	Dinosterol	Dinosterane	Dinoflagellates even when cysts are absent
Diatoms	Highly branched isoprenoid alkanes/alkenes	Highly branched isoprenoid alkanes	Blooming through upwelling
Prymnesiophytes	Long chain unsaturated ketones	Long chain unsaturated ketones	Surface sea-water temperatures
Chrysophytes	24- <i>n</i> -propylcholesterols	24- <i>n</i> -propylcholestanes	Marine setting
Green microalgae	Δ^7 -Sterols	5 α ,14 β ,17 β (H)-steranes	Freshwater/lacustrine input
Algae/cyanobacteria	Algaeans	Algaeans	Mainly freshwater/lacustrine
HIGHER PLANTS	Chromans/chromane precursors	Chromans	Salinity
Terrigenous angiosperms	Long chain <i>n</i> -alkanes Cutan	Long chain <i>n</i> -alkanes Transformed cutan	Terrestrial input (aeolian/fluvial)
	Sporopollenin	Transformed sporopollenin	
	Angiosperm lignin	Transformed angiosperm lignin	
	Polycadinene resins	Polycadinanes	
	Sporopollenin	Transformed sporopollenin	
	Gymnosperm lignin	Transformed gymnosperm lignin	
	Polycommunic acid resins	Transformed polycommunic acid resins	
	Specific triterpenoids	Specific triterpanes	Paralic input
Transitional plants (e.g. Mangroves)	Amide bound α,β -diOH-fatty acids	α,β -diOH-fatty acids	Shallow marine input
Seagrasses	Esterified α,ω -dicarboxylic acids Cutan Lignin	α,ω -dicarboxylic acids Transformed cutans Transformed lignins	Freshwater input
Freshwater plants			

The Holocene marine inundation of the south Florida peninsula has been well documented (e.g. Scholl 1964) and the effects of a transgressive regime on coastal sedimentation have been studied in some detail (e.g. Parkinson 1989). The south Florida peninsula has an extremely low relief and sea-level changes are recorded by sediments containing organic matter derived from various coastal and shallow marine vegetation types. The submarine and terrestrial floras (in this case seagrass and mangrove) are sensitive to the changes in salinity, amongst other variables, existing between the freshwater of the Everglades swamps to the marine conditions of the lagoonal mud-banks. An examination of particulate organic matter within the marine sediments of the bay failed to locate evidence for such a vegetational stratigraphy, as structured organic matter was rapidly reworked to amorphous masses (Frewin 1993) and this hindered the recognition of the relative position of the south Florida coastline. Root material may form as secondary fabrics in sediments, and was thus discounted from identification of colonizing communities. Root material was removed from sediment samples by sieving. Organic geochemical studies of the bay sediments isolated several groups of molecular markers pertinent to the study of backstepping submarine and terrestrial higher-plant types in Florida Bay.

Two organic marker parameters were used in the distinction of the two higher-plant sources. The relative contribution of C_{16} and C_{26}^+ α,ω -dicarboxylic acids were used to identify terrestrial higher-plant input and seagrass input, respectively. A typical mud-bank sequence is shown in Fig. 24. Using the markers described above, it can be concluded that seagrass colonization was occurring at the base of the sequence. The increased relative abundance of C_{16} chain lengths suggests that mangroves, or other terrestrial higher-plant material, were also located nearby, but colonization was not apparent at this particular point in the cored section. Further mangrove colonization was occurring higher in the sequence, in association with storm beach material. It is evident that seagrass input is very much reduced at this point in the core. In this way, the relative contribution of terrestrial and submarine organic colonizers existing in juxtaposition may be assessed.

Conclusions




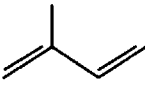


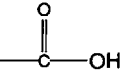
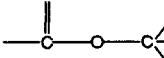
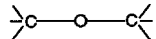
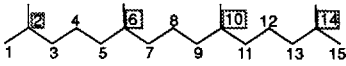
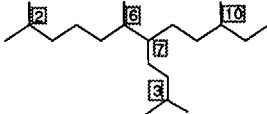
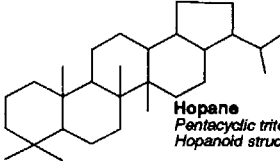
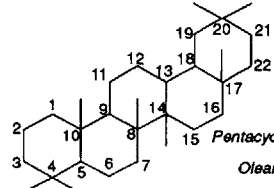
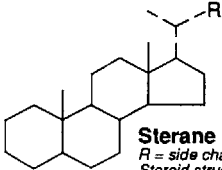
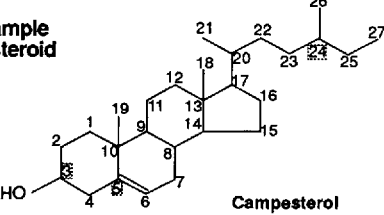
As a result of recent developments in organic geochemistry, i.e. determination of OSC and

analyses of $\delta^{13}C$ values of individual sedimentary compounds, it is possible to decode all information known to be present in sedimentary organic molecules, i.e.: (1) carbon skeleton structures; (2) positions of functional groups; and (3) stable carbon isotope ratios. The information strengthens relationships between molecular fossils (or biomarkers) and (palaeo)-biochemicals (Table 1). Furthermore, biochemical assemblages give clues to their precursor organisms and also reveal palaeoenvironmental conditions (i.e. temperature, stratification, salinity, etc.). The combined presence of OSC, dinosteroids, 24-*n*-propylsteroids (even in trace amounts), high amounts of C_{25} HBI hydrocarbons and the absence of long chain *n*-alkanes with odd over even predominance, bicadinanes and specific higher-plant triterpenoids (e.g. oleanane) characterize a marine environment. Likewise, palaeoenvironmental conditions and diagenetic processes are indicated by molecular and/or isotopic characteristics. For example, the presence of isotopically very heavy diaromatic carotenoid derivatives (less negative $\delta^{13}C$ values) indicate photic zone anoxia; the chroman ratio indicates hypersalinity vs. marine to fresh water conditions (even though the source organism is unknown); OSC indicate the presence of microbial sulphate-reducing activity, i.e. anoxia; isotopically heavy C_{25} HBI hydrocarbons indicate diatom blooming normally associated with palaeo-upwelling; the relative concentrations of di- and triunsaturated long-chain ketones derived from certain prymnesiophyte algae provide palaeo-surface seawater temperatures. Hence, biomarkers (or molecular fossils) can be upgraded to (molecular) palaeoenvironmental indicators.

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Appendix A

A simple guide to nomenclature in organic chemistry. For a more detailed appraisal of stereochemistry and chemical nomenclature in a geological context, the reader is referred to Peters & Moldowan (1993).

<p>Acyclic Alkanes These are simple hydrocarbons, containing only carbon and hydrogen.</p> <p style="text-align: center;">C_nH_{2n+2}</p> <p>Compounds with this same formula but differing structural rearrangements are called <i>isomers</i>. Compounds with a linear arrangement are given the prefix <i>normal</i> or <i>n-</i>.</p> <p><i>Unsaturation</i> occurrence of double bonds which can act as reactive sites (functional group)</p> <div style="display: flex; justify-content: space-around; align-items: center;"> <div style="text-align: center;">  <p>Suffix <i>-ane</i></p> </div> <div style="text-align: center;">  <p> <i>-ene</i></p> </div> <div style="text-align: center;">  <p> <i>-yl</i></p> </div> </div>	<p>The "isoprene" Sub-Unit This structure containing five carbon atoms is the basic sub-unit from which many biomolecules are formed. Larger compounds composed of such structures are termed <i>isoprenoids</i> or <i>terpenoids</i>.</p> <div style="text-align: center;">  <p>C_5 isoprene unit</p> </div>			
<p>Some Common Functional Groups and Linkages</p>				
<p>Alcohol</p>  <p>Suffix <i>-ol</i></p>	<p>Ketone</p>  <p> <i>-one</i></p>	<p>Acid</p>  <p> <i>-oic acid</i></p>	<p>Ester-bound</p>  <p> <i>-oate</i></p>	<p>Ether-bound</p>  <p> <i>-ether</i></p>
<p>Common Terpenoid Structures</p>				
 <p style="text-align: center;">Phytane (C_{20})</p> <p style="text-align: center;">2,6,10,14-tetramethylhexadecane (4 methyl groups at positions 2,6,10 and 14)</p>	 <p style="text-align: center;">C_{20} Highly branched isoprenoid (HBI) 2,6,10-tetramethyl-7-(3-methylbutyl)-dodecane</p>			
 <p style="text-align: center;">Hopane Pentacyclic triterpenoid structure. Hopanoid structure.</p>	 <p style="text-align: center;">Oleanane Pentacyclic triterpenoid structure. Oleanoid structure.</p>			
 <p style="text-align: center;">Sterane <i>R</i> = side chain Steroid structure.</p>	<p>Example of steroid</p>  <p style="text-align: center;">Campesterol</p> <div style="margin-top: 10px;"> <p>24-methylcholest-5-en-3β-ol</p> <p>24 = position of methyl group in side chain.</p> <p>5 = position of double bond. May also be referred to as Δ^5-steroid.</p> <p>3β = stereochemistry of functional group.</p> </div>			

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Modern and fossil mangroves and mangals: their climatic and biogeographic variability

JEAN-CLAUDE PLAZIAT

University of Paris-Sud, URA 723 – Département des Sciences de la Terre, Laboratoire d'Hydrologie, Bâtiment 504, F91405 ORSAY Cedex, France

Abstract: The variability of mangrove environments (mangals) has generally been underestimated, as has their distribution from temperate to subtropical climates and their histories in the Atlantic and Indo-Pacific biogeographic provinces. Subtropical, arid and equatorial mangals require different palaeoecological approaches. *In situ* fossilization is paradoxically very rare, and has often been misinterpreted, but current reworked shells, and human shell gathering (middens) provide valuable records of ancient mangals. The identification of ancient mangroves depends on the preservation of pollen or wood while the upward branching root system of *Avicennia* is another reliable indicator. The associated molluscan fauna may also be diagnostic, particularly if encrusting oysters are preserved with imprints of mangrove roots and bark. Several case studies are briefly reviewed and discussed: Holocene buried mangals of Abu Dhabi, Holocene shell middens of the Middle East, Miocene Japanese and European mangals documented by molluscs and pollen, and the Paleocene–Eocene mangals of western Europe. Problems concerning the evolution of the mangal biota and the differences between their distribution in ancient and modern climates forms the basis for discussion of the palaeogeographic and climatic significance of the palaeomangals reviewed in this paper.

Many geologists are familiar with mangrove environments characterized by diverse trees and shrubs, belonging to very different families, all with the unusual adaptation to life in intertidal salt waters of warmer climatic regions. However, few take into consideration the range and variability of mangrove environments: from desert to rain forest shorelines, from reef flats to estuaries and also from equatorial to temperate climates.

The chief species of mangrove trees (French: palétuviers) belong to the families Rhizophoraceae, Avicenniaceae, Combretaceae (*Laguncularia*) and Arecaceae (*Nypa*). These are viviparous trees developing from floating fruits or seedlings, taking root in the upper intertidal zone after a facultative flotation state in sea water. There is no rigorous definition of a mangrove but a strict association with the most typical mangrove tree vegetation is the common usage (see Barth 1982; Tomlinson 1986). Locally, mangroves characterize a narrow transitional belt between the marine and continental realms, above mean sea level, and they may also form a discontinuous tree-line along steeper shores (rocky or sedimentary slopes). However, they are better known as constituting extensive mangrove swamps or forests, a particular type of wet coastal biome which takes advantage of actively silting shores, and

estuaries, grading from fully marine to freshwater environments. These diverse ecosystems have been named mangals (Macnae 1968) (French: mangroves), an environmental term, that is now recommended by biologists (Chapman 1977; Por & Dor 1984), to include a mangrove dominated flora, the associated fauna and their biotope. Nevertheless, many English and American authors use 'mangrove' in the sense of mangal but usually in the adjectival form (e.g. mangrove swamp).

When viewed on a global scale (Fig. 1) mangroves are seen to occur in the warmer tropical belt, including equatorial rain forests, with local extensions to subtropical climates (average annual temperature below 20°C) in SE Africa, NE Asia and E Australia. Generally speaking, the eastern shores of the continents have larger latitudinal ranges (to 28–39°) than the western shores (4–28°) and Fig. 1 shows the opposing influences of warm ocean currents and both cold currents and winter winds. Such a distribution closely resembles that of the coral reefs, but with an extension into mild temperate climates. Most palaeogeographers tended to ignore these extensions out of the tropical belt while this author would suggest that they are an important key to the palaeoclimatic interpretations.

The Indo-Malayan areas provide the most

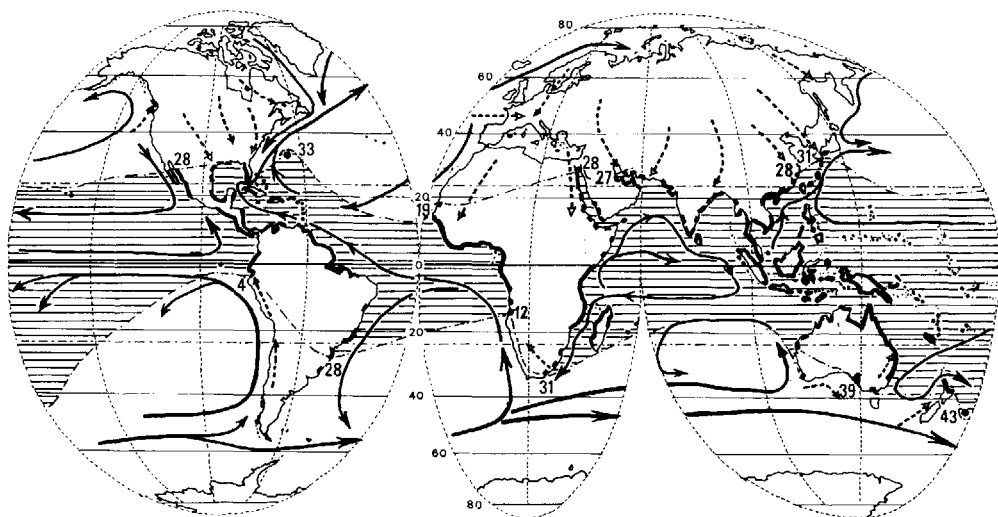


Fig. 1. Present-day mangal distribution (bold shorelines and dashed areas). The broadly tropical belt of mangrove occurrences is strongly modified by cold and warm ocean currents as well as the coldest winds generated by the winter polar air mass movements (dashed arrows). The eastern shores of each continent are favoured by both warmer sea currents and summer rains while the northernmost mangrove of Bermuda (33°N) and the southernmost mangroves of Chatham Island (43°S) demonstrate the influence of milder oceanic climates. Reference sources: Plaziat (1970*a, b*) and Chapman (1977), and monographs quoted in the text.

luxuriant expression of this biome with 41 mangrove plants (Barth 1982). This localized, equatorial richness paradoxically may have obscured the recognition of ancient mangals because fossil mangals also developed in subtropical and temperate regions. It is therefore important to recognize (Figs 2 & 3) that mangals range from the dwarf *Avicennia* thickets of desert shores and the *Kandelia* or *Avicennia* shrubs of higher latitudes (29–30°N, 35–44°S) to the 40m high *Rhizophora* and *Avicennia* sub-equatorial forested shores.

This variability is also expressed in the local floristic diversity [1–41 mangal plant species (Barth 1982; Tomlinson 1986)] and the associated faunal diversity, which generally decreases into higher latitudes. The ancient (Miocene) separation of the Atlantic and Indo-Pacific biogeographic domains (Dercourt *et al.* 1993) also induced differences both at the generic and specific level of floral and faunal components of present-day mangals. Therefore, it should be expected that their biogeographic distribution was different in Tertiary times when the Tethys seaway linked the Caribbean and SE Asiatic regions.

The similar marine adaptations of trees belonging to different families suggests that

other ancient plants, in Mesozoic or even Palaeozoic times, may also have adapted to this salty intertidal environment. However, the modern mangrove genera are only recorded back to the Paleocene. The notable exception to this is the palm tree *Nypa* whose significance in ancient mangals has been questioned as it grows in low salinity estuarine and back-mangrove swamp environments and even isolated freshwater swamps. Its pollen, *Spinizonocolpites* and fruits, '*Nipadites*' are locally common from late Cretaceous times onwards (Tralau 1964; Gee 1990). In addition to the problem of unrecognized ancient mangrove genera, the rare and often imperfect fossilization of most of the modern mangroves is a major constraint to the botanical recognition of ancient mangals. This introduces the question as to whether there are reliable criteria for the recognition of ancient mangals in pre-Neogene deposits, especially where plant tissue is not preserved. In other words, are there characteristic sediments, molluscs or crabs, which are incontrovertible indicators of ancient mangal ecosystems?

An exhaustive review of the components of present-day mangals is beyond the scope of this contribution. Botanical reviews by Muller

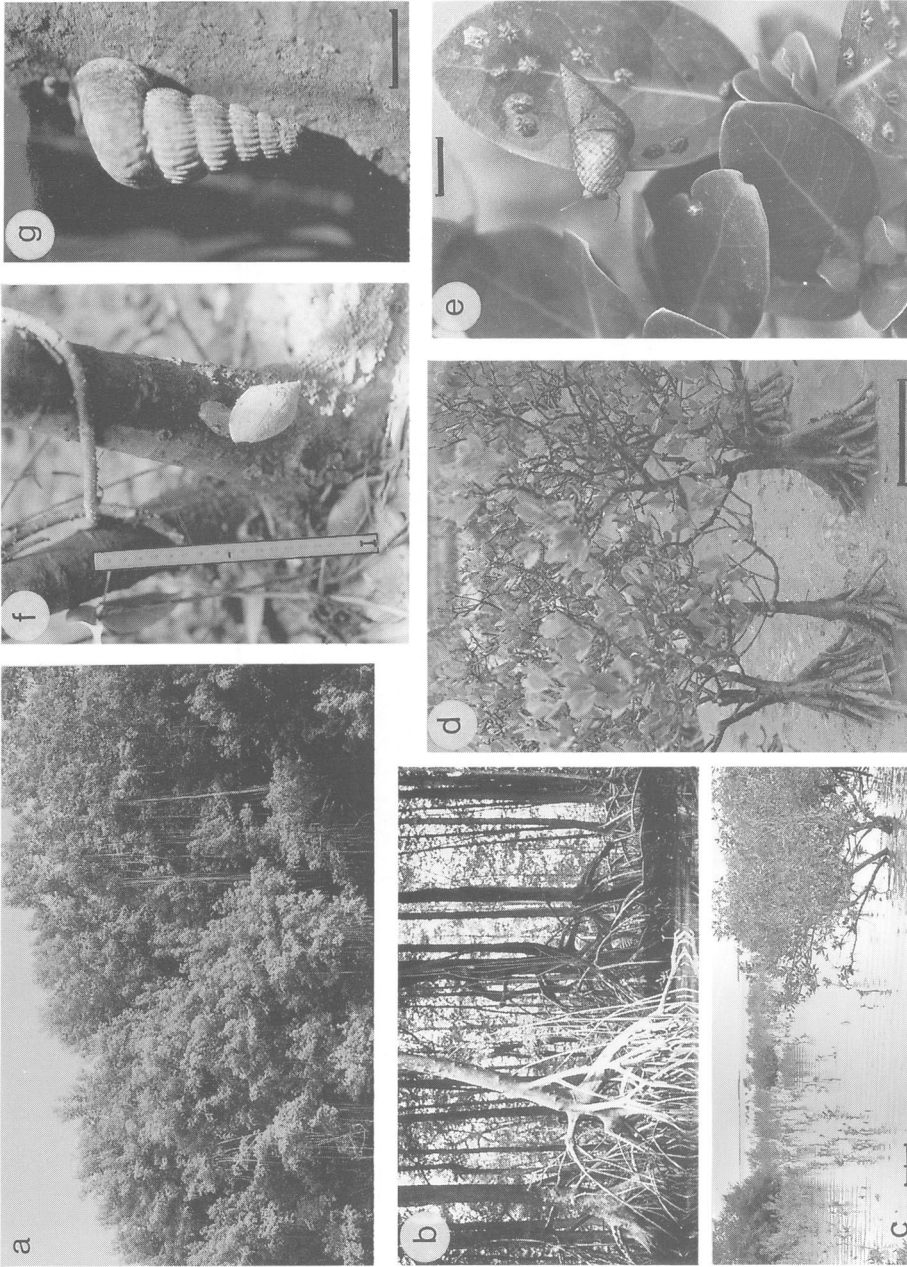


Fig. 2. (a) Equatorial mangal with 40 m high *Rhizophora* (and *Avicennia* not visible), Wouri river delta (latitude 4°N), Cameroon. (b) Internal glade in the highest tidal forest, same locality. (c) Flooded *Avicennia* shrubs, Persian Gulf, Saudi Arabia (27°N). (d) *Kandelia candel* at low tide, the northernmost rhizophoracean, Tanegashima (31°N), Japan. (e) *Littoraria melanostoma* and barnacles on tidally flooded *Avicennia* leaves, Xiamen (24°30' N), China. (f) Giant *Ellipticum* climbing on an *Aegiceras* trunk, Futien near Shenzhen (22°-30' N) China. (g) *Cerithidea* clinging 1.5 m higher by means of its dried mucus same locality. Scale bar: 20 cm, except for (f) and (g): 1 cm.

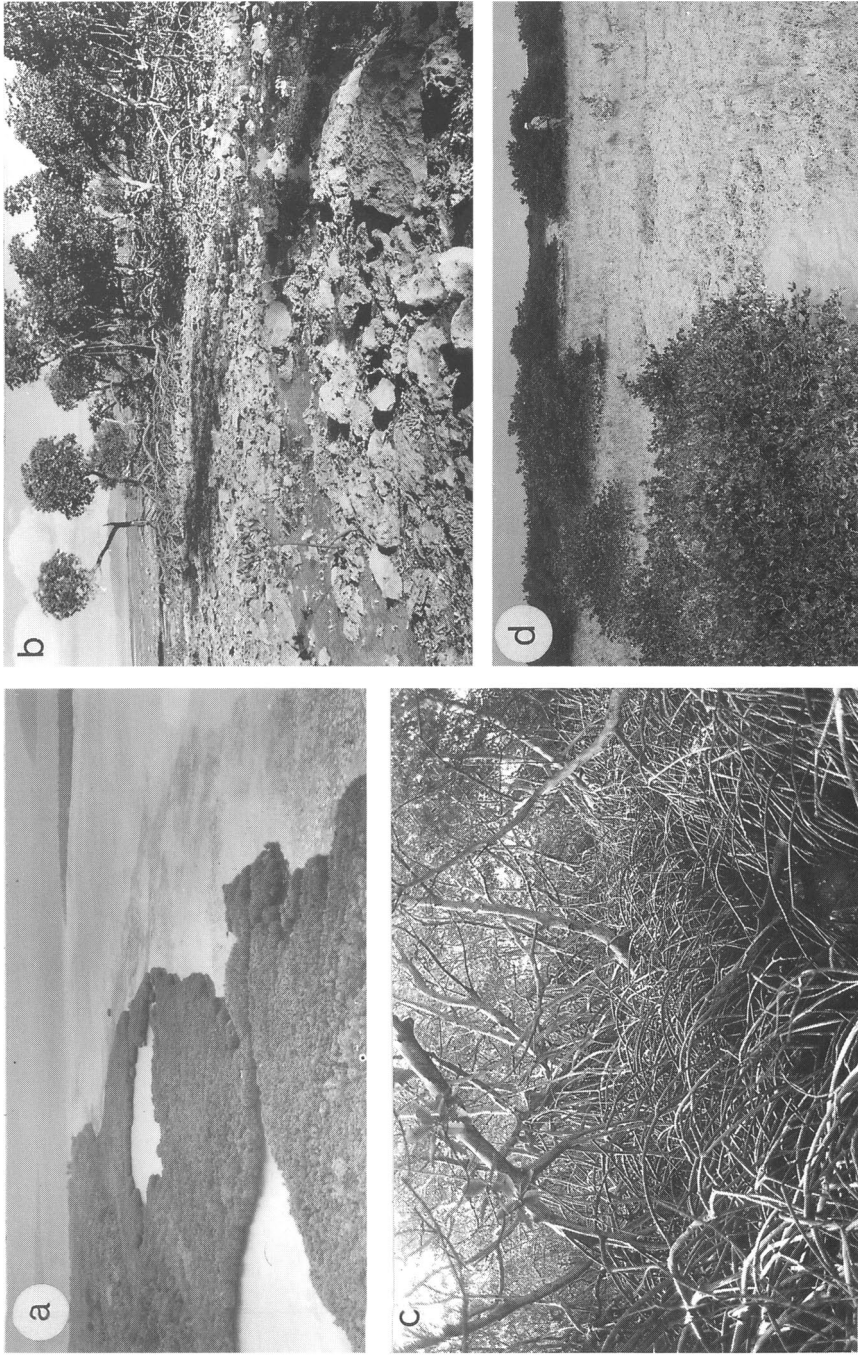


Fig. 3. (a) Mangal on the back-reef flat of Malekula (16°S latitude), Vanuatu, the classic reef-mangal association of the tropical belt. (b) A *Rhizophora* mangal encroaching over a fossil, uplifted reef, NE New Caledonia (21°S) showing a close superposition of different and successive environmental conditions. (c) Dense aerial rooting of a tropical *Rhizophora* mangal, Chichiriviche (11°N) Venezuela. (d) Dispersed dwarf *Avicennia* at low tide in a mangal, towards the limit of mangrove occurrence in the Arabo-Persian Gulf, Tarut (27°N) east Saudi Arabia.

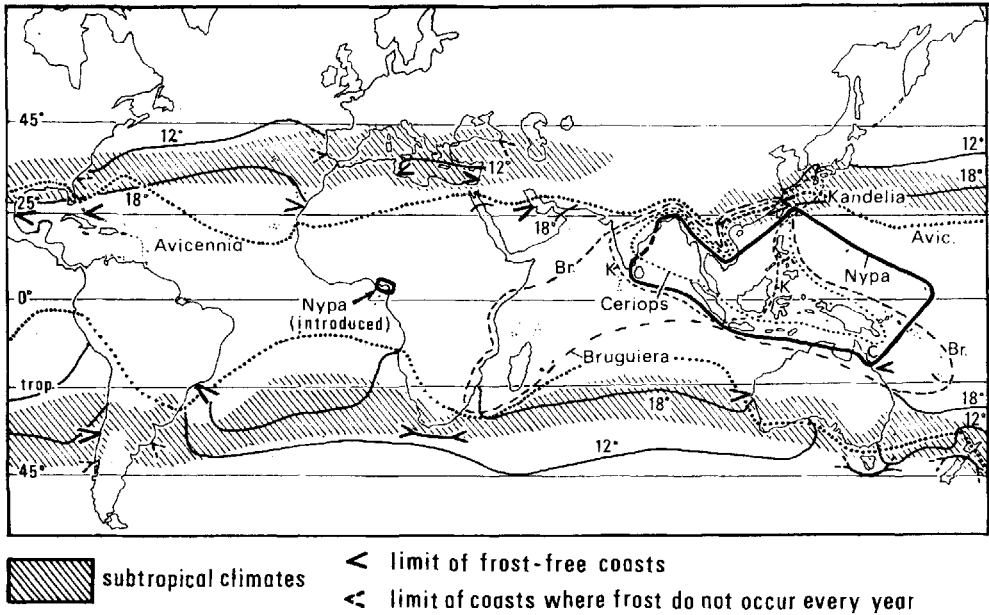


Fig. 4. Present-day distribution of mangrove genera (*Avicennia*, *Bruguiera*, *Ceriops*, *Kandelia* and *Nypa*) compared with climatic data: subtropical climates (mediterranean and humid subtropical), frost-free coastlines, minimum monthly average temperature of sea water and distribution of mangrove genera; after Plaziat *et al.* 1983, 1984c and others (see text).

(1981), Thanikaimoni (1987), Tomlinson (1986), and environmental studies by Macnae (1968), Chapman (1977) and Por & Dor (1984), are the best introductions to make use of the bibliographies published by van Tine & Snedaker (1974), Chapman & Johnson (1977) and Rollet (1981) and the congress contributions edited by Walsh *et al.* (1975).

In this paper the geographic diversity of mangals is discussed, and their preservation potential considered. Examples of ancient mangrove deposits are then described together with their palaeoenvironmental significance and finally the contributions made by mangals to reconstructing ancient climates and biogeography are discussed.

Geographic variability within the mangal biome

Global variability

The variability in mangal settings and components suggests that it is incorrect to consider the

diverse mangals as a single environment type. There are many different types that vary according to climatic, sedimentary and biogeographic contexts. Different descriptive names have been used to describe this variability: mangrove forest, mangrove swamp, reef mangrove or shura, mangrove shrubs, curtain, discontinuous line or isolate mangrove trees, besides the classic riverine, fringe and basin mangals (Lugo & Snedaker 1974).

According to the literature (cf. Tomlinson 1986), and the author's experience in French Guiana, Venezuela, Florida, Cameroon, Senegal, Egypt, Persian Gulf, Oman, Pakistan, Indonesia, China, Japan and New Caledonia, the tropical mangals are characterized by floras with more than three mangrove genera, associated with a tropical molluscan fauna. The widely distributed *Avicennia* tolerates seasonally weak frosts (New Zealand, Arabian coast of the Persian Gulf, southern USA) (Fig. 4). Subtropical climates (average annual temperature below 20°C, more than 350mm rain), as opposed to the tropical and arid climates, are usually

inhabited by stunted mangroves, though the subtropical eastern Australian shore possesses between three and eight mangroves despite occasional frosts.

Australian and Japanese mangals and reefs illustrate the influence of mild climate, i.e. the absence of hard frost. Higher diversity and higher latitude distribution of these so-called 'tropical' biomes reflect the milder regional conditions.

The winter invasions of cold polar air masses is a modern climate pattern as during most of the Cenozoic, ice-free poles, or at least very limited polar accumulations of ice, must have resulted in a globally milder seasonality and a lower gradient of climatic zonation (Plaziat 1970*b*, 1982, 1984*a-c*, 1986; Wolfe 1971; Daley 1972; Collinson 1990). The present distribution of ice-free lowlands coincides approximately with the 20°C average annual temperature which is also the proposed limit to the Tropical Realm (Fig. 4). Thus, a reduction of winter coldness should have a major influence on the distribution of the present tropical biota because of a poleward retreat of frosts, as these are the major limiting factor for plants. Mildness is locally favoured by the present-day oceanic currents fed by tropical waters. Mangroves as well as the reef-corals and 'tropical' molluscs take advantage of warm currents to expand poleward (e.g. for mangroves, Bermuda 33°N, E Australia 39°S, Japan 31°N, SE Africa 31°S, Chatham Island 43°S) and enter the temperate climatic zone (below 15°C annual average). It should always be remembered that we still live under the climatic influence of (reduced) polar ice-caps and this should be borne in mind when studying palaeo-subtropical climates of the European Tertiary.

On a global scale, *Avicennia* is the most resistant genus to low and high temperatures and to intense evaporation resulting in high soil salinities (up to 70‰ in New Caledonia; Baltzer 1970). Some Rhizophoraceae are also tolerant to low temperatures depending on the biogeographic provinces (e.g. Atlantic *Rhizophora*, Northeastern Asia *Bruguiera*, *Kandelia*), but they are excluded from hypersaline waters. Associated mangal faunas are also effected by these limiting factors which reduce organism size and diversity in subtropical zones (Plaziat 1984*a*). A few genera can extend from the tropical realm into adjacent climatic zones resulting in progressive faunal changes. Isolated mangrove clumps are usually devoid of their characteristic associated biotas. Their atypical faunas would make it difficult to establish the poleward limits of the ancient mangals in the

absence of phytal remains.

The biogeographic partition between Atlantic and Indo-west Pacific mangrove provinces is a modern feature. It reflects an isolation probably dating back to the middle Miocene (Dercourt *et al.* 1993). Therefore, the clear differences between their respective modern floras and faunas would not be expected to extend to early Tertiary times. In fact, many European mangal fossils belong to genera which are at present exclusively Indo-west Pacific (e.g. *Nypa*, *Ceriops*, *Sonneratia*, *Terebralia*, *Enigmonia*), whereas the Far East regionalism appears to have been important since the beginning of the Miocene times [*Chicoreus* (*Rhizophorimurex*), *Geloina*].

Local variability

Within any given mangal, the physical and chemical attributes of the environment may contrast dramatically from the external (marine) to the internal (landward) parts of the mangrove swamp. Along desert coasts and in high evaporative tropical climates the major gradient is an increase in salinity from the sea to bare sediment areas landward of mangroves (e.g. Red Sea, Senegal), whereas in humid climates the coastline is permanently of higher salinity (e.g. Cameroon, Guiana) (Baltzer & Lafond 1971; Plaziat *et al.* 1983). Similarly, tropical coasts with contrasting wet and dry seasons have drastic seasonal changes in the salinity gradient which may be a very selective stress (Plaziat 1982). In all these cases, as in grass salt-marshes, a biologic zonation results from the lateral gradients in physico-chemical factors. In the mangal, the local morphology of the bottom (channels, levees and enclosed basins) are highly influential (Baltzer 1969, 1982; Chapman 1977). Biotic zonation may be related to tidal flooding or height above datum (Berry 1964; Baltzer 1969; Chapman 1977). Another zonation of the mangal biota living below the canopy is related to the distance to open waters (open sea or channels) (Plaziat 1984*a*). It is worthy of note that larger channels may have a marine, lagoonal or estuarine fauna which is not representative of the mangal but is locally included within it. These interfingering marine or estuarine communities have been incorporated within the mangal fauna by some authors (Cantera *et al.* 1983; Zaninetti 1979) without reference to the characteristic mangal species or assemblages. At present, no complete and reliable review of modern mangal fauna indicators is available. According to personal experi-

ence, a palaeoecologist attempting to identify ancient mangals uses a small number of genera which extend back through the Cenozoic: mangroves including *Nypa* palm, crustacean decapods (Sesarinae, *Uca* s.l., *Thalassina*) and molluscs [*Terebralia*, *Telescopium*, *Chicoreus* (*Rhizophorimurex*), *Littoraria*, *Ellobium*, *Geloina*, circular *Isognomon*] as discussed by Oyama (1950), Plaziat (1975a, b, 1984a), as well as the pioneer biological advices by Fischer (1940) and Macnae (1968).

However, the mangal assemblages also include many organisms with a wider environmental distribution which may locally contribute the bulk of the fossilizable biota within a mangal: barnacles, oysters, gastropods (potamids, melanians, neritids) and bivalves (teredinids, mytilids). These non-specific organisms generally over-contribute to the skeletal record of the climax mangals and may, in some cases, produce the only remains of the mangals occurring near to their latitudinal limits which otherwise have impoverished faunas and floras.

Preservation of mangroves and other biological indicators of mangals

Wood and peat

The extensive mangrove forests seen today are, paradoxically, poorly recorded in the fossil record. Decaying wood in swampy environments produces acidic peats or sediments rich in organic matter in which the diagnostic remains may be scarce or absent. The best mangrove soil preservation observed by the author is part of a Holocene stunted *Avicennia* mangal from Abu Dhabi developed on carbonate sediments, in hypersaline conditions, which must have been near the limits of mangrove growth (Fig. 6). The phytal debris (fibres) of peats and the distinctive pink colour of *Rhizophora* peat may be also reasonably used to interpret sub-recent deposits (Spackman *et al.* 1966; Baltzer 1970), but the older silicified mangrove woods (review in Plaziat & Koeniguer 1983) are transported logs, buried some distance from the mangal. Similar preburial transport (flotation) is evidenced by fossil fruits, e.g. *Nypa* (Gregor & Hagn 1982; Plaziat 1984a-c; Collinson 1993) and seedlings of Rhizophoraceae from the London clay (Chandler 1951; Wilkinson 1981, 1983). The precise identification of the floral components of ancient mangals mainly relies on transported pollen grains, fruits and logs, generally collected in marine sedi-

ments, frequently some way from their original life environment. This may explain the incomplete and generally inaccurate knowledge of fossil mangroves.

Pollens and fruits

Palynology is the most informative method of identifying ancient mangroves, whereas fruits, along with fragments of wood and leaves, are usually occasional, lucky finds except in cases of exceptional preservation such as in the pyritic fruits of the London Clay (Reid & Chandler 1933; Chandler 1951, 1961, 1964, 1978; Wilkinson 1981, 1983; Collinson 1983).

The positive identification of fossil mangrove pollens is relatively recent, as prior to Sedova (1956) and Muller (1968; for description of *Spinizonocolpites*) the *Nypa* pollen was mistaken for that of a water lily (Kedves 1960). For recent reviews see Frederiksen (1985), Gee (1990), Harley *et al.* (1991) and Collinson (1993). In the tropical realm Tertiary mangrove pollens are now well known (e.g. Germeraad *et al.* 1969), whereas their discovery in intermediate latitudes is relatively recent. The *Avicennia* pollen appears confidently in Europe in the early Eocene (Sein 1961, also in Chandler 1964). More recently palynologists have referred some *Psilatricolporites* and *Retitricolporites* spp. to the Rhizophoraceae, *Avicennia* and *Pelliciera* (Chateauneuf 1980; Gruas-Cavagnetto 1991). However, the palynological taxonomy generally precludes any assignation to present-day taxa. The alternative palynological method is based on a direct comparison with present-day pollens. The relationship is thus expressed by direct reference to a modern species, for example aff. *Avicennia marina* or aff. *Sonneratia alba*. This implies that no botanical evolution took place since early Eocene times whereas a fossil terminology (*Palaeobruquiera* fruit) or a broader reference (Rhizophoraceae pollens, *Nypa* fruit) suggest that the ancient mangroves may differ and, accordingly, become more difficult to identify in older deposits.

Japanese palynologists have recognized fossil mangrove pollens relatively recently (Yamanoi *et al.* 1980; Yamanoi & Tsuda 1986). Thus it may be considered that the palynological identification of medium latitude, ancient mangroves began around 1960 but mainly developed around 1980.

The identification of fossil mangrove fruit is much earlier - *Nypa* has been known since the mid 18th century (Parsons 1758) and Rhizophoraceae fruits (*Palaeobruquiera*, *Ceriops*) have been identified since 1951 (Chandler, 1951).

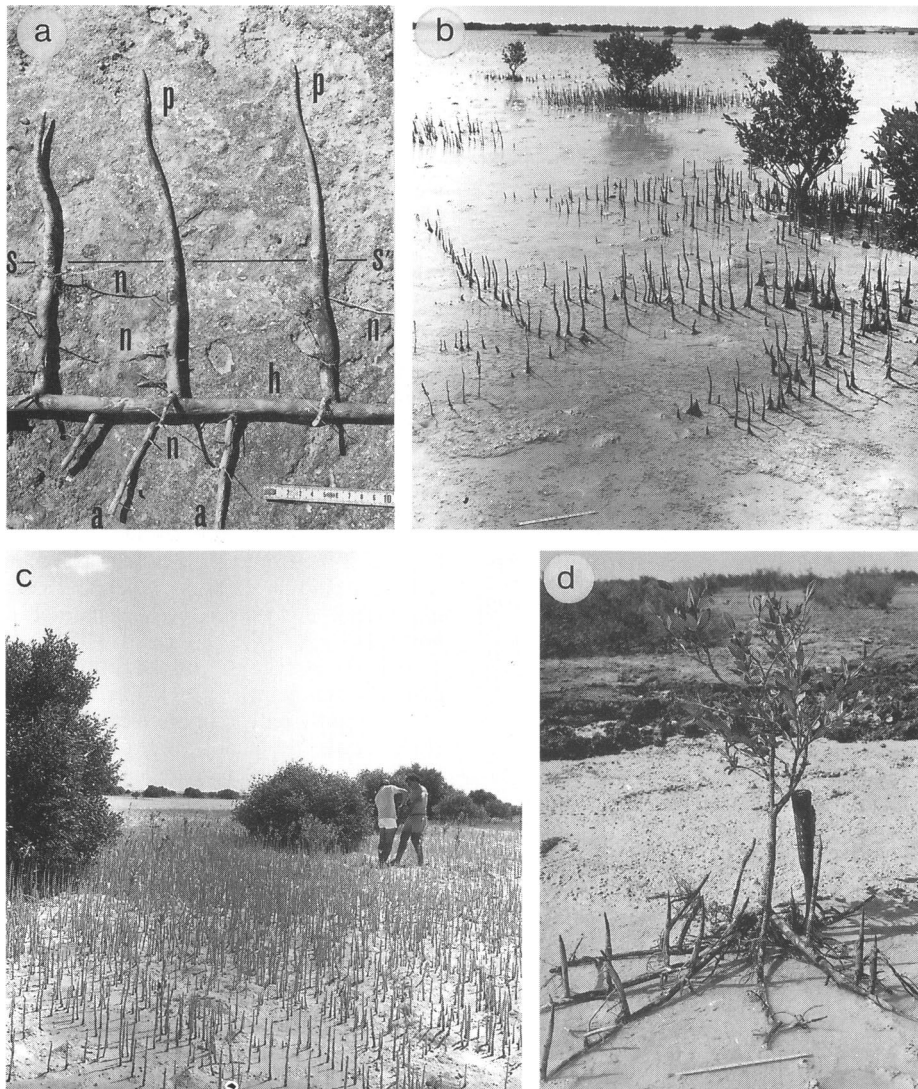


Fig. 5. *Avicennia* mangal of Ras al Khaf (Abu Dhabi, United Arab Emirates). (a) Unearthed roots – (s-s) was the sediment surface, (p) pneumatophores (aerial roots) branching from the horizontal root (h), (a) anchoring roots, (n) nutritive rootlets. (b) Scattered shrubs on the tidal carbonate mud-flat. The radiating horizontal roots may be traced by their aligned pneumatophores. (c) Higher mangroves (2-4m) and denser pneumatophores. (d) An unhearthed young *Avicennia*. The characteristic root network comprises the horizontal roots and branching upwards pneumatophores. Scale: 20 cm.

Root systems

Other indicators of ancient mangroves are the complex root networks of *Avicennia* (and *Sonneratia*) characterized by the striking association of vertical and radiating horizontal roots, vertical pneumatophores (aerial roots) branching upwards, and rising several decimetres out of

the soil, and the feeding roots penetrating downwards (Fig. 5). A pioneer publication on so-called fossil *Avicennia* root network by Hoffmeister & Multer (1965) is based on the description of such an orthogonal network of 'calcified' roots in a Pleistocene calcarenite of Key Biscayne (Florida). Recent field and thin-section observations by the author reveal that

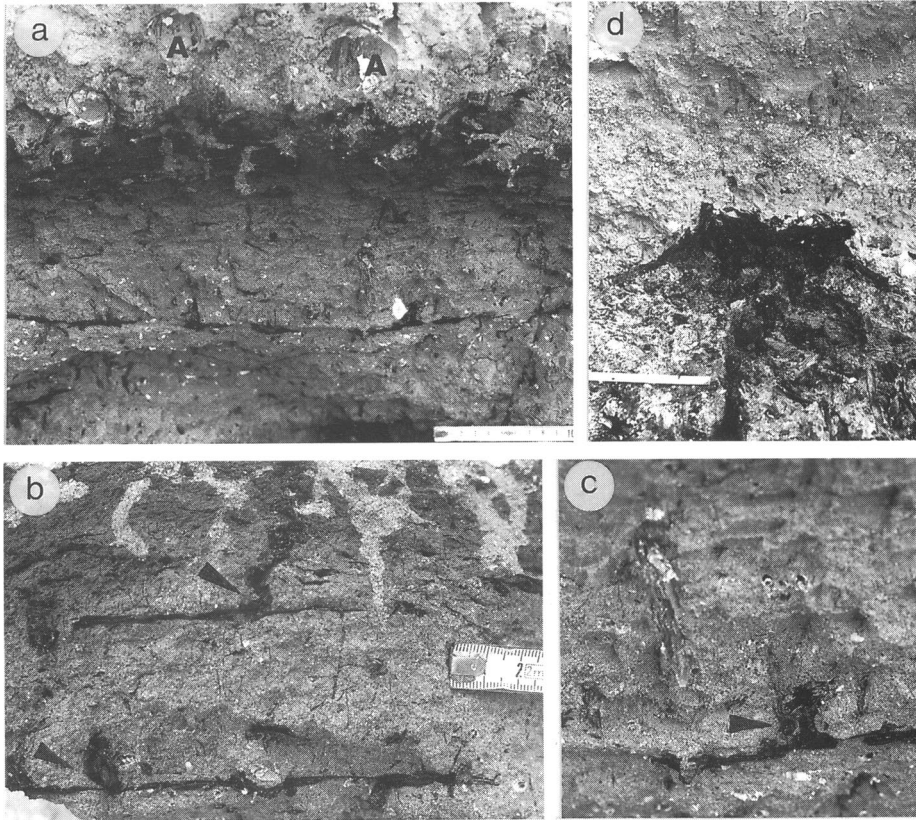


Fig. 6. Holocene *Avicennia* mangal paleosol. Um al Nahr canal, Abu-Dhabi (UAF). (a) The uppermost organic matter-rich horizon is overlain by a lagoonal, transgressive muddy sand [with *Anodontia* shells (A) in life position] and locally burrowed (white infills). (b) & (c) The diagnostic upward-branching pneumatophores (arrows). (d) A buried stump with a well preserved *Avicennia* wood structure (J.-C. Koeniguer identification) dated 6500 years BP.

this is in fact a rhizolith network developed in a Pleistocene eolianite and not a fossil mangal. The vertical roots branch downwards or are independent from the horizontal network. This pattern is a common character of dune vegetation. Moreover, the concentric organization of the carbonate filling and coating of the root channels are typical of those described from carbonate rhizoliths (cf. Klappa 1980; Jones & Ng 1988) and they do not preserve any anatomical structures. Other interpreted *Avicennia* roots published without illustration of the diagnostic pneumatophores would also need re-examination, as the same may be the case for the Miocene '*Avicennia* mangrove roots' from Arabia of Whybrow & McClure (1981) and the Oligocene '*Avicennia* roots' of Bown (1982) from Egypt. It is shown below, in an example from a

Holocene mangrove from Abu Dhabi (Fig. 6), that the characteristic upward branching of the *Avicennia* pneumatophores can be preserved in fossil mangrove soils.

Molluscs

Molluscs have the most fossilizable hard parts (shell) of the mangal fauna. However, the intense dissolution of their apices or umbones, during life, suggest that the fate of most of the shells of epibiont as well as endobiont gastropods and bivalves is complete disintegration when buried in the acid mangroves of humid climates (Philippon & Plaziat 1975; Plaziat 1975a, b, 1984a). Most of our core samples through superficial deposits are devoid of recognizable shell remains. The best chance of preservation is

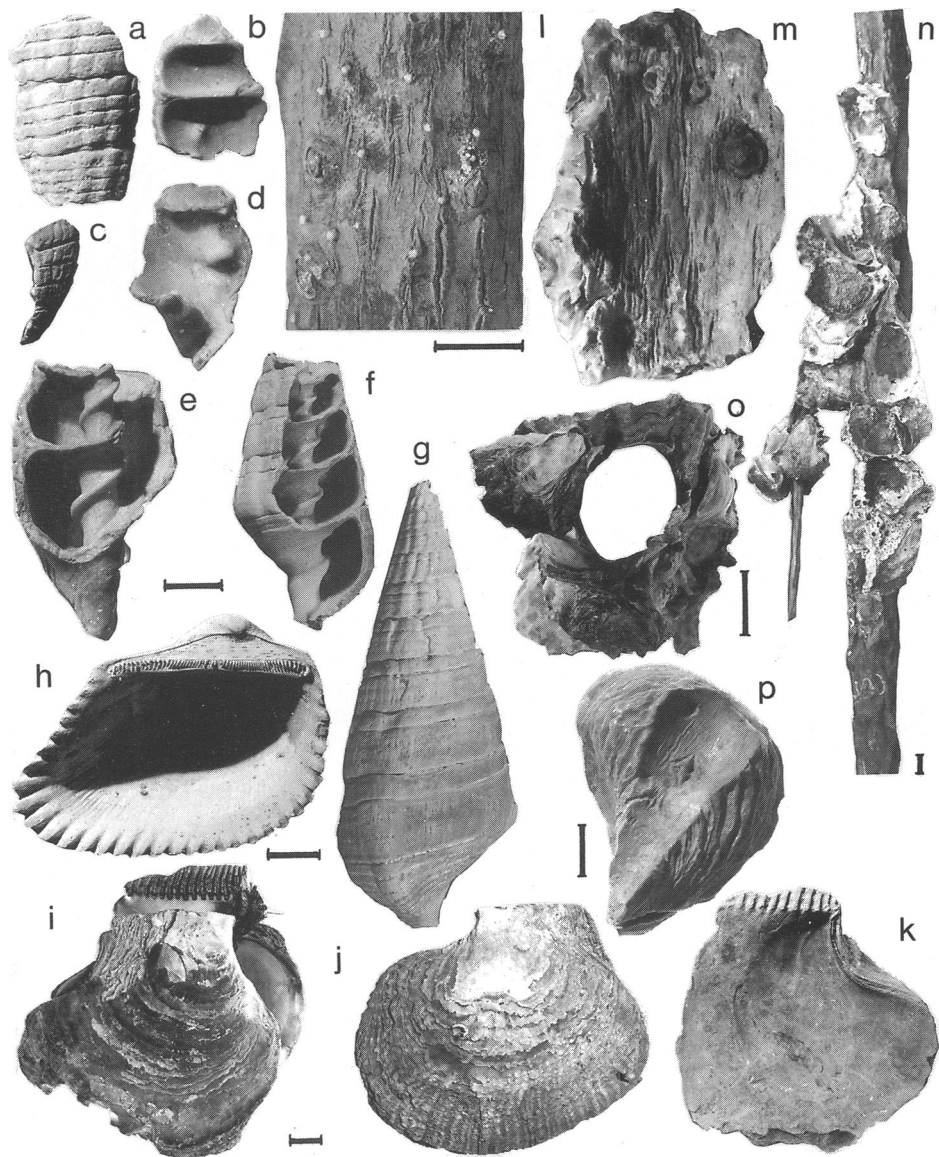


Fig. 7. Mangal shells: living, Recent and Palaeocene. (a)–(g) *Terebralia palustris* from Holocene shell-middens. The best preservation (g) suffered a labrum break whereas the most characteristic chips (a–d) result from longitudinal strokes generally made with pebbles in order to extract the desired meat. (h) *Anadara* from a tidal channel of the same Qurm mangal midden, west of Muscat (Oman). (i)–(k) *Isognomon ehippium*, the so-called ‘flat-oyster’ byssally attached to tidally flooded mangrove trunks. (i) & (j) New Caledonia. (k) Qurm midden. (l) & (m) The cracked bark of a *Rhizophora* stilt root and its imprint by an oyster shell. Wouri delta, Cameroon. (n) & (o) Oyster clump of an intertidal *Rhizophora* silt root. (o) Axial view of the cylindrical composite collar, Diahot river estuary, New Caledonia. (p) A late Paleocene oyster (*Ostrea unciifera*) with a subcylindrical imprint ornamented with longitudinal cracks similar to the *Rhizophora* root bark (Early Sparnacian, Rieux-en-Val, Aude, France, cf. Plaziat 1970). Scale bar: 1 cm.

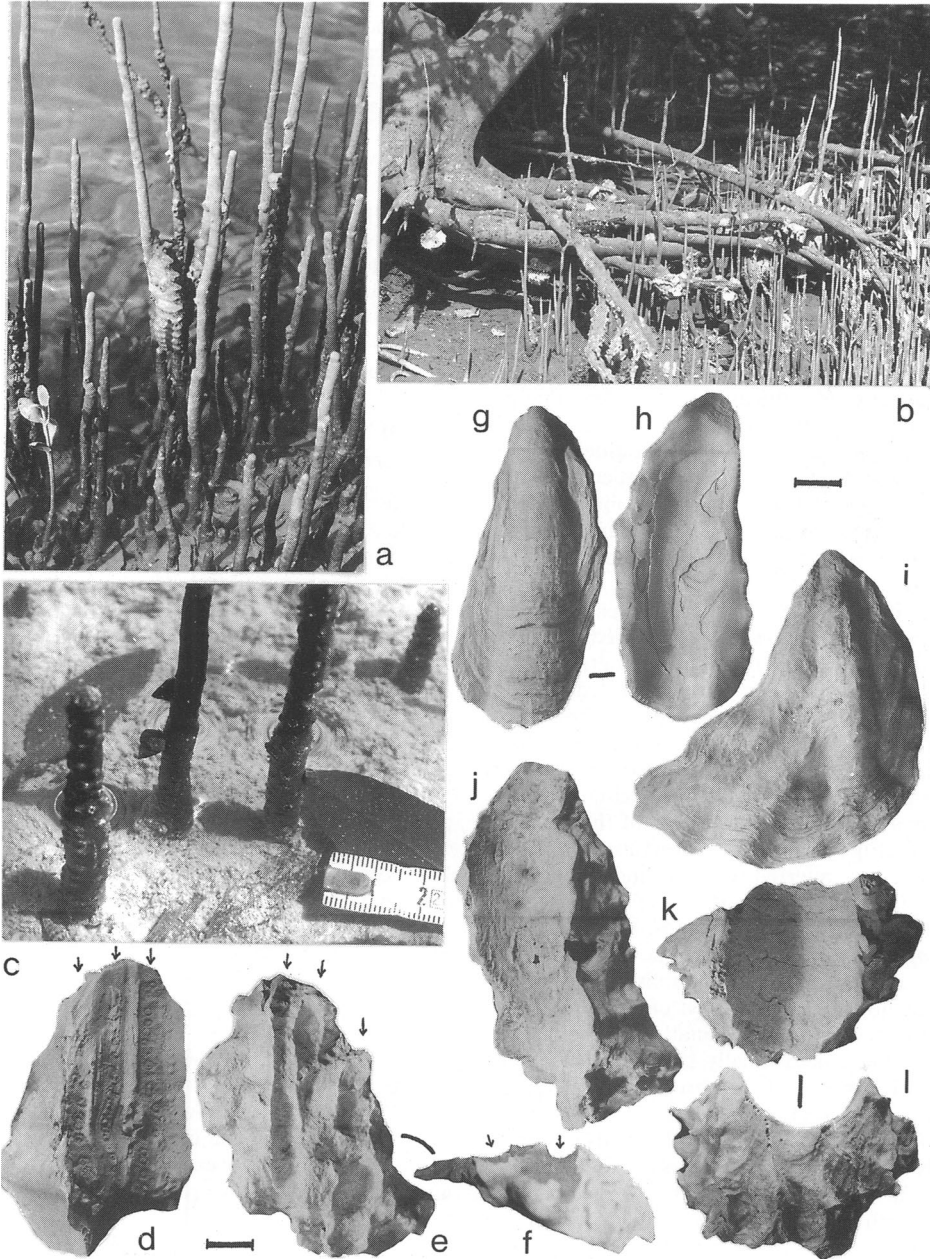


Fig. 8. Characteristic morphologies of oysters encrusted on the diverse types of *Avicennia* roots. (a) & (b) *Saccostrea cucullata* on pneumatophores and horizontal roots unearthed by the natural erosion of a channel bank. Qurm mangal, west of Muscat, Oman. (c) 'Breathing' apertures or pneumatodes on the pneumatophores. Same locality. (d)–(f) Pneumatophore prints with the diagnostic pneumatodes moulded by the right valve of oysters. Holocene midden (5500 years BP) north of Hurghada, Gulf of Suez, Egypt. (g)–(i) The left valves of oysters encrusting small roots or pneumatophores. The external morphology reproduces exactly the root curvature while the internal curvature is attenuated. (j)–(l) Right valve moulding of larger, horizontal roots. Same shell-midden 2 km from a vanished mangrove site, Deir um Deheis Abu Shaar. Scale bar: 1 cm.

given by the lateral transport of shells, quickly followed by burial in a fine-grained (less permeable) sediment. The acid waters of mangals show limited dissolution of shells in marine settings where the low pH (6–3) is buffered by the seawater salinity. In the smallest mangals, on backreefs or in arid bays, carbonate sedimentation is an additional buffer also acting during diagenesis. Thus, carbonate muds and marls are the most favourable sediments for shell preservation, whereas siliceous sands are the worst, due to their long lasting permeability. Paradoxically, the smaller backreef mangals are better documented by their molluscs than the luxuriant equatorial mangal forests.

Depending on their biogeographic province, the generic identification of a few mangal molluscs are reliable but rare indicators of Neogene mangals (see below). In older deposits (Paleogene, Cretaceous) these characteristic taxa may have been replaced by other mud-creeping snails, tree climbers and shallow burrowers, the reliability of which must be locally demonstrated.

The only time-independent evidence is given by oyster shells showing the detailed moulding and xenomorphic growth of mangrove aerial roots on which they were encrusted (Plaziat 1970*a, b*). A precise comparison of these fossil imprints with the modern *Rhizophora* bark cracks on prop roots, or pneumatode prints on *Avicennia* pneumatophores and exhumed roots, allows a reliable demonstration of their mangal origin (Figs 7 & 8). Unfortunately, many authors have referred to any cylindrical print as mangrove roots, and it is well known that oysters also encrust gorgonids, coral branches (*Acropora*) or drifted wood. The unreliability of some of the previously published references should not negate this type of evidence which requires the critical examination of the imprint morphology, occasionally corroborated by the local occurrence of mangrove pollen (Gruas-Cavagnetto 1991).

The favourable storm or flood dispersion of shells from mangal biotopes is highly influenced by local geomorphology. Thus a steep, rocky coast with a narrow mangrove belt will give a better chance of shell preservation than the huge, acidic delta mangals within which the biogenic carbonate products are recycled on site. In the more extensive mangals, transportation in deep tidal channels is the best chance for shells to escape dissolution (Vieillefon 1970; Plaziat 1984*a*).

Prehistoric human's exploitation of seafood can also lead to the preservation of mangal shells in the recent past. Near-mangal kitchen- or shell-

middens are variably sized accumulations of discarded oysters, *Terebralia* and other molluscs. These occur in the supralittoral zone where the shells can escape from the usual diagenetic disintegration (Figs 7 & 8). Archaeologists are increasingly aware of the need for a palaeoecologic approach for the reconstructions of ancient ways of life, which leads to collaboration with malacologists (Priour 1990; Glover 1991), sedimentologists (Fairbridge 1976) and ethnographers (Meehan 1982). The palaeoclimatic and palaeogeographic evolution of Quaternary shores will profit by this collaboration, especially in intermediate latitudes where the climatic and sea-level changes successively favoured and precluded mangal development (see below).

Examples of palaeo-mangals and their palaeoenvironmental significance

The 'lure of the mangal' (Musgrave 1929) may be the source of unsupported identifications of ancient mangals (see Plaziat & Koeniguer 1983). A critical examination of all evidence, as reviewed above, is necessary for their positive identification. Improvements in palaeoecological methods, especially with an appropriate reference to the closest modern mangals, will hopefully lead to more precise palaeoclimatic and environmental reconstructions of the various palaeomangals. The following examples have been selected to illustrate mangals from different periods as well as the environmental range contained within fossil mangals. French and Japanese contributions, including first-hand data, have been intentionally emphasized compared to the well-known and more easily found publications in English.

The Holocene mangal of Abu Dhabi

The famous sabkhas of Abu Dhabi emirate on the Persian Gulf side of the Arabian peninsula (c. 24°N), are better known for their evaporites than for their dwarf mangals (Figs 5 & 8; Baltzer *et al.* 1994). This Holocene, regressive, carbonate and evaporite sequence, results from sedimentation in bays locally fringed by *Avicennia* mangals (Evans *et al.* 1969; Purser 1973; Purser *et al.* 1988; Kenig 1991). These are typical mangals of the mid-latitude hot and arid belt. A lagoonal seagrass facies, with vertical roots and *Anodontia* shells in life position, is interbedded between both transgressive and the regressive mangrove associated with microbial mat facies. This association was revealed in pits dug across the sabkha flat during the initial field studies of Evans *et al.* (1969) and detailed during our more

recent research (Purser *et al.* 1988). The newly excavated ship canal for the Um al Nahr port presents a spectacular, continuous 70 m section, along which a transgressive mangal has been preserved. Within this buried section, the *Avicennia* root network and stumps (identification by J.-C. Koeniguer) are preserved as carbonaceous and woody remains (Fig. 6). The associated molluscan fauna includes the atypical lagoonal taxa: *Potamides conicus* (ex. *Pirenella conica*; Lozouet 1986) and *Brachidontes variabilis*. The main interest of this outcrop is the unquestionable preservation of an *Avicennia* root network with its diagnostic upward-branching pneumatophores (Fig. 6b & c).

Prehistoric and more recent mangal shell-middens

Since the latest Palaeolithic times humans have accumulated piles of shells near to the harvesting sites, either at their feeding places (settlements) or at shell-opening places, such as on the shore. The mangal origin of these shells provides important evidence of the former existence of mangals in areas from which mangals have now disappeared (e.g. Gulf of Suez, SE Oman) or have become impoverished (e.g. Persian Gulf).

The importance of mangals as sources of seafood has been known for a long time (Fairbridge 1976) but its relative value was not always well understood. It is now assumed that the shell-gatherers are most frequently fishermen with complementary shell contribution by women and children (Meehan 1982; Biagi *et al.* 1984; Figuti 1992). The latter contributors may explain some unusual shell selections such as the occurrence of dead encrusted shells, inedible or 'aesthetic' shells in some middens.

Mangals are an important source of proteins: the tree oysters occur everywhere, whilst *Terebralia palustris*, *Geloina* and *Isognomon* are characteristic of the Indo-West Pacific shores. However, as oysters also encrust rocky shores they cannot always be regarded as a mangal contribution. In the RH6 midden (Durante & Tosi 1977) adjacent to the present-day Qurum mangal (Ras-al-Hamra near Muscat, Oman), the oyster shells have abundant mangrove root imprints, thus demonstrating that people from the 3rd millennium principally exploited mangal molluscs, mainly oysters, then in second rank *Terebralia* and scarce *Isognomon* (Figs 7 & 8). The best root prints are perfect counterparts of pneumatophores and larger horizontal roots of *Avicennia* exhumed by channel bank erosion, as is the case today with *Saccostrea cucullata* living in the Qurum mangal (Fig. 8a & b).

On the Egyptian Red Sea coast local occurrences of mangroves are documented from the late Pleistocene, Last Interglacial 5e substage (around 122 000 years BP), and in the middle Holocene (4th millennium) according to dated molluscan shells (Reyss *et al.* 1993; Plaziat *et al.* in press). The generic triad of *Saccostrea-Terebralia-Isognomon* is the characteristic mangal assemblage of the Pleistocene back-reef shores and inter-reef embayments, from Berenice to the entrance of the Gulf of Suez (Figs 7a-g & 8d-i). During Holocene times (5300-6100 years BP) in the northernmost locality of Abu Shaar (North of Hurghada) the same *Saccostrea cucullata* and *Terebralia palustris* have accumulated in middens 1-2 km from the present-day mangal at Deir um Deheis. Today, these species live only south of the entrance of the Red Sea in richer mangals. This suggests an important environmental change to the south through increased precipitation and winter temperatures, favouring mangal development. Valuable information on the timing of the Quaternary climatic optima in the absence of mangrove tree remains rely on these anthropogenic molluscan assemblages.

Along the Indian Ocean coast of Oman, middens of the 5th to 3rd millennia with variable contributions by *Terebralia* and oysters indicate the positions of vanished lagoons, now converted to sabkhas and partly buried below aeolian sands (Plaziat 1990). The ancient Arabian people of these areas probably had a diverse diet founded mainly on fishing. Scattered clusters of broken *Terebralia* shells on the edge of a high cliff may be a corroborative observation interpretable as a trace of bait preparation. In this case the *Terebralia* should not be considered only as a scaffold. Such a collaboration with archaeologists is a promising research venture. Quaternary changes of the climate certainly would benefit from such studies of mangal shells; for example *Terebralia palustris* made brief excursions into the Persian Gulf (Abu Dhabi, Bender Abbas) and *Telescopium telescopium* temporarily settled on the shores of Iriomote Island (southernmost Japan island, NE of Taiwan) in the last centuries (Plaziat, ¹⁴C unpublished dates), but do not occur there today.

The Miocene mangals of mainland Japan

A molluscan fauna considered to be associated with mangal environments of early to middle Miocene age (15.5-16 Ma; N8) was published by Oyama as early as 1950. This interpretation has since been confirmed by palynology 30 years

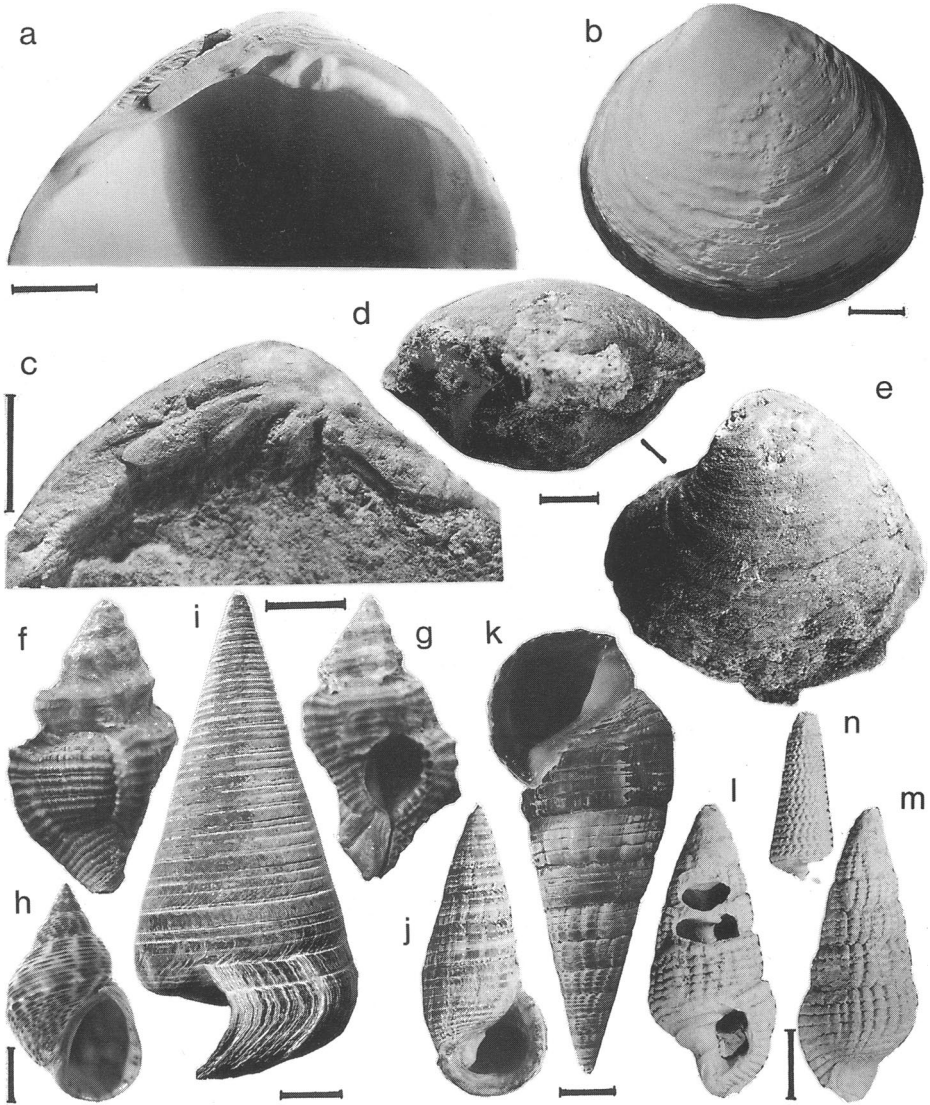


Fig. 9. (a) & (b) *Geloina coaxans*, the largest cyrenid of the Pacific mangals and its characteristic hinge, Okinawa island, Japan. (c)–(e) Fossil *Geloina* from the early middle Miocene, north of Hiroshima, Japan. (f) & (g) *Chicoreus* (*Rhizophorimurex*) from a Singapore mangal. (h) *Littoraria scabra*, the most typical snail of the Indo-West Pacific mangals. However, its fragile shell generally impedes its fossilization. New Caledonia. (i) *Telescopium telescopium*. Delta mangal of the Mahakam river, E Kalimantan, Indonesia. (j) & (k) *Terebralia sulcata* and *Terebralia palustris* from an Okinawa mangal, Japan. (l) & (m) *Terebralia bidentata lignitarum* and (n) *Tympanotonos margaritaceus*, European Miocene potamids associated with an *Avicennia* mangal at Puisserguier, Hérault, France. Scale bar: 1 cm.

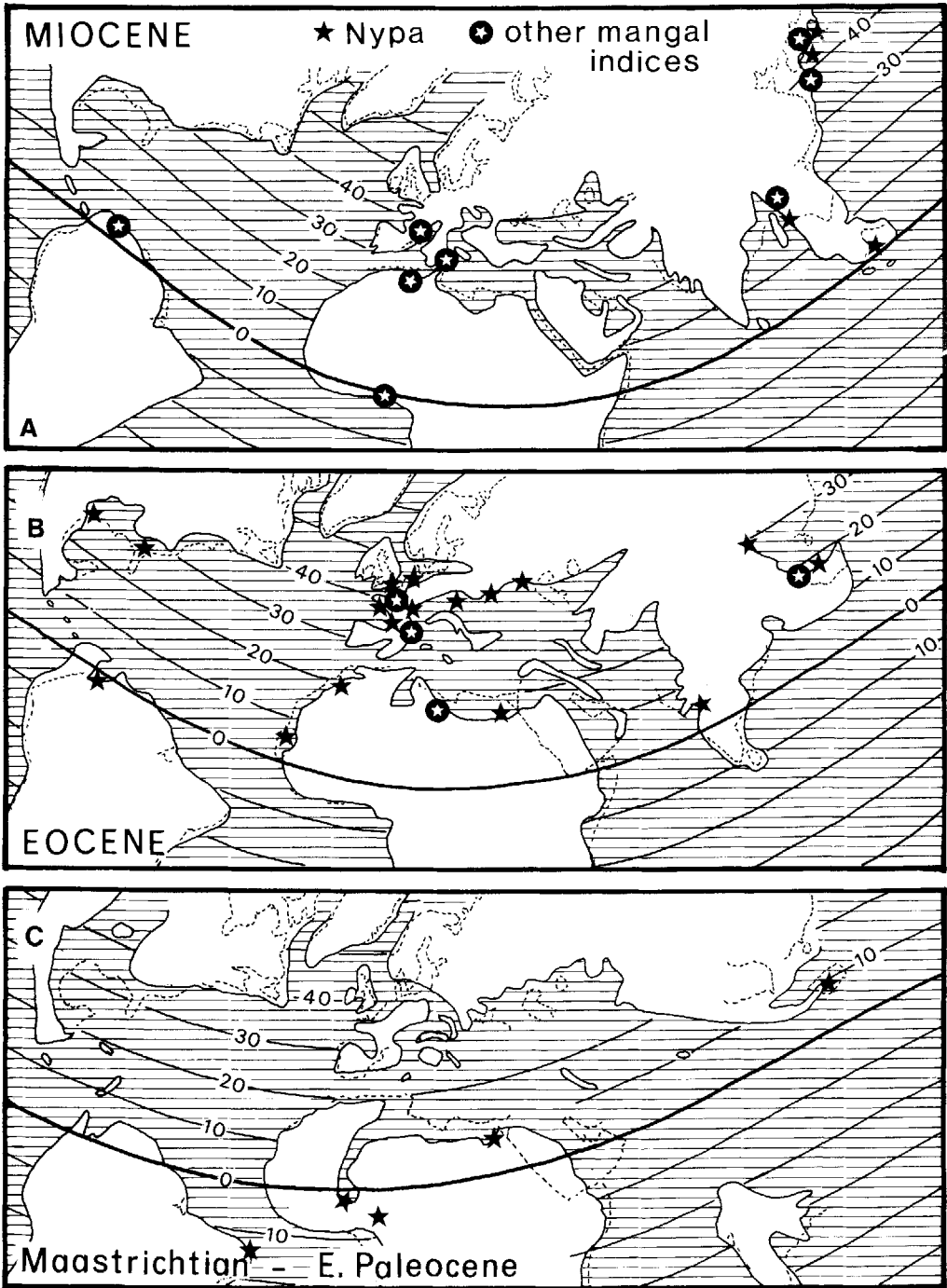


Fig. 10. Palaeogeographic distribution of northern hemisphere mangal indices from: (A) early middle Miocene mangrove pollens, *Nypa* pollen and molluscs, (B) latest Paleocene–Eocene: pollen, wood and fruits of mangroves and *Nypa*, and molluscs. (C) Maastrichtian–earliest Paleocene *Nypa* fruits and pollens. Palaeogeographies according to the Tethys project (Dercourt *et al.* 1993). Reference sources in Tralau (1964), Muller (1968), Plaziat & Koeniguer (1983) Plaziat 1984c and many others.

later (Yamanoi *et al.* 1980; Tsuda *et al.* 1981). The Toyama prefecture basin is located in the coastal area of the Sea of Japan, NW of Tokyo near 37°N (42°N palaeolatitude; cf. Chiji *et al.* 1990). Oyama (1950) interpreted a group of four Miocene molluscs [*Littoraria*, *Telescopium*, *Chicoreus* (*Rhizophorimurex*), and *Geloina*] as the key genera of a mangal biocoenosis '*Telescopium-Geloina*' by analogy with the present malacofauna of subequatorial mangals (Singapore, Palau) (Fig. 9). Other, larger potamidids (*Terebralia* and extinct *Vicarya*) were not included in this diagnostic group. This mangal interpretation has never been questioned. Similarly, Okamoto and Terachi (1974) described a *Crassostrea-Cyclina-Geloina* assemblage of molluscs from north of Hiroshima as a possible 'mangrove tropical or subtropical environment'. Subsequent analyses emphasized the diagnostic importance of *Geloina*: '*Geloina* bearing mollusc assemblage' of Itoigawa (1978), '*Vicarya-Geloina* association' of Ozawa *et al.* (1986). The climatic significance of these palaeo-mangals later became their main interest, with a progressive shift in interpretation from a subtropical (Itoigawa 1978) to a tropical environment of formation (Horikoshi 1981). This was confirmed by the discovery of various mangrove pollens in many *Geloina*-bearing sites (Yamanoi *et al.* 1980; Yamanoi & Tsuda 1986; Tsuda *et al.* 1986): *Bruguiera*, *Sonneratia*, *Excoecaria*, *Avicennia*, *Rhizophora*, *Ceriops*, *Scyphiphora* and *Nypa* in south and central Honshu, and northwards to the Noto peninsula (42°N palaeolatitude) (Fig. 10). More recently, decapod crustacea (*Thalassina*, *Sesarma* and *Scylla*) have been found in these Miocene mangal biotas (Karasawa 1990; Karasawa & Nishikawa 1991).

A careful study and re-examination of the Miocene molluscan fauna, together with other evidence for hot climates (coral reefs, nautiloids, insects, tortoises), led to the interpretation of a brief tropical episode *c.* 16 Ma (Tsuda *et al.* 1984), or the 'tropical spike' of Itoigawa (1989). This climatic event is also named the 'Mid-Neogene Climatic Optimum' by Itoigawa & Yamanoi (1990). Taking into account the diversity of the mangroves and molluscs this suggests that the nearest present-day equivalents of these Miocene mangals are in the Philippines and Hainan islands. This is more than 20° south of the Miocene Japanese mangals. A rigorous study of this tropical invasion is still in progress and shows that sediments with the warm arcidpotamid faunas of Korea and Hokkaido, as described by Yoon (1989) and Kanno *et al.* (1988), have yielded no mangrove pollen (Yamanoi Unpublished work). The high diver-

sity of the Miocene mangals is the best evidence of a major climatic optimum different from the other Neogene (Tsuchi 1992) to present-day optima.

The actualistic approach of the Japanese malacologists probably explains their precursory role in the identification of ancient mangals. This has not been revealed to western researchers until very recently. Meanwhile, parallel but independent work resulted in the same climatic reconstructions in Europe.

The Miocene mangals of southwestern and central Europe

French and Spanish *Avicennia* mangroves of Miocene age are among the latest discoveries of fossil mangals. This interpretation is supported by the associated pollen, *Retitricolporites oleoides*, which is very close to that of the eastern *Avicennia marina* (Bessedik 1981). In sites from both Languedoc and Catalonia the precise age of this mangrove (and reef) episode is also dated by N8 foraminifera as occurring near the Burdigalian-Langhian boundary (*c.* 16 Ma) (Bessedik 1985; Bessedik & Cabrera 1985; Negretti *et al.* 1990). This is a local confirmation of the worldwide early mid-Neogene climatic optimum, demonstrated by mangrove remains up to 41–44°N of latitude (Fig. 10). An attempt to combine the malacological information with these palynological data has been attempted by the author; *Potamidides* sp. and a *Terebralia* (*T. bidentata lignitarum*) are present at Sant-Paul-d'Ordal, Catalonia (unpublished observations) as well as in mangal sites in the Languedoc (Miquel 1897) (Fig. 9 l, m). The same *Terebralia* still occurs during the late Miocene (early Messinian) in southern Spain (38°N; Archambault-Guézou *et al.* 1979) whilst *Avicennia* pollen is recorded from early Miocene (Bessedik 1985) to the early and late Messinian of Sicily (37° 30'; Suc & Bessais 1990) and Algeria (Chikhi 1992). This Miocene mollusc-pollen association supports the value of *Terebralia* as a mangal marker – a relation well established for *Terebralia palustris* in Quaternary times (Braithwaite *et al.* 1973; Plaziat 1984a). However, its unequivocal association with mangals further back in time from the Quaternary may be questioned (Plaziat 1984a–c); for example, the Korytnica clay of southern Poland (50°N) has been interpreted as adjacent to a mangal (Radwanski 1974; Baulk & Radwanski 1977) on the basis of the occurrence of *Terebralia*. The 'suggested' *Rhizophora* (Radwanski 1974, mangrove tree drawn in his fig. 5) should perhaps be changed for an *Avicennia*, although the presence of a

mangal at this latitude requires palynological confirmation. The NN5–NN6 biozone of the Polish assemblage being later in time than the worldwide mid-Neogene climatic optimum; thus a mangal occurrence at such a high latitude would be particularly surprising. The author suggests that the European Miocene sites with *Terebralia* should be re-studied before the Miocene species of this gastropod genus can be accepted as a reliable mangal index.

The Palaeocene–Eocene mangals of western Europe

The London Clay flora, based mainly on pyritized fruits, a relatively rare fossilization, gives the best known flora of this age, with mangrove seedlings (Chandler 1951, 1961, 1978; Wilkinson 1981, 1983; Collinson 1983) referred to *Palaeobruquiera* and *Ceriops*. The earliest identification of *Nypa* fruit (*Nipadites*) by Parsons (1758) has been confirmed by Reid & Chandler (1933), Tralau (1964) and Collinson (1993). An early Eocene mangal occurring at the 41°N palaeolatitude was so surprising that the autochthony of these buoyant *Nypa* fruits has been questioned (Van Steenis 1962). Durand & Ollivier-Pierre (1969) answered this question by the co-occurrence of *Nypa* pollen and fruits in southern England. Corroborating data for the proximity of these mangroves are scarce. The tree anomiid *Enigmonia* (Wrigley 1936; Le Renard 1990) is usually regarded as a reliable indicator of mangrove environments but the author has recently collected present-day specimens fastened under intertidal rubble (South China). Fortunately, Sein (1961) has observed rare *Avicennia* pollen while Gruas-Cavagnetto (1976) has revealed that '*Rhizophora*-looking' pollen is present in several London Clay and other English Eocene sites.

In the Paris Basin (38°N palaeolatitude) apart from *Nypa* fruits, palynology has aided the documentation of Ypresian mangroves with *Nypa*, aff. *Bruquiera* and the facultative mangal fern *Acrostichum* (Gruas-Cavagnetto *et al.* 1980*a, b*) in a preserved paleosol. Chateauneuf (1980) also recorded cf. *Bruquiera*, cf. *Rhizophora*, *Avicennia* and *Pelliciera* in the early-middle Eocene of the Paris Basin and Guinet & Gruas-Cavagnetto (1986) added *Avicennia* from the Channel Auversian.

In southern France (32°N palaeolatitude) numerous late Paleocene to early Eocene shore deposits have a common muddy facies. The first attempt to demonstrate the presence of mangal palaeoenvironments (Plaziat 1970*a, b*) was based on a synecologic study of molluscs; especially

oyster prints, similar to those of present-day *Rhizophora* prop-root oysters (Fig. 7p). *Nypa* fruits (Fritel 1921; Plaziat 1984*b*) and pollen (Médus 1977; Médus in Plaziat 1984*c*) were the first botanical corroborations of a preserved mangal, but only the Ilerdian deposits coincide with a climatic optimum (cf. Plaziat 1983, 1986). Much later, a complete palynological demonstration was given by Gruas-Cavagnetto *et al.* (1988) and Gruas-Cavagnetto (1991), the latter with Sonneratiaceae, *Pelliciera*, Rhizophoraceae (*Bruquiera*), *Avicennia* and the prevalent *Nypa* from the middle Ilerdian. In northern Spain, the record of *Nypa* pollen (Haseldonckx 1972, 1973) and fruit (Llompert 1977; Soudet & Plaziat Unpublished work) in the early to middle Eocene has been extended up to the late Eocene by fruit occurring north of Barcelona (Alvarez Ramis 1982; Biosca & Via 1988).

The recognition of early Tertiary mangals is much more difficult than Neogene examples and may raise some important questions. The botanical affinities of pollen morphotypes are not always obvious. The use of 'cf' and crude family names by authors suggests some questions on the reliability of plant identification in some ancient pollen para-taxa. This may result in part from the remote stage of evolution of the mangrove families. Thus, the importance of oyster root-prints must be emphasized and these must be carefully discussed (cf. Plaziat 1970*a, b*). Concerning the occurrence of *Nypa* dominated mangals, more information is needed on their associated present-day fauna (Plaziat 1984*c*). This is the topic of recent field investigations in Indonesia by the author.

Possible Mesozoic to Palaeozoic mangals

The occurrence of *Nypa* fruit and pollen in the Cretaceous is the only reliable link between the Cenozoic and more ancient mangals (Muller 1968; Jähnichen 1990) (Fig. 10). The '*Terebralia*' interpreted to indicate a mangal in the latest Cretaceous deposits of Sicily by Carbone *et al.* (1989) and '*Brachidontes*' shell buried side-by-side with Cenomanian '*Acerites*' leaves (Retallack & Dilcher 1981) should not be considered as reliable evidences for mangals. The Jurassic conifer *Pseudofrenelopsis* (pollen *Classopolis*) gives a good example of a 15 year-long debate concerning a problematic mangal indicator, from the first interpretations favouring a mangrove environment (Wall 1965; Batten 1974; Retallack & Dilcher 1981) to the various contributions refuting its marine location (see Plaziat & Koeniguer 1982; Francis 1983). Many 'Jurassic mangals' have been based on the identification

of *Classopolis* (e.g. Macquar *et al.* 1977). In the same way, a *Cordaites* has been considered to be a Carboniferous mangrove (Cridland 1964). However, this interpretation is disputed as it is based only on the occurrence of prop-roots. The continental habitat of aerial-rooted *Cordaites* has recently been demonstrated by Aassoumi *et al.* (1992). Similarly, the interpretation of early-middle Cretaceous angiosperms and Triassic lycopods or Palaeozoic seed-ferns as mangroves by Retallack (1975) and Retallack & Dilcher (1981) should not be accepted until more detailed studies have been undertaken. As the biological features, such as aerial breathing roots and viviparity, are not diagnostic criteria for mangroves it will be difficult to demonstrate an unambiguous adaptation to the marine swamp environments in these extinct groups.

The contribution of ancient mangals to palaeogeography and palaeoclimatic reconstructions

Demonstrated examples of mangal soils are excessively rare (Gruas-Cavagnetto *et al.* 1980*a, b*; above examples). The best environments for mangal shell preservation occur in a narrow, marine, peri-mangal belt, whilst pollen and fruits may be transported far away seawards by wind and flotation (Muller 1959). Wind may also disperse mangrove pollen landward. Thus, the precise location of the mangal is rarely preserved but its intertidal biota (oysters and other amphibious molluscs) remains a good bathymetric reference and general indicator of ancient shoreline environments.

The estuarine setting of mangroves and *Nypa* may extend far inland (*Rhizophora* more than 100 km inland in W Africa (cf. Monteillet & Plaziat 1980, 1981); *Sonneratia* 90 km and *Nypa* 50 km in NE Sumatra, personal observation). This fluvial distribution clearly answers the question on the reliability of the *Nypa* pollen as a seashore indicator (Ollivier-Pierre & Caratini 1984). This palm tree probably acquired its brackish swamp ecology in Cretaceous times but as it can spread further upstream than marine nannoplankton its pollen *Spinizonocolpites* may be incorporated in adjacent continental sediments while the floating fruit tend to disperse downstream and sink at a distance from the shoreline (Plaziat 1984*b, c*; Collinson 1993). However, the co-occurrence of preserved fruits and pollens are not infrequent (Durand & Ollivier-Pierre 1969; Plaziat 1984*b*; Collinson 1993) and palynological studies are still needed in most of the fruit-bearing deposits.

The climatic significance of the ancient man-

gals is a more fundamental question. The climatic distribution of the present-day mangroves has been discussed above and the typical subequatorial mangal distribution does not apply to many of the fossil mangroves. Many fossil mangals occur at relatively high to medium latitudes (Fig. 10). The western European Miocene *Avicennia* clearly suggest a mangal living close to its geographic limits at the 37–55°N palaeolatitudes. The synchronous Japanese mangals show a more diverse flora, with eight mangrove species and a subequatorial looking fauna at 40–42°N palaeolatitudes. A general comparison between the fossil and present-day biotas suggests at least a 20° northward shift of the climatic zonation for the Japanese Miocene (cf. the Philippines Islands). A similar poleward shift may have occurred with the Miocene European mangals as the northernmost present-day analogues are in the Gulf of Oman. Such a latitudinal shift on the basis of today's climatic zones would suggest a change in average annual temperature of c. 12°C, which is most unlikely.

The influence of fluctuations of the polar ice-caps is the most likely explanation of the difference between present-day and earlier Tertiary distributions. During ice-free episodes the meteorological characteristics of air circulation must have been different from 'glacial' episodes. The thermal gradient would have been reduced and the polar air incursions into the subtropical latitudes would have been precluded. The author and many palaeobotanists have proposed that a limited global rise of temperature (less than 5°C) would be enough to permit most of the tropical biota, presently excluded from the subtropical domain by freezing, to expand widely towards the poles (Plaziat 1970*a, b*, 1984*a–c*, 1986; Wolfe 1971; Daley 1972; Collinson 1990). Thus, during periods of global climatic optima, such as the last Quaternary Interglacial (stage 5e), the mid-Neogene (16 Ma) optima and periods presumed to have more or less ice-free poles (e.g. the early to middle Eocene, 54–40 Ma), cannot be interpreted directly according to the present-day climatic belts (cf. Adams *et al.* 1990). The episodic or long-lasting expansions of the mangal into higher latitudes (Plaziat 1970*b*; Muller 1980) gives a clear indicator for these climatic optima providing that the appropriate modern analogues are used. For example, the monthly distribution of rainfall is important as the mangal is favoured by summer rains which reduce the withering effects of summer high temperatures. The distribution of the present-day 'humid subtropical' climates (eastern shores

of the American and Eurasian continents) vs 'mediterranean' (western shores) suggests that there would be different effects of a limited temperature rise on the biota of coastal swamps occurring at say 40°N. Tropical biota benefit from the summer rainy season and expand in the subtropical areas whereas the dry summer and winter of mediterranean areas limit their extension. In Miocene times the eastern Asian coasts have been affected by the northward expansion of the diverse eastern tropical mangals of Hainan and the Philippines whilst the Mediterranean coasts would have only received the stunted mangal of the western Indian ocean (e.g. Gulf of Oman, Red Sea). On the other hand, the European Eocene may have been favoured by the ubiquitous Tethyan biota on the margin of this circum-global seaway and a more humid climate around the higher latitudes of the London-Paris Basin (Plaziat 1986). A more thorough mixing of oceanic water masses driven by the attenuated thermal contrasts would also have contributed to the climatic mildness at these palaeolatitudes. This may partially settle the conflict between isotopic and biotic evidence on Tertiary temperatures (Adams *et al.* 1990) as the facilitation of global seawater mixing would possibly result in the lowering of intertropical water temperatures.

Conclusions

Along with coral reefs, hot deserts and rain forests, mangrove swamps are generally regarded as typical of low latitude, present-day tropical climates. However, beyond this simplified picture there are considerably more useful data for palaeoclimatic analyses based on the actual diversity of present-day mangals. This critical review indicates, however, that the correct identification of ancient mangals is not easy and that many mistakes have been made in the past. Unambiguous indicators of mangal environments are preserved mangrove fruit and pollen along with root network and stem tissue, and the associated molluscan fauna, especially oysters which have overgrown roots and preserve a basal bark imprint. More detailed case studies are clearly needed, but examples reviewed in this paper already show that a number of independent researchers have contributed to an improved interpretation of preserved fossil assemblages referable to mangals. These examples range from the Paleocene to the Holocene and include a variety of climatic and biogeographic settings within the palaeo-subtropical belt. Fossil mangals can be used to identify climatic optima during the Cenozoic but

this information is strongly controlled by the variations in mangrove diversity which in turn is related to the biogeographic provinciality.

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Palaeo-oxygenation: effects and recognition

PETER A. ALLISON,¹ PAUL B. WIGNALL² & CARLTON E. BRETT³

¹*Postgraduate Research Institute for Sedimentology, The University, PO Box 227, Reading, RG6 2AB, UK*

²*Department of Earth Sciences, University of Leeds, Leeds LS2 9JT, UK*

³*Department of Geological and Environmental Sciences, University of Rochester, Rochester, New York 14627, USA*

Abstract: Oxygen is a bio-limiting element for metazoa and one of the most important factors influencing species diversity and abundance in the marine realm. Equally, the absence of oxygen is generally considered to be essential for the inhibition of microbial decay and the formation of organic-rich sediments. As such, the determination of depositional palaeo-oxygenation values of ancient rocks has become a fundamental quest for the palaeoecologist and mudrock sedimentologist. In this paper the development of the tripartite anaerobic–dysaerobic–aerobic terminology for oxygen-related biofacies and the recent additions of the exaerobic and poikiloaerobic biofacies are reviewed. The new, non-genetic, oxygen-restricted biofacies (ORB) scheme is also presented. Chemosymbiotic life strategies have been suggested to be important in many extinct black shale taxa but a glance at modern chemosymbionts casts doubt on the significance of this mode of life in ORB. A review of lowest dysaerobic benthic forms throughout the Phanerozoic reveals the repeated occurrence of a few morphologies almost exclusively derived from the brachiopods and bivalves. Geochemical indices of palaeo-oxygen levels are also reviewed.

The recent renaissance in the development of criteria for the determination of palaeo-oxygen values has led to the recognition of a considerably greater variety of dysaerobic biofacies in the geological record. This is illustrated with two case studies, the first, from the celebrated Burgess Shale of British Columbia, shows a depositional environment dominated by a fluctuating oxycline. The second case study, from widely separated earliest Triassic marine sections, illustrates the possibility of a widespread (global) dysoxic event at this time.

Oxygen is an essential requirement for metazoan life (Rhoads & Morse 1971). In the marine realm sea water contains about 8 ml/L of dissolved oxygen. Oxygen is removed principally through respiration and is replaced largely by diffusion from the air but also by the photosynthetic activities of aquatic plants. A reduction in the concentration of dissolved oxygen can have disastrous consequences for marine life leading to a reduction in diversity and ultimately to mass mortality. This is the principal reason for palaeontological interest in palaeo-oxygenation. Petroleum geologists have long recognized the relationship between carbon-rich sediments and facies deposited under low oxygen conditions (Curtis 1980). This led to the assumption that low oxygen conditions promoted the preservation of organic carbon and led to the formation of organic-rich source rocks. This view has, however, been contested; the alternative being that organic-rich facies are a result of high carbon input which has in turn lowered oxygenation (Henrichs & Reeburgh 1987; see discussion in Allison & Briggs 1991).

In this overview the effects of oxygenation on biofacies and sediment chemistry, and how such features can be used as indicators of palaeo-oxygenation, are examined. Oxygen is but one stress which can limit the diversity of benthic life, others include temperature, substrate consistency (see Goldring, this volume), water turbidity and general environmental stability. Thus, palaeontological data alone can be potentially misleading in the assessment of levels of oxygenation limits. A holistic approach which involves as many techniques as possible (palaeontological, sedimentological and geochemical) should therefore be favoured. A variety of geochemical, palaeoecological and taphonomic criteria have been developed recently; the validity of these techniques in different circumstances are reviewed. The use of some of these techniques is illustrated with two contrasting case studies. The first is an outcrop scale study of the Middle Cambrian Burgess Shale of British Columbia and a variety of mainly sedimentologic and palaeoecological techniques are used to argue for the existence of

a fluctuating oxycline. The second study focuses on the earliest Triassic marine record and uses a series of geochemical and palaeoecological techniques to show that global levels of seawater oxygen were lowered at that time.

History of research

Terminology

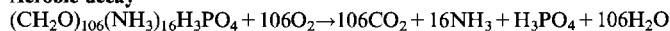
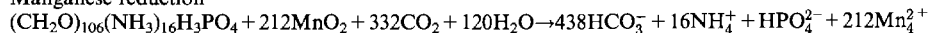
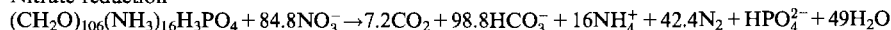
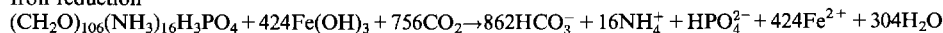
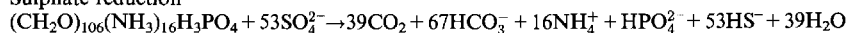
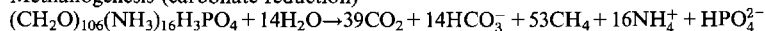
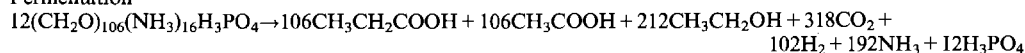
Dissolved oxygen in sea water has long been recognized as an important influence on biotic composition (Walcott 1911) and fossil preservation (Weigelt 1989). For this reason, considerable research effort has focused on the characterization of palaeo-oxygenation within ancient marine environments. Recent work has used biotic diversity and sediment fabric to define low-oxygen restricted palaeoenvironments. One of the first of these systems was based upon modern observations in a range of oxygen deficient basins in the Black Sea, Southern Californian Continental Borderland and Gulf of California (Rhoads & Morse 1971). This study recognized three important oxygen controlled biofacies, termed aerobic ($O_2 > 1$ ml/L), dysaerobic (O_2 between 1 and 0.1 ml/L) and azoic ($O_2 < 0.1$ ml/L) which were considered to be critical in controlling the composition of the benthic biota. Azoic in this case was probably synonymous with euxinic which is defined not on oxygen content but on the presence of free dissolved hydrogen sulphide (the absence of oxygen is, in the general case, a prerequisite for free sulphide) within the water column above the sediment-water interface (e.g. Tyson & Pearson 1991). It is important to note here that although the terms anoxic and anaerobic are often used synonymously they actually refer to different things: the suffix 'oxic' refers to levels of dissolved oxygen and is therefore a descriptor of environments. However, the suffix 'aerobic'

refers to metabolic processes and should properly be used to describe modes of life or biofacies. The tri-partite classification of Rhoads and Morse (1971) was modified by Byers (1977) who replaced the term azoic with anaerobic (Table 1). Further nomenclatural additions included the term 'exaerobic' (Savrda & Bottjer 1987). This was based upon a study of the Miocene Monterey formation of California and was coined to describe the biofacies associated with oxygen concentrations near the anaerobic-dysaerobic boundary. This was characterized by laminated sediments in association with shelly fossils which the authors believed may have been chemosymbiotic (harbouring sulphide-oxidizing bacteria within their cells). Such organisms are known in the modern marine realm but are restricted to localities which can yield both dissolved sulphide and oxygen.

The term poikiloaerobic was introduced by Oschmann (1991) in recognition of the fact that dissolved oxygen concentrations are commonly highly dynamic and can vary on an annual scale. His study of the Upper Jurassic Kimmeridge Clay Formation of Western Europe suggested that the oxygen concentrations indeed varied on an annual scale, as they do in some modern shelves and epeiric basins, such as the Mid-Atlantic Bight and the North and Baltic Seas (see Wignall 1994 for discussion). Two additional, almost synonymous, terms – suboxic and hypoxic – have been used to describe very low levels of dissolved oxygen. Suboxic (Breck 1974; Tyson & Pearson 1991) is used to define waters which contain dissolved NO_2 liberated by nitrate reduction (see later discussion) and is characterized by dissolved oxygen concentrations of less than 0.2 mL L^{-1} . Hypoxic is used to define a similar range of concentrations but is independent of NO_2 levels (Tyson & Pearson 1991).

Table 1. *Terms used in description of ancient and modern levels of oxygenation (see text for sources of terms)*

Term	Definition
Aerobic	Normal benthic fauna, no oxygen restriction
Dysaerobic	Impoverished benthic fauna stressed by low bottom-water oxygen values
Anaerobic	No benthic fauna present due to lack of oxygen
Exaerobic	Specialized benthic fauna perched between anoxic and dysoxic conditions
Poikiloaerobic	Low diversity, opportunistic benthic fauna responding to fluctuating but generally low benthic oxygen values
Oxic	> 1.0 ml/L
Dysoxic	1.0 – 0.2 ml/L
Suboxic	0 – 0.2 ml/L (nitrates reduced)
Anoxic	0 ml/L
Euxinic	0 ml/L (free H_2S in water column)

Table 2. Idealized profile of microbial decomposition pathways in marine sediment**Aerobic decay****Anaerobic decay****Manganese reduction****Nitrate reduction****Iron reduction****Sulphate reduction****Methanogenesis (carbonate reduction)****Fermentation****Oxygen and decay**

All sediment pore-waters, regardless of the level of dissolved oxygen present in overlying sea water, will eventually become anoxic. Oxygen is depleted during aerobic respiration by both metazoa and microbes. At the sediment surface oxygen can diffuse into the sediment from the overlying water column but, as sediment accumulates, this becomes increasingly difficult and finally sediment pore-waters become anoxic. In this paper we are primarily concerned with palaeo-oxygenation of the overlying surface waters and not sediment pore-waters, thus discussion of the latter is limited to the extent that it is dependent on the former.

The most fully understood degradation pathway for organic carbon is that of aerobic respiration (Table 2). During this process organic carbon is combined with oxygen and broken down to yield carbon dioxide and water. If the rate of carbon deposition exceeds that of oxygen supply, however, anoxia results. Under anaerobic conditions microbes utilize a series of alternative electron acceptors. In an idealized sediment profile these reactions are stratified (Bernier 1981) with each one providing a lower free-energy yield than the one above. Very few sediment profiles are ideal though, and many sediment pore-water profiles are considerably complicated by the presence of a burrowing infauna. The most obvious departure from the ideal concerns sulphates, which are abundant in marine pore-waters but occur in very low concentrations in most freshwaters. Conversely, nitrates are present in higher concentrations in freshwater than they are in marine environ-

ments. Thus, the thickness of the individual reduction zones varies according to pore-water ion concentrations and this, in turn, reflects depositional environment. Sediment heterogeneity may also lead to a departure from the idealized stratification. For example, where carbon content in the sediment varies, so too will the demand for oxygen and other electron acceptors. Thus, the microbial stratification described above can occur around accumulations of organic carbon such as faecal pellets or organism carcasses. An additional variation on the ideal case is brought about by burrowing activity since this can increase the effective surface area of sediment exposed to the overlying water and thereby permit greater diffusion of oxygen and other electron acceptors into the sediment. This diffusion, and therefore any microbial stratification, is centred around the burrow.

The association of anoxic conditions with accumulations of carbon-rich sediments is generally accepted as proof that anoxia inhibits decay and is an instrumental factor in the preservation of organic carbon in sediment (e.g. Curtis 1980). This is supported by rate measurements (Jahnke *et al.* 1982), which show that aerobic degradation in deep-sea sediments is faster than anaerobic decay. However, laboratory experiments using fresh (Foree & McCarty 1970) and aged organic matter (Westrich & Bernier 1984) suggest that rate of aerobic decay is broadly similar to that of anaerobic decay. Henrichs & Reeburgh (1987) have suggested that many of the rate measurements available for anaerobic environments were derived from deep-water settings where carbon was subjected to

lengthy periods of aerobic decay prior to deposition. Conversely, measurements of aerobic decay rate were generally from shallow water environments where the carbon was deposited was relatively fresh. Thus, Henrichs & Reeburgh (1987) suggest that reduced rate of decay of organic carbon in anaerobic settings is simply a function of the relative decay resistance of the carbon molecules in that setting. The reduced rate of carbon utilization reflects not the degradative pathway, but molecular composition. This view is contested by Emerson & Hedges (1988) who believe that anaerobic decay can be slower than aerobic decay if the carbon source is refractory. This hypothesis is supported by reports on the decomposition of lignin, which degrades much more slowly under anaerobic conditions than in an aerobic system (Benner *et al.* 1984). Canfield (1989) showed that only a small reduction in rate between aerobic and anaerobic conditions is necessary to account for the accumulations of organic matter in anoxic and euxinic sediments.

Some of the physical and chemical properties outlined above may vary according to sediment lithology. Temperature, for instance, can have a pronounced effect on decay rate, in general a twofold increase in rate may be expected for a 10°C rise in temperature (Smith 1986). Permeability variations may affect the transport of pore-water nutrients to degradative bacteria; lower permeability in muds impedes oxygen supply to microbes, thereby promoting anoxia. Supply of nutrients is also affected by bioturbation since this can increase the effective surface area of a sediment thereby promoting heightened diffusion of nutrients (Aller 1980). Porosity may vary by a factor of two or more in 'seemingly uniform' sediment and this may produce a similar heterogeneity in rate of decay (Allison 1990). Sedimentation rate will also affect decay rate. Rapid burial will distance a carbon source from the overlying water and impede diffusion of electron acceptors into the sediment. This will lead to an attenuation of the layering of microbial decay reactions and enhanced levels of preservation.

Palaeo-oxygenation: effects and detection

The biota

The underlying principle behind the Rhoads and Morse (1971) model is that a declining oxygen gradient causes a decrease in the benthic faunal diversity until a zero point is reached at the anaerobic-dysaerobic divide. Therefore, the ranking of samples by diversity is in effect

revealing a palaeo-oxygenation gradient (Wignall 1990). Despite the numerous recent additions to the literature on black shale faunas, this fundamental principle has remained unchallenged as it is supported by a great body of data from modern oxygen deficient environments (e.g. numerous references in Tyson & Pearson 1991).

Rhoads and Morse (1971) noted that calcareous-shelled taxa were preferentially eliminated at low oxygen values with the result that dysaerobic faunas were dominated by soft-bodied worm taxa. Byers (1977, p. 6) rather over-simplified the situation by defining a dysaerobic biofacies as 'calcareous epifauna lacking, but sediment bioturbated due to the activities of resistant fauna.' In fact, as Rhoads & Morse (1971) had noted, and more recent studies have reiterated, shelly taxa (particularly echinoderms) can be abundant in modern oxygen-deficient settings (e.g. Savrda *et al.* 1984; Vercoetere *et al.* 1987).

The soft-bodied fauna can provide important information for evaluating palaeo-oxygen gradients. Under declining seafloor oxygen levels, burrows become smaller and shallower with the result that the simple measure of burrow diameter can be used as a palaeo-oxygen indicator (Savrda & Bottjer 1986). Specific ichnotaxa have also been considered diagnostic of dysaerobic biofacies; *Chondrites* is the prime example (Bromley & Ekdale 1984). This approach is fraught with difficulties, however, as many trace fossil taxa exhibit secular changes in their environmental preference through the Phanerozoic (Bottjer *et al.* 1988, and this volume). Thus, *Chondrites* is rarely found within Jurassic black shales whilst it is common in such facies in the Cretaceous (Wignall 1991).

Chemosymbiosis

In the past few years the recently discovered life strategy of sulphide-oxidizing bacterial symbiosis in many marine invertebrate groups has led to the frequent suggestion that a chemosymbiotic life strategy may have been important in many extinct black shale taxa (e.g. Savrda & Bottjer 1991). Organisms which utilize this lifestyle harbour sulphide-oxidizing bacteria within their tissues. The bacteria combine sulphide with oxygen deriving energy for themselves and produce sulphate as a by-product. These bacteria are 'farmed' by the metazoan host which ultimately ingests the microbes. A variety of bivalves and worms have been found to exist in this way (Grassle 1985) but all of them require a source of both

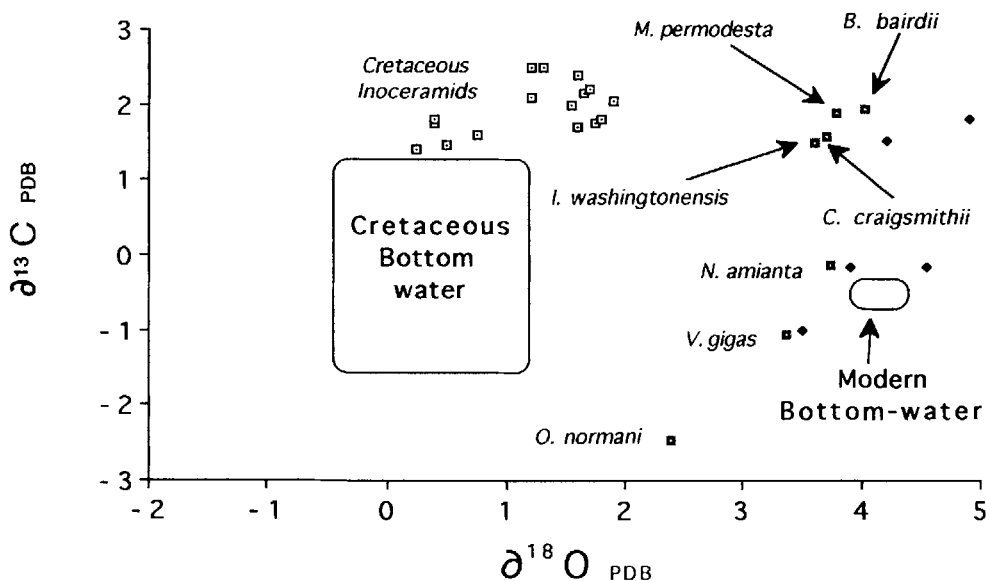


Fig. 1. Oxygen and carbon isotope plot of shell material sampled from chemotrophic (*V. gigas*), mixotrophic (*I. washingtonensis*) and heterotrophic (others) organisms. Filled diamonds (*Calypptogeania* sp.) and inoceramid data from MacLeod & Hoppe (1992).

sulphide and oxygen. Such organisms have been found in deep-water environments around oceanic vents (Grassle 1985), petroleum seeps (Seilacher 1990) and large decomposing carcasses such as whales (Allison *et al.* 1991). They also occur in shallow water where the oxygen supply is restricted and the anoxic–oxic interface is close to the sediment surface. Such environments can exist in seagrass banks where the sediment carbon content is high (promoting sulphide production) and circulation is baffled by the seagrass (Seilacher 1990). The identification of such organisms in the fossil record is difficult. Nearly all modern species of lucinids have this life habit and there is therefore some uniformitarian justification for assuming that the same is true of ancient representatives of the same group, although other groups of bivalves include species capable of chemosymbiosis. Seilacher (1990) has suggested that certain morphological characters, such as tubular shell spines and pores in shell structure, could be indicators of chemosymbiosis, although such features are usually lacking in modern chemosymbionts. Attempts have been made to use shell chemistry to define this mode of life. MacLeod & Hoppe (1992, 1993) studying Cretaceous inoceramids considered that the carbon and oxygen isotope composition of the shells was unusual in that both were unusually positive relative to

bottom-water equilibrium. The oxygen values were used to demonstrate conclusively that the bivalves were in fact benthic and not planktic. The carbon values (Fig. 1) were compared with those obtained from three individuals of *Calypptogeania* sp., a known chemosymbiont which had apparently similarly anomalous values. Thus, a chemosymbiotic habit was postulated for the inoceramids. However, this argument was contested by Grossman (1993) who argued that MacLeod & Hoppe's (1992) characterization of bottom-water equilibrium was in error and that the inoceramids did not therefore have an unusual carbon isotope composition. The uniformitarian aspect of MacLeod & Hoppe's (1992) conclusions can also be criticized. Their characterization of the isotopic composition of chemosymbiont shells was based upon three specimens of one species. Here data is included from a variety of species collected live from the Santa Catalina Basin off the coast of California (see Allison *et al.* 1991 for depositional environment). The organisms were sampled from the vicinity of a large whale carcass which was supporting a chemosymbiotic community. The shelly species collected included the benthic scavenging ophiuroid *Ophiothalmus normani*, the chemosymbiotic bivalves, *Vesicomya gigas* and *Idasola washingtonensis*, and the heterotrophic gastropods *Mitrella permodesta*, *Coc-*

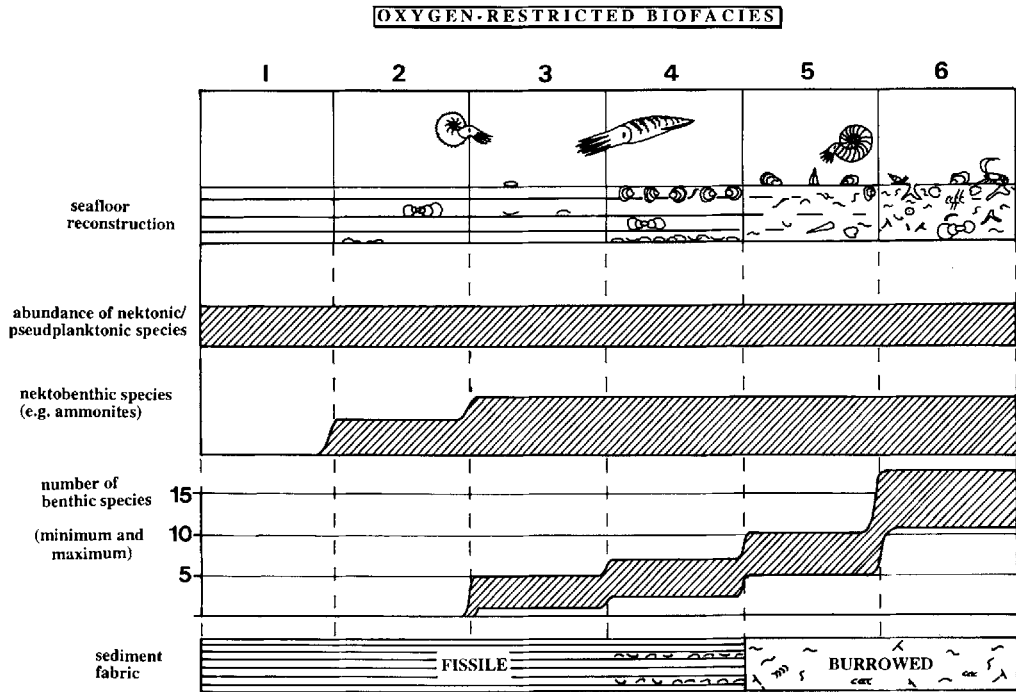


Fig 2. Classification scheme for oxygen-restricted biofacies (ORB) derived mostly from data on the fauna and lithologies of the British Jurassic [from Wignall & Hallam 1991, with slight modifications (cf. Wignall, 1994)]. This shows from top to bottom: (i) diversity of nekton and pseudoplanktonic components of the fauna, assumed not to be controlled by the benthic oxygen levels and therefore not varying; (ii) diversity of nektobenthos (e.g. ammonites); ORB 1 contains no nektobenthos due to the inferred occurrence of hydrogen sulphide in the bottom waters; (iii) number of benthic species shown gradually increasing as benthic oxygen values increase from ORB 3–6, ORB 1 and 2 are anaerobic biofacies and so contain no benthos; (iv) change in sediment fabric type from planar laminated to homogeneous, burrowed fabrics around the ORB 4–5 transition.

linella craigsmithii, *Bathibembix bairdii* and *Neptunea amianta*. In all, except the last two examples, the trophic state of the species was defined by biochemical assays (Demming *et al.* 1990). The isotopic composition of the shells varied widely with total overlap between the different groups (Fig. 1). Thus, shell composition cannot be used as an indicator of chemoautotrophy.

Exaerobic biofacies

Many of the principles of black shale palaeoecology have been derived from the uniformitarian approach, i.e. applying modern-day observations to the past. Unfortunately many ancient black shales consist of biofacies not seen at present. In particular, laminated sediments with

some bedding planes covered in one or a few species of bivalve are common in the past (Morris 1980; Hallam 1987) but they have not been observed forming at the present day. Savrda & Bottjer (1987) termed this the exaerobic biofacies. The definition of the exaerobic biofacies has undergone considerable modification in its brief history. In their initial case study Savrda & Bottjer (1987) noted the presence of infaunal bivalves at the transition between barren, laminated (anaerobic) biofacies and burrowed (dysaerobic) biofacies of the Monterey Formation of California. They therefore considered that the exaerobic biofacies recorded some environment teetering on the edge of anoxia. Subsequently the exaerobic biofacies was defined to consist of epifaunal taxa encountered within laminated strata

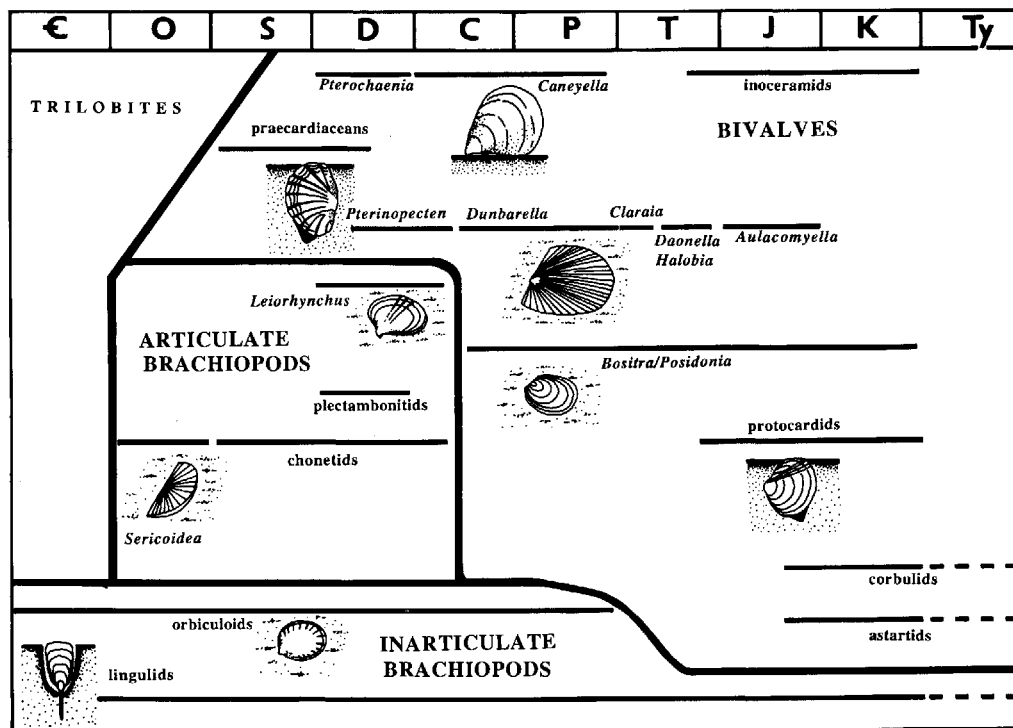


Fig. 3. Summary of the ranges and modes of life of the more common lower dysaerobic taxa of the Phanerozoic. The faunas show a secular change from trilobite to brachiopod to bivalve-dominated forms in the Palaeozoic. Inarticulate brachiopods form a constant component of lower dysaerobic communities. Note the repeated evolution of the 'paper pecten' - type morphology from *Pterinopecten* to *Aulacomyella* and the similarity of this form to the chonetiform brachiopods (*Sericoidea*, chonetids) of the earlier Palaeozoic.

(Savrda & Bottjer 1991). The absence of infauna from the exaerobic biofacies was attributed to the presence of bacterial mats for which the presence of a grazing fauna of ostracods, foraminiferans and small echinoids was held as evidence of their former presence (Savrda & Bottjer 1991). It should be noted that this definition now excludes the original type example.

The latest definition of the exaerobic biofacies includes many black-shale faunas which have previously been interpreted to indicate environmental conditions fluctuating between true anoxia and short periods of dysoxia; during the latter phases transient colonization by both infaunal and epifaunal taxa occurred (Wignall & Myers 1988; Oschmann 1991). This is a distinct genetic classification to that of the exaerobic concept and the terms 'episodically dysaerobic'

(Wignall & Myers 1988) and 'poikiloaerobic' (Oschmann 1991) have both been proposed.

Oxygen-restricted biofacies

The foregoing discussion highlights a debate in which black-shale environments are closely tied to a genetic classification scheme. This has tended to obscure the basic utility of species abundance as a simple measure of relative palaeo-oxygen levels. Thus, the non-genetic, oxygen-restricted biofacies (ORB) scheme has been proposed (Wignall & Hallam 1991). ORB are defined simply by their number of species and the sediment fabric (Fig. 2). One of the few drawbacks of this approach is the strong sample-size dependence of species diversity - a sufficiently large sample must be available for analysis. ORB 1 and 2 are equivalent to

anaerobic biofacies and are characterized by a total absence of benthic forms. ORB 3 and 4 contain only a few benthic species which can be either very rare (ORB 3) or prolifically abundant on some bedding planes (ORB 4). ORB 4 is equivalent to the contentious exaerobic, poikilo-aerobic or episodically dysaerobic biofacies noted above. ORB 1–4 generally occur in finely laminated and/or fissile strata but once benthic species diversity exceeds around five species then there is a change to strata with a more obviously bioturbated fabric.

Dysaerobic faunas through the Phanerozoic

Due to the ease of definition of dysaerobic biofacies (ORB 3–6) it is possible to judge the secular changes in dysaerobic communities through the Phanerozoic from a literature review. Upper dysaerobic assemblages (ORB 5 and 6) essentially appear to record slightly impoverished subsets of the typical aerobic assemblages found in contemporaneous mudstone facies (e.g. Wignall 1990). Thus, their evolutionary changes parallel those seen in offshore mudstone communities of the Phanerozoic (Jablonski *et al.* 1983). The detailed composition of the subsets can however be significantly different from those of aerobic assemblages; Kammer *et al.* (1986) noted that late Palaeozoic dysaerobic assemblages are dominated by vagile molluscs rather than the sedentary brachiopod populations of aerobic facies. The detailed documentation of the changes in upper dysaerobic communities is beyond the scope of this paper.

In contrast to upper dysaerobic communities many of the lower dysaerobic communities (e.g. ORB 3 and 4) of the Phanerozoic appeared to have consisted of taxa more-or-less unique to black-shale facies (Fig. 3). For the Cambrian, trilobites are dominant in every marine habitat (Jablonski *et al.* 1983) but they are replaced by brachiopods from the Ordovician, although trilobites continued to occur as minor components of lower dysaerobic assemblages until the Silurian – dalmanitid trilobites occur in Wenlock black shales for example (Calef & Hancock 1974). Ordovician lower dysaerobic assemblages consist of both inarticulate brachiopods, particularly the orbiculoid *Schizocrania* (Brenchley & Pickerill 1993) and lingulids, and articulate brachiopods (e.g. the strophomenacean *Sericoida*). The lingulids are one of the most persistent components of black shale communities as they are encountered in this facies from the Early Cambrian to the Cretaceous (Fig. 3). The orbiculoids are not quite as long ranging as

there are no convincing records from black shales after the Permian (the so-called orbiculoids of the late Jurassic Kimmeridge Clay have been shown to be patelliform gastropods; Wignall 1990). The articulate brachiopods show considerably more taxonomic variation, although similar morphologies tend to occur again and again. Thus, the chonetiform *Sericoida* is replaced by true chonetids, particularly *Protochonetes*, in the Silurian and Devonian (Calef & Hancock 1974; Thayer 1974).

The Silurian witnessed the first appearance of bivalves in examples of ORB 3 and 4 with the praecardiacean genera *Cardiola* and *Dualina* being particularly common, whilst their relative *Buchiola* is encountered in Devonian black shales (Kammer *et al.* 1986). The mode of life of this extinct group has not been fully evaluated but their morphology is generally reminiscent of modern shallow infaunal bivalves (Wignall & Simms 1990). Bivalves had become the dominant taxon encountered in black shales by the Devonian and a number of different life strategies have reappeared repeatedly since then, although individual genera have commonly been derived from quite distantly related families (Wignall 1994). *Pterochaenia* was the first representative of a tall, quadrate, symmetrical, epibyssate morphotype that was to reappear again in *Caneyella* in the Carboniferous and, most successfully, in the inoceramids of the Mesozoic. The highly characteristic 'paper pecten' morphotype (broad hinge line, numerous radial ribs, well developed ear in right valve) is also first seen in the Devonian, with the appearance of *Pterinopecten* and its direct descendants, *Dunbarella* (Carboniferous–Permian) and *Claraia* (Early Triassic), continuing to be encountered in prolific numbers on black-shale bedding planes. By the Late Carboniferous brachiopods had been ousted from lower dysaerobic communities and bivalves almost exclusively dominated black-shale faunas from the Carboniferous to the Cretaceous. A few gastropod taxa, particularly aporrhoids, begin to appear in black shales from the late Jurassic onwards but they never rival bivalves in abundance (e.g. Wignall 1990). Unfortunately the post-Cretaceous story is too poorly known for trends to be assessed due primarily to the rarity of black-shale facies in the Tertiary. However, the descendants of the low oxygen-tolerant corbulids of the Jurassic can still withstand dysoxic conditions today (Lewy & Samtleben 1979).

The overall macroevolutionary trend in black shale faunas is very similar to that seen in the marine invertebrate record as a whole, with trilobites being replaced by brachiopod-domi-

nated faunas which, in turn, are replaced by bivalves (Fig. 3). However, this transition occurs much sooner in black shale environments – brachiopods were not displaced from shelf communities until the Triassic (Jablonski *et al.* 1983). Therefore, rather intriguingly, many lower dysaerobic faunas of the Palaeozoic can be considered rather modern in aspect.

This brief review also highlights a number of other interesting aspects of lower dysaerobic assemblages. Contrary to the predictions of the exaerobic biofacies, very low, bottom water oxygen levels do not necessarily produce epifaunal assemblages. Shallow infaunal taxa can be common in black shales (e.g. the lingulids, praecardiaceans and several heterodont genera in the Jurassic are all prolific in many developments of ORB 4). None the less epifaunal forms are common and byssally- and pedically-attached taxa are frequently encountered in many black-shale taxa. For many species the attachment site is rather enigmatic. In particular both *Schizocrania* and most species of *Claraia* have a pedicle and byssus, respectively, that was constrained to emerge through a narrow slot ('keyhole') orthogonally to the plane of their shell. This implies that they were firmly adpressed to a hard substrate – a rather strange conclusion for black-shale dwelling taxa. The functional morphology and palaeobiology of this form is clearly worthy of further study.

Taphonomy

Bottom-water anoxia has long been associated with heightened levels of fossil preservation, be it either articulated hard parts of multi-element skeletons such as arthropods, echinoderms and vertebrates, or preservation of soft tissues (Seilacher 1970; Seilacher *et al.* 1985; Allison 1988a). Research into decomposition in sediment has focused upon the fate of disseminated organic carbon (Emerson & Hedges 1988). Very few studies have attempted to assess rates of degradation of heterogeneous accumulations of organic matter such as macro-organisms. Early studies suggested that anoxia did indeed reduce the rate of decay (e.g. Hecht 1933; Zangerl & Richardson 1963; Zangerl 1971). Recently, however, experiments on the decay of crustaceans in jars filled with anoxic mud (Plotnick 1986; Allison 1988a) showed that anaerobic decomposition was rapid, thereby demonstrating the ineffectiveness of anoxia as a precursor to the fossilization of soft parts. This is supported by mass balance calculations (Allison 1988a) which demonstrate the high oxygen requirement

for aerobic decomposition (1 g dry weight of soft tissue requires 671 cm³ of oxygen for complete respiration), while anaerobic sulphate-reduction will decompose twice as much organic matter, mole for mole, as an equivalent amount of aerobic respiration. Jørgenson (1977) calculated that even in oxygen saturated sea water a particle greater than 2 mm in diameter would be anaerobic at the centre. Indeed, given size/surface area constraints on oxygen diffusion it is obvious that any large carcass must decompose essentially anaerobically. Thus, water column anoxia is unlikely to influence decay rate. A complete absence of oxygen will, however, isolate a carcass from scavengers and thus prevent skeletal disarticulation. Experiments carried out on the seabed of the Santa Catalina Basin off the coast of Southern California showed that fish could be stripped of flesh and bones disarticulated within 2–3 days (Smith 1985). The principal scavenger in this cold (4°C), deep (1200 m), dysoxic environment (O₂ content is 0.4 ml/L) is an ophiuroid! However, an absence of oxygen is not the only way of excluding scavengers; rapid burial will perform the same task although this can usually be identified from sedimentological features.

The respiratory by-products of anaerobic microbial metabolism include several ionic species (Table 2) which can promote the formation of early diagenetic minerals (e.g. Coleman 1985). The most well known of these are calcite, siderite and pyrite, but the formation of these minerals does not necessarily imply that the overlying water column was anoxic. All fine-grained sediments will become anoxic eventually, often within a few centimetres of the sediment surface. Ironically, the presence of such minerals can, in some circumstances, be an indication of an aerobic water column. For example, pyrite forms as a result of microbial sulphate reduction, the resultant hydrogen sulphide reacting with a variety of iron compounds to produce first iron monosulphide and then pyrite (Berner 1984). Sulphate reduction is an anaerobic process but certain morphologies of pyrite can only be formed under broadly oxic conditions within anaerobic micro-environments. For example, pyritized soft tissues, or in fact any concentration of pyrite around organic carbon can only occur where the overlying seawater is to some extent aerated. In this case the organic-carbon source decomposes producing a localized anoxic micro-environment which is a source of sulphide. Dissolved iron, liberated by iron reduction, can react with the sulphide at source to produce pyrite (e.g. Hudson 1982; Brett & Baird 1986; Allison 1988b; Briggs *et al.*

1990; Canfield & Raiswell 1991). Conversely, in an environment where water above the sediment surface is anoxic, a carcass decomposes anaerobically without forming a sulphate-reducing micro-environment. In such a setting sulphide production is disseminated throughout the sediment and extends above the sediment-water interface. Dissolved iron is rapidly titrated from solution, forming evenly disseminated pyrite. When this has been utilized, the dissolved sulphide attacks slow-reacting iron minerals such as magnetite and biotite (Canfield 1991).

Geochemistry

A fundamental dichotomy separates the way in which palaeoecological and geochemical indices are used to evaluate palaeo-oxygen values. Palaeoecological indices record the response of the benthic biota to a declining oxygen gradient whilst for geochemistry the important divide is that between anoxic and oxic conditions because it is the anoxia which gives black shales their unique geochemical signature (as detailed below).

Sedimentation rate and organic carbon flux to the sediment are amongst the most important factors controlling the anoxic-oxic (redox) boundary within the sediment. This raises the question of why all sediments do not have an anoxic geochemical signature. In fact, anoxic compounds such as pyrite do form in broadly oxic sediments within anoxic micro-environments but they rarely survive burial due to their rapid rate of oxidation in sediments that are being actively irrigated by a burrowing fauna (Canfield & Raiswell 1991).

Total organic carbon and hydrogen index

The occurrence of a high total organic carbon content (TOC) in sediments is often taken to indicate low oxygen conditions, although whether such high values are the cause or consequence of bottom-water anoxia is the subject of considerable debate (Pedersen & Calvert 1990; Wignall 1994). Henrichs & Reeburgh (1987) pointed out that a high TOC could simply be due to high surface-water productivity and thus a high benthic flux of organic carbon. Whilst such a flux will generate a high benthic oxygen demand due to decay any resultant oxygen deficiency will simply be a consequence of the high TOC values, but it does not necessarily suggest that it was a cause of enhanced preservation. None the less, high TOC values in sediment almost certainly indicate that benthic oxygen levels were low at the time of

deposition.

A related indicator of anoxia is the hydrogen index (HI); this is based on the fact that organic carbon compounds are affected by condensation reactions during diagenesis which led to the formation of kerogens. Such compounds can be subjected to pyrolysis, which has in fact become the standard tool for assessing source rock maturity (see Tyson & Pearson 1991). HI is expressed as the amount of material extracted by pyrolysis (the pyrolysate) in mg g^{-1} TOC. Carbon which has been subjected to aerobic decay will generate a smaller quantity of pyrolysate than that which was deposited in an aerobic environment. The quantity of pyrolysate is, of course, dependent upon other factors such as burial depth and so the HI is usually only used as an indicator of palaeo-oxygenation in a relative sense, for example down a particular section of core (see Emeis *et al.* 1991).

Rare earth element anomalies

In an oxic environment cerium is removed from sea water by co-precipitation with metal hydroxides and becomes concentrated in sediments relative to other rare earth elements. In an anoxic setting this does not happen and the cerium concentration in sediments is in the same proportion to other rare earth elements as it is in sea water (Wright *et al.* 1987). Thus, to use abundance of cerium as an indicator of oxygen levels it is necessary to know what the past sea-water concentrations of these elements were. This can be determined from analysis of fossil biogenic phosphates. The rare earth element content of *in vivo* phosphatic biominerals (e.g. bone, teeth and some shells) is usually three to four orders of magnitude greater than that of oxygenated sea water, although the proportion of individual elements is the same (Wright *et al.* 1987). Cerium content is usually expressed as a cerium anomaly, Ce_{anom} relative to the other common rare earths La and Nd (Wright *et al.* 1987):

$$\log [3Ce_n/2La_n + Nd_n],$$

where n is an international standard value. In this scheme a negative anomaly results from a depletion in cerium and is indicative of an oxygenated environment.

Uranium

The advent of multi-channel, field-portable gamma ray spectrometers has greatly facilitated the rapid assessment of palaeo-oxygen levels

in black-shale facies. Spectrometers also have the additional advantage over other assessment techniques of not requiring the collection of samples enabling them to be used inexpensively in borehole studies. Spectrometers measure the gamma-ray emissions of naturally occurring radionuclides which, in mudrocks, are usually potassium, thorium and uranium. It is the concentrations of U that are most important to the study of palaeo-oxygen values.

In oxic conditions U occurs as soluble and stable uranyl (U^{6+}) carbonate complexes whilst at the redox boundary it forms the even more soluble uranyl ion (Langmuir, 1978). However, in anoxic conditions much less soluble uranous (U^{4+}) fluoride complexes are formed. It is this reaction which is responsible for the enrichment of black shales in U, although the actual mechanism of enrichment is poorly understood and the phase in which U is incorporated is also the subject of speculation (Anderson *et al.* 1989). Anderson and his co-workers observed that anoxic samples only require 2–3 min exposure to oxygen for pore-water concentrations of U to rise by a factor of six. This is undoubtedly due to the rapid formation of the uranyl ion and it emphasizes how important persistent anoxia is to the formation of U-rich black shales.

A potential problem with using U concentrations for measuring palaeo-oxygen levels is caused by the occurrence of U in heavy mineral phases of clastic sediments. This detrital component of uranium (U_{det}) must be distinguished from the authigenic enrichment caused by anoxia (U_{aut}) because the gamma ray spectrometer only measures the total U (U_{tot}) content of the sediment. This dilemma can be resolved by examining the U content of aerobic mudrocks in which all the U is of detrital origin. By examining a large data set, Myers & Wignall (1987) showed that for such mudrocks the Th/U ratio is nearly always between 3 and 5. In black shales the ratio is commonly less than 3, the decrease being due to the addition of authigenic U. Thus, the U_{aut} component can be calculated from spectrometer data as:-

$$U_{aut} = U_{tot} - U_{det}$$

The detrital component can be calculated as:

$$U_{det} = Th/3.$$

This errs on the safe side because for many mudrocks the Th/U ratio is closer to five.

The calculation of authigenic U values has been shown to be of great value for palaeo-oxygen analysis, particularly of non-calcareous mudrocks (Wignall & Myers 1988). For limestones any U content must presumably be of

authigenic origin in the absence of any detrital material but the nature of U incorporation into carbonate phases is poorly known. U has strong affinities for francolite, so the possibility that high values are due to the abundance of this mineral rather than to intensely anoxic conditions must be discounted.

Degree of pyritization

Pyrite is by far the most abundant authigenic mineral formed under anoxic conditions and in environments with water column anoxia it may be very abundant indeed. It is therefore tempting to quantify this abundance as a measure of ancient oxygen values.

In most oxygen-poor marine environments hydrogen sulphide is present in abundance and the main constraints upon how much pyrite forms are the degree of oxygen deficiency and the abundance of iron. Not all iron reacts to form pyrite for some of it is incorporated in rather inert phases such as clay minerals. It is therefore the proportion of reactive iron incorporated into pyrite which is of most significance. Raiswell & Berner (1985) have quantified this as their degree of pyritization (DOP) of reactive iron index:

$$DOP = \frac{\text{pyritic iron}}{(\text{pyritic iron} + \text{acid soluble iron})}$$

Comparison with palaeoecological data has shown that dysaerobic sediments tend to have DOP values between 0.5 and 0.75 whilst anaerobic sediments typically have values in excess of 0.75 (Raiswell *et al.* 1988).

Recently the use of DOP has been complicated somewhat by the realization that the reactivity of iron-bearing minerals depends upon the duration of their exposure to hydrogen sulphide (Canfield *et al.* 1992). Thus sedimentation rate is introduced as another unconstrained variable affecting DOP. This tends to limit the quantitative utility of this index as proposed by Raiswell *et al.* (1988), although high values can still be taken to indicate oxygen deficiency. A severe practical constraint on the use of the index is caused by the very rapid oxidation of pyrite during weathering; very fresh samples are required.

Case studies

The foregoing discussions have highlighted the considerable diversity of techniques that have been developed over the last few years for measuring palaeo-oxygen values. The following

two case studies demonstrate that, by applying a selection of these procedures, previously inferred palaeo-oxygen values are in need of revision. Thus, the celebrated and supposedly anoxic Burgess Shale environment was probably dysoxic whilst many of the carbonate facies of the earliest Triassic, far from being normal marine, are probably dysaerobic facies.

The Burgess Shale

The Middle Cambrian Burgess Shale of British Columbia is world renowned for the abundance and diversity of soft-bodied fossils which it contains. To date tens of thousands of specimens have been collected (Conway Morris 1986). Most of the fossils have been recovered from two quarries on the east side of Mount Field in British Columbia. The fossils are enclosed within thinly laminated mudrocks (the 'thick' Stephen Formation) which abut against a steep-sided carbonate stratigraphic unit (the Cathedral Formation). The laminae are continuous and are between a few mm and 2 cm thick. In general the laminae alternate between two types. The coarser is a mudstone/siltstone couplet with variable amounts (10–40%) of silt-sized grains of carbonate and quartz. This type of lamination typically has an erosive base with scours varying from 0.1 mm to 1 cm in depth and fines up. The second lithology is finer grained and contains very little silt-sized material; it has a base which lacks erosive features and it displays no grading. The muds have variously been interpreted as: (1) turbidites; (2) turbidites influenced by contourites; and (3) tempestites (see Allison & Briggs 1991 for discussion). The limestone block has been interpreted as either a platform margin with a relief of some 170 m or a part of a carbonate ramp. Rapid deposition in conjunction with anoxic conditions has been invoked to account for preservation, although neither will automatically reduce decay rate (Allison 1988a).

The fossil-bearing strata are worked at two quarries on the SW face of Mount Burgess overlooking the town of Field in the Yoho National Park. In the lower quarry (Walcott's Quarry) the sequence is composed of alternating carbonate and silty units. The former fine upwards and are generally parallel bedded, although they do occasionally contain convoluted beds and some very small scours. These scours are usually lined with coarse quartz grains and occur within the limestone beds. They were obviously deposited as several events. The intervening clastic muds are banded with faint alternating laminations and possibly some weak

ripples. Ripples should not form in muds because of grain size constraints but could do if the clay minerals flocculated prior to deposition. The fossils are found in the mud layers. The sediments are surprisingly quartz rich, containing as much as 43% in some cases with the remainder being composed of micas and carbonates. The latter is problematic since carbonate concentrations in excess of 10% preclude the use of Degree of Pyritization analysis as a measure of palaeo-oxygenation. However, thin-section fragments of organic carbon are common (presumably soft-bodied skeletal detritus) and are often associated with clusters of framboidal pyrite. For pyrite to form there must be a source of carbon to feed the bacteria, a source of sulphate which can be reduced and a source of iron which can combine with hydrogen sulphide. For pyrite to form as clusters around organic material the water overlying the sediment must be oxic and not euxinic as has been previously supposed (see previous discussion).

The upper (Raymond's) quarry does not contain conspicuous carbonate layers and is a rather monotonous sequence of graded silt/mudstone layers with interspersed shell beds. Macroscopically the unit contains a number of undescribed trace fossils including a number of 'Planolites-like' traces which are filled with shelly fragments. In transverse section these structures are clearly defined as gutters produced by vortex flow. However, very clear *Diplocraterion* has been collected *in situ* from Raymond's quarry. Clearly, the presence of such burrows indicates that the unit was oxygenated at least briefly. There are also abundant low diversity shell beds composed of hyoliths, brachiopods or trilobites. Analysis of the brachiopods shows that they occur in a variety of orientations and frequently include several different size classes and orientations.

Depositional oxygenation for the Burgess Shale is evidenced by pyrite morphology, trace fossils and abundant monospecific shell beds. These features occur either alone or together but are restricted to certain levels in the sequence. Elsewhere, the presence of dispersed pyrite which is not always associated with organic carbon is evidence of a euxinic environment. Clearly then the depositional oxygenation fluctuated during deposition.

Earliest Triassic carbonates

Earliest Triassic sections of the world exhibit a remarkable uniformity of facies, particularly in the basal-most Griesbachian stage where finely laminated micrites and marly micrites character-

ize nearly all localities (e.g. Wignall & Hallam 1992). Such facies are not noticeably enriched in organic carbon and they have generally been considered to record normal marine conditions. However a variety of lines of evidence suggests that oxygen deficiency or even total anoxia may have characterized deposition, discussed below.

Fauna and sedimentology The impoverished faunas of the earliest Triassic consist almost exclusively of a few species, typically *Lingula* and the bivalves *Claraia* and *Unionites*. *Lingula* is well known from dysaerobic facies throughout the Phanerozoic (Fig. 3) whilst *Claraia* (a 'paper pecten' morphotype) is again typical of many dysaerobic faunas; its direct ancestor *Dunbarella* is one of the commonest genera in late Palaeozoic black shales. The fauna is generally exceedingly abundant on a few bedding planes whilst the intervening bedding surfaces are barren of fossils.

The fine lamination and absence of burrowing is strongly suggestive of anoxic bottom-water conditions. However, the Griesbachian sediments were formed in the immediate aftermath of the Permo-Triassic mass extinction and the absence of an active infauna could alternatively be a consequence of a lack of biomass following the extinction event.

Geochemistry Carbonates generally have rather low pyrite contents due to the severe iron limitation of pyrite formation in carbonate depositional systems. However, tiny pyrite crystals are common at many levels in Griesbachian micrites and they are commonly concentrated as lags at the base of minor storm-winnowed laminae (cf. Wignall & Hallam 1992). This indicates that the pyrite was present in the surface sediments and that it was not oxidized by storm events – both features are indicative of anoxic or even euxinic conditions. If the lower water column was anoxic then abundant pyrite would have been able to form due to presence of soluble iron(II) in such euxinic conditions.

Whilst only modest amounts of TOC are present in most Griesbachian marine sediments, recent geochemical analysis of the Gartnerkofel core from southern Austria has shown it to be volatile, marine organic matter that would be unlikely to be preserved in normally oxygenated bottom waters (Wolbach *et al.* 1994). The low values of TOC may be due to a low organic carbon flux to the sediments (which in turn may reflect low primary productivity) or, alternatively, a high carbonate production rate or a

combination of both.

REE analysis of conodont apatite from the Dinwoody Formation (Griesbachian Stage) of the western United States has shown it to lack a Ce anomaly – a phenomenon characteristic of anoxic conditions (Wright *et al.* 1987; also see above). Whether such a phenomenon is indicative of global anoxia is open to debate but, at the very least, it can be inferred that the large Early Triassic seaway of this region was subject to anoxic conditions.

Despite the low values of TOC, the weight of evidence suggests that the Griesbachian witnessed a widespread phase of dysoxic or anoxic carbonate deposition. That such inferences can be made is due to the battery of multidisciplinary techniques that are now available for the analysis of palaeo-oxygen values.

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Fossil indicators of nutrient levels.

1: Eutrophication and climate change

M. D. BRASIER

¹ *Department of Earth Sciences, Parks Road, Oxford OX1 3PR, UK*

Abstract: Both phosphorus and nitrogen are elements essential to life. Availability of these biolimiting nutrients therefore exerts a major control on the carbon cycle through ocean productivity, bringing about changes in ocean-atmosphere chemistry and climate. This review begins with a brief account of the biological importance of phosphorus and nitrate to the cell, and introduces current terminology relating to the interlinked carbon-nutrient cycles in the oceans. Nitrate-limited, eutrophic ecosystems are associated with modern upwelling zones, characterized by high rates of delivery of new phosphorus, high rates of new primary production and export production. Fossil indicators include high accumulation rates of biogenic silica, apatite, baryte and organic matter, plus non-spinose, smaller planktonic foraminifera. Examples from biomineral chemistry include indications of high Ba/Ca, high Cd/Ca and increased differences between $\delta^{13}\text{C}$ in planktonic and benthic foraminiferal test calcite. Such eutrophic indicators are shown to have peaked during glacial phases in the Quaternary, supporting a model in which Milankovitch-related reductions in solar isolation influenced the availability of nutrients, increasing primary productivity and lowering the levels of atmospheric carbon dioxide.

The aim of this review is to explore ways in which high levels of nutrient availability and primary productivity may be recognized from the fossil record. This has great relevance to Quaternary climate change, but there is also the need for comparable approaches to questions of nutrient levels, climate change and evolution in much earlier periods. An Eocene case history is examined in an accompanying paper (Brasier, this volume), which reviews the recognition of low levels of nutrients from the fossil record. Ultimately, it is hoped to pursue similar approaches to ancient events, such as those in the Cambrian (e.g. Cook & Shergold 1986; Brasier 1992a, b).

The importance of nutrient minerals containing phosphate and nitrate to the fertility of the soil is familiar in everyday life. The presence of nutrients in adequate amounts ensures healthy plant growth and the rapid accumulation of biomass, beneficial in the annual yield of crops. The same is essentially true in the oceans, which form the subject of this review. Primary productivity of the ocean plankton is now thought to play a major role in the buildup or decline of the 'greenhouse' gas carbon dioxide. The relationship between the nutrients and productivity may therefore provide a clue to climate history. Nutrients also have growing relevance to a range of pollution-related problems. These include the response of delicate ecosystems to human effluent, fertilizer and detergent run-off, methane, and CO_2 from fossil fuels which may

contribute to 'global warming'. Not least, nutrient levels may hold important clues to major episodes of evolutionary diversification and mass extinction. Nutrient-related studies can therefore provide an important dimension to geology and environmental palaeontology (see Table 1).

Nutrients and the biosphere

Some basic terms

Useful working definitions relating to nutrient, oligotrophy and eutrophy are given by Hallock (1987). In this paper, the term **nutrient** refers particularly to inorganic **biolimiting nutrients** (e.g. dissolved nitrate and phosphate in sea water) rather than to organic **preformed nutrients**. The terms **oligotrophic** and **eutrophic** are qualitative terms used to refer to regimes of low and high biolimiting nutrient availability, respectively, and their associated levels of primary productivity. **Eutrophication** here refers to those changes in conditions which bring about higher nutrient availability and raised levels of primary productivity.

Biolimiting nutrients and the cell

Four elements are commonly regarded as biolimiting nutrients: phosphorus, nitrogen, iron and silicon. Phosphate ions are essential to life: for energy metabolism, nucleic acid metabolism

Table 1. *Importance of nutrient studies in the earth sciences (with some basic sources)*

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1. **Fertility/productivity of the oceans:** this is directly controlled by the availability of biolimiting nutrients (P, N, Fe, Si; e.g. Broecker & Peng 1982).
 2. **Climate and atmosphere history:** modelling of Holocene and earlier climate changes draws extensively upon proxies for ocean palaeoproductivity (e.g. Broecker & Peng 1982; Berger *et al.* 1989; Summerhayes *et al.* 1992). Nutrients may be implicated in the amplification of Milankovitch cycles in $p\text{CO}_2$ that bring about climate change (e.g. Shackleton & Pisias 1985) and in carbon burial events that brought about the oxygenated atmosphere in the Proterozoic (e.g. de Marais *et al.* 1993).
 3. **Pollution:** risk assessment for modern anthropogenic pollution and 'global warming' requires comparative studies of ecosystem response to nutrient increase (e.g. Hallock 1988; Summerhayes *et al.* 1992).
 4. **Carbonate sedimentology:** nutrients may have controlled the rate of carbonate production and bioerosion (e.g. Hallock & Schlager 1986; Hallock 1988).
 5. **Hydrocarbons:** modelling of organic-rich sediments and hydrocarbon facies requires distinction between productivity-driven, oxygen minimum zone impingement and barred basin models (e.g. Tyson & Pearson 1991).
 6. **Fertilizer resources:** origin of phosphorites and associated uranium source rocks is often linked to upwelling of nutrients (e.g. Cook & Shergold 1986).
 7. **Carbon isotope stratigraphy:** interpretation requires distinction between productivity and carbon-burial models (e.g. Schidlowski & Aharon 1992).
 8. **Wider evolutionary significance:**
 - (a) evidence for high productivity during radiations in early Cambrian (e.g. Cook & Shergold 1986; Brasier 1992a, b) and Palaeocene (e.g. Corfield & Shackleton 1988);
 - (b) evidence for productivity collapse during mass extinction events at major geological boundaries (e.g. Magaritz 1989);
 - (c) evidence for increased extinction of 'oligotrophs' during mass extinction events (e.g. Hallock & Schlager 1986; Hallock 1988).
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and for buffering the ionic strength within the cell. Hence there is a relatively fixed requirement for phosphorus in living algae and protists, on average incorporated at a ratio of about one atom for every 106 atoms of carbon (known as the 'Redfield ratio'; Redfield *et al.* 1963). Since this is greater than the naturally occurring ratio of phosphorus to carbon outside the organism, cellular storage of phosphorus is beneficial, notably in the form of adenosine triphosphate (ATP). Phosphorus intake must be obtained from fluids surrounding the cell in autotrophic

organisms, but can be supplemented by intake from food in heterotrophic organisms. This phosphorus intake must be balanced by excretion of Ca^{2+} ions, to prevent the precipitation of insoluble hydroxyapatite within the cell (Simkiss & Wilbur 1989).

Nitrogen is also an essential element since all amino acids, proteins and nucleic acids contain it. Nitrogen ions are present in a number of forms in sea water, including ammonia (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), organic N and particulate N, all of which can be classified as nutrients. The demand for nitrogen by living marine algae and protists is for about 16 atoms of nitrogen to every one atom of phosphorus (Redfield *et al.* 1963), even when nitrogen concentrations have fallen very low. Although more than three-quarters of the atmosphere is made up of nitrogen it is not in a chemical form that can be used by the biosphere, and living matter also depends upon the process of biological **nitrogen fixation**. This specialized intracellular process is undertaken largely by groups of bacteria, such as cyanobacteria, whose synthesis of NH_4^+ is passed on through the food chain in a series of oxidation steps that lead to NO_2^- and NO_3^- , which together with organic and particulate N can all be classified as nutrients. The existence of six possible oxidation levels for nitrogen means that this element has special importance as an oxygen-donor or oxygen-acceptor in microbial metabolism (Delwiche 1970). Eukaryote plants then take up this synthesized ammonia or nitrate for their own amino acids, from the water column or porewaters, from where it is passed on to animals through the food chain.

Recent attention has focused on the role of iron as a biolimiting nutrient, which is required in the synthesis of chlorophyll, some photosynthetic electron transport proteins and for the reduction of CO_2 , SO_4 and NO_3^- during photosynthetic production of organic compounds (e.g. Martin and Fitzwater 1988). Those authors argue that Fe ions are less available than P or NO_3^- in some nutrient-rich ocean surface waters away from terrestrial or sediment influence. Hence, Fe availability may limit surface productivity in eutrophic areas.

The role of silicon as a nutrient is less conspicuous. Silica ions are essential to diatoms (which are a major element of modern phytoplankton) both to make the skeleton and for DNA synthesis (Ludwig & Volcani 1986). Theoretically, therefore, silica may be biolimiting to diatoms, e.g. in many freshwater habitats. In upwelling regions of the ocean, however, where diatoms bloom in enormous numbers, it

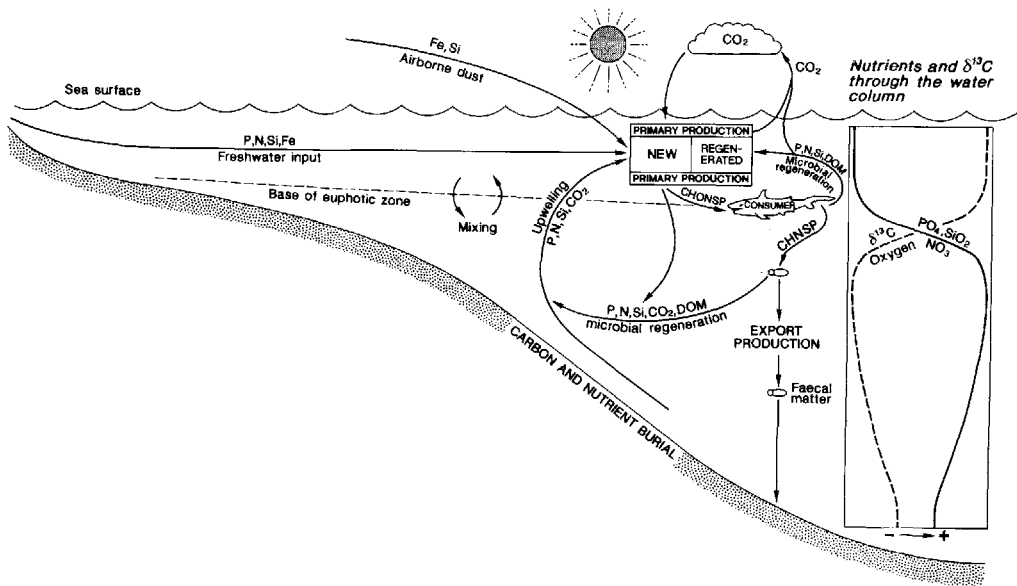


Fig. 1. Diagram to illustrate nutrient cycling and the biological carbon pump. The right-hand side schematically shows the changing concentrations of nutrients, $\delta^{13}\text{C}$ and oxygen with depth. Major biogenic processes are given in capital letters. DOM = dissolved organic matter.

is P and N rather than Si that control levels of productivity (Calvert 1965; Garrison & Douglas 1981).

Biological processes in nutrient cycles: basic principles

The biosphere (empirical formula $\text{C}_{106}\text{H}_{212}\text{O}_{106}\text{N}_{16}\text{PS}$) is conspicuously 'hungry' for P and N, the more so since both the hydrosphere and lithosphere are markedly depleted in these elements, relative to C, H, O and S. Where light and temperature are optimal, the availability of these dissolved **biolimiting nutrients** (P, NO_3^- or NH_4^+ , plus Fe and Si) largely controls **primary production** by photosynthesis.

Optimal conditions for primary production are largely confined to coastal regions of the continental shelf. This is where the highest levels of mean primary productivity and benthic biomass are found at present, and both factors contribute towards oxygen-depletion of the bottom sediments (Tyson & Pearson 1991, pp. 2-3; Table 1). Coastal processes, therefore, may largely control the rate of turning of the carbon cycle, and the interlinked biochemistry of the oceans (Fig. 1). Several terms widely used in productivity research are explained below.

Gross primary productivity is the total amount

of energy fixed in organic matter per unit of time, regardless of whether the organic matter is used for growth or respiration. Levels of gross primary productivity are greatly influenced by light (higher when more illuminated) and temperature (greater when warmer). Gross primary productivity is also influenced by nutrient availability, brought about by changes in the rate of mixing of surface and deeper waters, or by fluvial run-off (e.g. Smith *et al.* 1981). These factors, and associated primary productivity, are known to vary with the seasons and within or between latitudes (e.g. Tait 1980; Tyson & Pearson 1991).

Net primary productivity is the energy fixed in photosynthesis less the energy lost during respiration and 'leakage'; i.e. it is the amount available for growth (Krebs 1972). The amount depends not only upon nutrient uptake but also upon metabolic rates, which may vary directly with temperature, nutrient levels and between species (Hallock & Schlager 1986).

New production arises from photosynthesis in response to the supply of nutrients (mainly nitrates) brought from below the photic zone, e.g. during upwelling episodes (Berger *et al.* 1989). **Regenerated production** relies on the recycling of nutrients within that zone, while **export production** refers to the amount of

production 'exported' (by gravitational sinking) below the euphotic zone, and is the factor most relevant to geological questions of carbon and nutrient burial. It should be emphasized here that export production tends to be highest in regions of episodic, high, new production and least in areas of stable regenerated production (Berger *et al.* 1989).

Similar concepts apply to the phosphorus cycle: the input of **new phosphorus** (i.e. inorganic sources; e.g. Table 2), the pathways of biologically **regenerated phosphorus** through the ecosystem and the **exported phosphorus** which is removed into sediments. It should be noted that unlike nitrogen, phosphorus is not cycled through the hydrosphere and atmosphere in the vapour phase; the P cycle is therefore strongly tied to the biosphere–lithosphere cycles.

A range of biological processes is involved in the removal of photosynthetically fixed carbon and nutrients from surface waters into the aphotic zone (i.e. **export production**): e.g. grazing by zooplankton and fish, and the sinking of larger faecal pellets (e.g. Table 3; see also references in Berger *et al.* 1989). The rate of export by this 'biological pump' is closely tied to

levels of primary productivity and hence to the supply of nutrients in surface waters. The rate of export may therefore govern the cycling speed of the carbon cycle: i.e. fast when nutrients are freely available and slower when nutrients limit primary production.

Once the flux of organic matter has arrived on the seafloor it may suffer one of two fates. Firstly, it may be converted into biomass by biological processes such as deposit feeding and bacterial respiration, with a resultant release of respiratory carbon dioxide, plus P and N compounds. Secondly, it may be incorporated into the sedimentary record, perhaps to form hydrocarbon-rich black shales, phosphorites or biogenic cherts. These three lithologies are typically associated in nutrient-rich, oxygen-depleted conditions.

All of these processes are closely reflected in the geochemistry of the oceans. For example, the photic zone is strongly depleted in the nutrients P, N and Si (Fig. 1). It is also depleted in the light isotope of carbon (^{12}C relative to ^{13}C) since this is preferentially taken up into organic matter during photosynthesis. The ratio between these carbon isotopes is measured as $\delta^{13}\text{C}\text{‰}$ relative to

Table 2. Factors which could raise nutrient levels and primary productivity, encouraging eutrophication in surface waters of the past

BIOLOGICAL

1. **Increased nitrogen-fixation by cyanobacteria** and other microbes, raises nitrate availability, e.g. in the coastal photic zone when light, temperature and nutrients are optimal (e.g. Codispoti 1989).
2. **Bioturbational regeneration of organic matter, phosphorus, silicon** and other minerals from deeper sediment layers to the sediment–water interface and overlying water column (e.g. Schink & Guinasso 1977; Aller 1980, 1982; Hottinger 1987).
3. **Vertical migration of zooplankton** recycles nutrients obtained from deeper waters, as may happen during diurnal or breeding cycles (Angel 1989).

PHYSICAL

4. **Increased fluvial run-off**, important for delivering more P, Fe (and N in recent decades), at all latitudes (e.g. Rabelais *et al.* 1991), such as might develop during regression (e.g. Bramlette 1965; Broecker 1982; Schildowski & Aharon 1992).
5. **More wind-transported dust**, bearing Fe particles, e.g. at times of low sea level during Quaternary, at all latitudes (e.g. Martin & Fitzwater 1988).
6. **Stronger ocean–atmosphere circulation**, delivering more P, N, Si and trace elements into surface waters at all latitudes, e.g. from cooler climate, stronger climatic gradients, greater insolation during Quaternary (e.g. Shackleton & Pisias 1985).
7. **West coast upwelling**, delivering more P, N, Si and

trace elements into surface waters, especially at low altitudes (e.g. Cook & McElhinny 1979).

8. **Equatorial upwelling** delivering more P, N, Si and trace elements into surface waters, especially at low latitudes (e.g. Cook & McElhinny 1979).
9. **Dynamic upwelling**, delivering more P, N, Si and trace elements, at all latitudes (e.g. Froehlich *et al.* 1982).
10. **Seasonal changes in the thermocline**, delivering more P, N, Si and trace elements, at all latitudes (e.g. Tyson & Pearson 1991).
11. **Drop in temperature**, which brings about a fall in metabolic rate, and nutrient and food requirements, leading to relative eutrophication (e.g. Hallock *et al.* 1991).
12. **Nutrient release** from P-rich guano and palaeosols during sea-level rise on carbonate platforms (e.g. Neumann & MacIntyre 1985).
13. **Rapid transgression** of a nutrient-rich, oxygen-depleted water mass on to an 'oligotrophic' platform (e.g. Schlanger *et al.* 1987).
14. **Overturn of the water mass owing to unstable density gradients** (e.g. warm saline bottom waters, cool fresh surface waters), bringing nutrients abruptly to the surface (e.g. Berger 1982; Wilde & Berry 1986).
15. **Overturn of the water mass owing to sudden tectonic movements** in the basin, leading to tsunamis which bring nutrients abruptly to the surface (e.g. Taira 1982).
16. **Overturn of the water mass owing to a meteorite impact**, leading to tsunamis which bring nutrients abruptly to the surface (e.g. Hallock 1988).

the PDB standard (see Williams *et al.* 1989). Since photosynthesis shows a preference for ^{12}C , the $\delta^{13}\text{C}$ of surface waters is affected by the availability of biolimiting nutrients. Thus a trend towards more positive carbon isotopes in the $\delta^{13}\text{C}$ of planktonic calcium carbonate (or organic matter) cannot take place unless there is an adequate supply of P, nitrates, Fe or Si.

Nutrients and isotopically light CO_2 are returned to the water column at greater depths, mainly by microbial **rem mineralization** of organic matter. This leads to a vertical gradient in $\delta^{13}\text{C}$ and nutrient in the water column (Fig. 1) and a strong inverse correlation between PO_4 concentrations and $\delta^{13}\text{C}$ of sea water. Hence, Broecker & Peng (1982) regarded the latter as a proxy record for reconstructing changes in the PO_4 content of various water masses. Thus, a more negative $\delta^{13}\text{C}$ in sedimentary or biomineral carbonates may indicate a higher dissolved PO_4 content (owing to regeneration and low removal by photosynthesis), while a more positive $\delta^{13}\text{C}$ may indicate the converse.

The role of bioturbation Burrowing is likely to

have considerable effect upon nutrient regeneration. By destroying microbial mats it has the potential to disrupt nitrogen-fixation (Brasier Unpublished work) and is thought to allow regenerated P to escape into the overlying water column (Hottinger 1987). Burrowing also increases the silicon flux by a factor of ten (Schink & Guinasso 1977; Aller 1980) owing mainly to an enormous increase in the area of the sediment-water interface represented by the burrow walls.

Burrowing also moves organic matter and nutrients between geochemical reaction zones, displacing anaerobic zones downward and increasing the amount of faster, aerobic recycling within the upper layers of the sediment (e.g. Aller 1982). Organic material (including mucus burrow linings and faecal pellets) is pushed further down into the aerobic zone by deeper burrows, where regeneration is less efficient, aiding the burial of organic matter (e.g. Reimers 1989). The effects of bioturbation on carbon burial will therefore vary according to rates of sedimentation, steepness of the redox gradient and the depth and intensity of bioturbation

Table 3. Factors which could promote lower levels of nutrients and primary productivity, hence reducing eutrophic conditions in surface waters of the past

BIOLOGICAL

1. **Larger size of phytoplankton cells** enhances the export of organic carbon and nutrients below the photic zone (e.g. Degens *et al.* 1985; Legendre & Le Fevre 1989).
2. **Larger zooplankton faecal pellet size** enhances the export of carbon and nutrients below the photic zone (e.g. Peinert *et al.* 1989).
3. **Export and burial of calcitic skeletons** (e.g. nannoplankton, foraminifera) can remove much associated P from surface layers of the ocean (e.g. Codispoti 1989).
4. **Export of and burial of apatitic skeletons, phosphatized calcitic skeletons and organic matter**, also removes some P, especially in phosphorites (e.g. Codispoti 1989; Brasier 1992a).
5. **Increased numbers of suspension feeders and grazers** in surface waters, acts as a control on eutrophication by cropping phytoplankton (e.g. Stachowitsch 1991).
6. **Mid-water denitrification** (i.e. nitrate reduction), typical in oxygen minimum zones at low latitudes, reduces levels of nitrate in surface waters, lowering primary productivity (e.g. Codispoti 1989).
7. **Bioturbational burial** of organic matter and associated P, especially where accumulation rates are high (e.g. Jumars *et al.* 1989; Jumars & Wheatcroft 1989) could remove nutrients from the sediment-water interface, especially if sedimentation rates are high.
8. **Decreased nitrogen fixation**, such as might happen

through extensive burrowing of cyanobacterial mats, could reduce the availability of biolimiting nitrate (e.g. Codispoti 1989; Brasier 1992a).

9. **Nutrient-sealing**, by microbial mats, could reduce the escape of regenerated nutrients from sediments into overlying waters (e.g. Hottinger 1987).

PHYSICAL

10. **Reduced fluvial run-off**, as during a transgression, reduces the delivery of nutrients from the land (see Table 2).
11. **Increased carbon and nutrient burial**, as during a transgression (e.g. Broecker 1982; Schidlowski & Aharon 1992) or during phosphogenic events (e.g. Codispoti 1989; Brasier 1992a), removes nutrients into sediments.
12. **Downwelling** ('antiestuarine circulation'), mainly at low latitudes, pulls down nutrients from surface waters (e.g. Hottinger 1987).
13. **Scavenging of sea-water phosphorus by submarine volcanic activity**, results in P-depletion of bottom waters, such as currently happens above modern ocean ridges (Freely *et al.* 1990). Ridge activity and ridge length may therefore affect the nutrient cycle.
14. **Warmer climate** with reduced climatic gradients and slower bottom water circulation, slows the delivery of nutrients into surface waters (e.g. Fischer & Arthur 1977).
15. **Increased temperature**, brings about a rise in metabolic rate and a higher nutrient and food requirement (Hallock *et al.* 1991).
16. **Prolonged density stratification**, owing to warm, dense, saline bottom waters, traps nutrients below a pycnocline (e.g. Thiersten 1989; Jeppson 1990; Brasier 1992b).

(Berger *et al.* 1989; Jumars *et al.* 1989).

The relationship between burrowing organisms and trophic supply has been examined by Jumars & Wheatcroft (1989). Firstly, one must acknowledge the problems. The intensity of bioturbation, for example, is not an index of food density: abundant food will encourage abundant organisms and hence many burrows; but scarce food also requires increased searching by fewer benthos. Furthermore, nutrient-poor substrates may arise either from a low supply of food or from its low quality. Although these factors are difficult to separate, they tend to covary. A second problem relates to the likelihood that much bioturbation responds not to contemporaneous productivity of the overlying water mass but to earlier productivity events preserved in the sediment. Thus, deposit feeding burrows may be exploiting earlier productivity events preserved within the sediment; but associated suspension feeding burrows may be exploiting later productivity levels above the sediment-water interface.

For a given food quality, however, it can be surmised that benthos adapted to oligotrophic regimes need to maximize their food intake as follows: (1) economies on the 'search time' taken to find an item of food (encouraging 'efficient' behavioural strategies); (2) separation of ingested or egested products (encouraging, for example, the crossing over earlier traces); (3) economies on the amount of sediment shifted (encouraging parsimonious directional behaviour, re-use of burrows) because burrowing is the most expensive form of locomotion; (4) increase in the 'retention time' of food in the gut (favoured by a larger or longer body size, or a more voluminous gut). Many of the features are characteristic of those animals which formed the deep sea *Nereites* ichnofacies (Seilacher 1967), where storm or turbidite sedimentation interrupts a food supply that is invariably low (see Goldring this volume).

It is possible that onshore-offshore trends in ichnofacies (e.g. Seilacher 1967; Frey & Seilacher 1980) are related to parallel changes in nutrient concentration and supply. For example, near-shore communities, dominated by suspension feeding 'trace fossils' such as *Skolithos* and *Diplocraterion*, may well reflect nutrient-enriched coastal waters. Offshore communities, dominated by grazers and farmers, such as *Helminthoida* or *Palaedictyon*, may have been responsive to a lower quality of supply. If so, it follows that anomalous distributions of ichnofossil taxa, such as *Nereites* ichnofacies in littoral waves of the Cambrian (Crimes 1992) may reflect not only the inadequate supplies of food

in the deep sea until later times but also the patchy quality of food in shallow waters. Changes in the proportion of suspension feeders, however, need not indicate an increase in vertical flux, since they are largely dependent on horizontal flux of particles and it may be this that changes.

Eutrophic vs oligotrophic conditions

The processes discussed above can be highly sensitive to changes in nutrient level. This sensitivity comes sharply into focus when comparisons are made between ecosystems living in two very different conditions of nutrient supply: 'eutrophic' and 'oligotrophic' conditions.

Eutrophic conditions are characterized by high and oscillating levels of nutrient supply, and high net productivity. Good examples of this are to be found in areas of upwelling off the west coast of Africa, and in the NW Indian ocean (e.g. Summerhayes *et al.* 1992). Ecosystems adapted to such '**green water**' conditions form the subject of the present paper.

Oligotrophic conditions are characterized by low and stable levels of supply, and lower net productivity. Good examples of this include coral reefs of the Caribbean, Indian Ocean and especially the central Pacific Ocean (e.g. Hallock & Schlager 1986; Hallock 1988). Ecosystems adapted to these '**blue water**' conditions form the focus of an accompanying paper (Brasier this volume).

Table 4 attempts to summarize the generalized characteristics of ecosystems living under eutrophic (i.e. 'green water') and oligotrophic (i.e. 'blue water') conditions, as often represented in the literature (e.g. Margalef 1965; McArthur & Wilson 1967; Hallock & Schlager 1986). The commonly given view is that oligotrophic environments tend to support communities with higher species diversity than eutrophic ones, and contain more specialized species. Many of these species pursue the classic '**K-strategy**' features of larger body size, slower growth rate and a less opportunistic reproductive strategy. These **K-strategists** are protected from their **r-strategy** competitors by factors such as lack of nutrient resources in the environment (Hottinger 1987). If the nutrient levels of an oligotrophic-adapted system rise too high, blooms of plankton reduce water clarity (i.e. 'green water') and limited water transparency will shift primary production further towards the phytoplankton. Secondary production will then shift to suspension feeders, at the expense of benthic algae and deposit feeders or grazers.

Table 4. Generalized characteristics of eutrophic vs oligotrophic ecosystems compiled from sources in the text

	Eutrophic	Oligotrophic
New nutrient supply	High, unstable	Lower, more stable
Net productivity	High, especially plankton	Lower, especially benthos
Water clarity/colour	Low ('green') (or 'red tides')	High ('blue')
Diversity	Low	Higher
Dominance	High	Lower
Reproduction	Frequent, opportunistic, often sexual	Less frequent, more predictable, often asexual cloning
Progeny	Numerous	Less numerous
Juvenile mortality	High	Lower
Body size	Small	Larger
Growth rate	Fast	Slower
Population size	Large	Fewer
Population stability	Unstable, mass mortality	More stable
Trophic strategy	Generalist	More specialist
Benthic feeding method	E.g. suspension feeders	E.g. grazers, symbiotic forms
Symbiosis/dependence	Less	More
Food utilization	Inefficient	More efficient
Food chain length	Short	Longer
Food tiers	Few	Many
C and P loss to sediment	High	Low
C and P regeneration	Low	High
Associated microbes	Endoliths, denitrifiers, sulphate reducers, sulphide oxidizers, magnetotactics (Rhoads <i>et al.</i> 1991)	Aerobes
Marine vertebrates	Common	Scarcer
Bioerosion levels	Higher	Lower
Associated sediments	Dolostone concentrated, pelagic limestone, phosphorite, black shale, diatomite, etc.	Oolitic limestone, shelly-benthic limestone, framework reefs, red to grey muds, stromatolites/microbialites

Eutrophic conditions bring about high plankton productivity that supports a high biomass, including large schools of fish. Among the invertebrates, suspension feeders appear to be favoured by eutrophic conditions, leading to peaks in density and diversity. The turritellid gastropods, for example, are most diverse in those coastal regions that experience seasonal upwelling, where they can dominate the macrofauna (e.g. Allmon 1988, 1992). This success is attributed to an abundance of suspended food sources and/or their preference for cooler waters. Suspension feeders also predominate in the vicinity of eutrophic Adriatic waters, where their consumption of plankton and organic matter may even help to keep down the level of eutrophication and anoxia (e.g. Stachowitsch 1991).

Nitrate- vs phosphate-limited ecosystems

Another way of looking at these contrasts is to identify the major biolimiting nutrient: i.e. nitrate or phosphate (Codispoti 1989).

Nitrate-limited ecosystems include those

adapted to eutrophic conditions, such as the upwelling areas off the west coasts of South America and Africa. Here, the nitrogen compounds exert a relatively short-term control on primary production which experiences many short-term (e.g. annual) fluctuations (e.g. Codispoti 1989). The reasons for these fluctuations appear to be as follows: upwelling delivers 'new phosphorus' into surface waters, encouraging 'new production' of phytoplankton. Excess phosphate (e.g. faecal matter) and silica (e.g. diatom frustules) are 'exported' into shelf sediments under such conditions. Surface blooms sink and decay in waters below the photic zone, where aerobic respiration of organic matter by bacteria consumes large amounts of oxygen, leading to the development of an 'oxygen minimum zone'. Anaerobic respiration therefore begins to take over, especially by denitrifying (i.e. nitrate-reducing) bacteria. An expanding zone of nitrate reduction at this stage means that surface phytoplankton encounter a shortage of nitrate nutrients and are no longer able to bloom because of 'nitrate limitation'. Such negative feedbacks reduce the production of organic

matter, allowing oxygen concentrations to rise again and aerobic respiration to resume (Codispoti 1989).

Over the span of Quaternary glacial cycles a shortage of iron nutrients may have reduced productivity during interglacial transgressions, due to the reduced transport of land-derived dust particles to the oceans (Martin & Fitzwater 1988). On the geological time-scale, however, phosphate limitation is likely to have been more important (Codispoti 1989). The average residence time for P is relatively long (c. 100 000 a) compared with that for combined N in the oceans (c. 10 000 a; Codispoti 1989). Three factors may push shallow marine ecosystems towards **phosphate limitation**: (1) extensive nitrogen fixation/nitrite oxidation by bacteria (so that P becomes the main limiting nutrient); (2) greater density stratification, especially in epeiric seas (so that P recycling is restricted both vertically and laterally); and more speculatively, (3) massive removal of P into sediments (e.g. Codispoti 1989; Brasier 1992a, b). Reefal communities and those of land-locked epeiric basins, such as the Red Sea, Arabian Gulf and Mediterranean Sea, provide modern examples of such phosphate-limited ecosystems (e.g. Littler & Littler 1984). Thus, both the phytoplankton and benthic plant biomass are phosphate limited in the increasingly eutrophic Adriatic Sea (e.g. Justic 1991).

Both nitrate- and phosphate-limited ecosystems are vulnerable to rapid changes in the level of supply. Conspicuous modern examples of this include El Niño events and anthropomorphic pollution of fluvial run-off. The El Niño events of the last two decades have involved changes to the normal pattern of wind circulation, bringing about warmer surface waters in tropical areas, e.g. off the NW coast of South America. Here, the nitrate-limited pelagic ecosystems may suffer mass mortality because the upwelling of cool, P-rich waters falters, so that surface waters become warm and stagnant (Heinze & Wefer 1992). Phosphate-limited coral reefs also suffer from bleaching at these times, mainly due to raised temperatures (Brown & Ogden 1993). Even more serious may be the current disruption of coastal ecosystems by polluted fluvial run-off, enriched in P (mostly bound to organic matter), solid nitrogenous wastes and dissolved ammonium, NO_3^- and NO_2^- ions (Fisher *et al.* 1988). This eutrophication brings stress to phosphate-limited communities, such as coral reefs, where it may suppress the rate of carbonate accumulation (e.g. Hallock & Schlager 1986). In nitrate-limited coastal ecosystems, eutrophication can lead to a bloom of primary producers, and

thence to oxygen depletion of the water column and seafloor, causing particular stress to the benthos (e.g. Rabalais *et al.* 1991).

Biological vs physical factors

Some of the natural factors which could raise nutrient levels in surface waters of the past have been widely discussed in the literature (Table 2). However, the distinction between various biological and physical processes is not easy to make in the geological record. It requires an interdisciplinary approach, involving integrated studies of sediments, fossils and geochemistry in time and space. Such an approach is best demonstrated by current studies of Quaternary to Recent climate change (e.g. within the Ocean Drilling Program, or ODP), reviewed below.

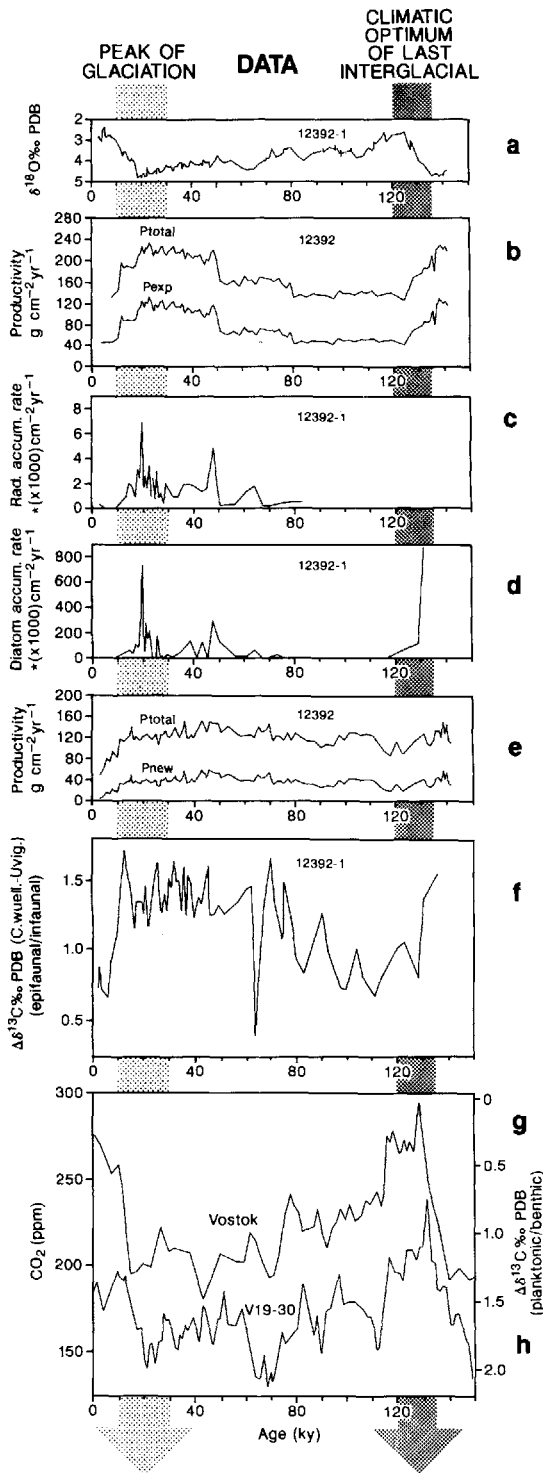
Palaeoceanographers have identified the importance of physical factors, such as winds and upwelling (Table 2, factors 5–9). Beyond the ‘ice-house’ world of the Quaternary, however, other physical factors may have applied, including some that are distinctly catastrophic (Table 2, factors 13–16) and these may be applicable to the study of mass extinction events. The role of biological factors (Table 2, factors 1–3) should also be considered; these may be relevant to the Precambrian–Cambrian boundary interval, for example, when there was an ‘explosive’ increase in bioturbation and zooplankton (Brasier 1992a).

Although biological factors may be of limited importance in raising nutrient levels in surface waters, they appear to play a very important role in lowering nutrient levels and eutrophication (Table 3, factors 1–9). Each of these biological factors has been regarded as a kind of feedback, that slows down or even halts the development of oxygen-depleted and toxic conditions. Physical factors listed here (Table 3, factors 10–16) represent the converse of physical factors listed in Table 2.

Hence, there are many physical factors capable of raising nutrient levels and primary productivity towards eutrophication (Table 2). Some of them are quite abrupt and could have potentially catastrophic effects upon the biota. Adverse ecological effects of eutrophication may be kept in check by a wide range of biological factors (Table 3). Some of these, therefore, could serve as useful markers for the onset of eutrophication.

The fossil evidence for ocean eutrophication

A succession of exciting discoveries in recent years has led to the realization that nutrients and



INTERPRETATION

- a** Heavier oxygen isotopes in epibenthic foraminiferid *Cibicidoides wuellerstorfi* from deep sea cores indicate episodes of increasing ice volume (after Sarnthein *et al.* 1992).
- b** Ocean productivity estimates derived from %Corg and equations indicate higher productivity with cooler climate. Ptotal = total productivity; Pexp = export productivity (after Sarnthein *et al.* 1992).
- c** Estimated accumulation rates of radiolarians; maxima indicate high productivity in surface waters at times of cooler climate (after Abrantes 1991).
- d** Estimated accumulation rates of diatoms; maxima indicate high productivity in surface waters at times of cooler climate, and notably during the peak of glaciation (after Abrantes 1991).
- e** Ocean productivity estimates derived from transfer functions on planktonic foraminiferal assemblages, involving equations in Sarnthein *et al.* (1992). Ptotal = total productivity; Pnew = new productivity. Shows minimal productivity during warm interglacial phases (after Sarnthein *et al.* 1992).
- f** Difference between carbon isotopes of epifaunal and infaunal benthic foraminifera, indicate changing carbon isotopic gradients within sediment. Maxima are attributed to high surface productivity and greater pore-water oxidation of organic matter during colder phases (Abrantes 1992).
- g** Carbon dioxide ppm in Vostok ice core from Antarctica shows maxima during interglacials and minima during glacial phases (Barnola *et al.* 1987).
- h** Difference between carbon isotopes of planktonic and benthic foraminifera in core V19-30 from eastern equatorial Pacific, shows a changing isotopic gradient through the water column, attributed to maximal surface productivity during cold phases (Shackleton & Pisias 1985).

Fig. 2. Palaeobiological evidence for eutrophic episodes off west Africa during Quaternary glacial maxima (c. 20 ka and 130 ka BP), obtained from deep-sea core site M12392 [(a)–(f)]. These are correlated, below, with $\delta^{13}\text{C}$ data in core V19-30 from the eastern equatorial Pacific (g), and carbon dioxide ppm from the Vostok ice-core in Antarctica (g). An interpretation for each curve is given on the right-hand side. In (f), C.wuell.-Uvig. refers to the $\Delta\delta^{13}\text{C}$ difference between epifaunal *Cibicidoides wuellerstorfi* and infaunal *Uvigerina peregrina*.

climate may be intimately linked through the influence of eutrophication on the 'greenhouse gas' carbon dioxide. One important aim for palaeoclimate research has therefore been to find 'proxy' indicators for the nutrient status of the oceans through climatic cycles, such as those of the Quaternary. Before discussing this (next section) it will be useful to review the fossil indices for ocean eutrophication discussed below and summarized in Table 4. These can be divided into palaeobiological and fossil geochemistry indicators. Examples given here are mainly from the Quaternary–Recent (Fig. 2).

Palaeobiological indicators

Siliceous plankton and benthos Major biogenic silica deposits such as those of the Miocene Monterey Formation of California have long been thought to accumulate during past episodes of high ocean productivity (e.g. Calvert 1966; Garrison & Douglas 1981; White *et al.* 1992). Recent studies of sediment traps on the deep ocean floor confirm that fluxes of siliceous diatom and radiolarian skeletons are indeed good indicators of high ocean productivity (Takahashi 1986; Schrader & Sorknes 1991). Accumulation rates of diatoms, radiolarians and biogenic opal can therefore be derived from ancient sediments and used to provide estimates of past ocean fertility (Tiedemann *et al.* 1989; Abrantes 1991, 1992) with accuracies that now approach 80%. This method, for example, confirms that ocean productivity was highest during the glacial phase *c.* 50–10 ka ago (Fig. 2c & d; Sarnthein *et al.* 1992). It should be noted, however, that diatoms are more vulnerable than radiolarians to solution in the water column or within sediments, and the comparative preservation of siliceous microfossils must therefore be analysed (Abrantes 1992).

Since diatoms predominate in the highly fertile 'core' of most upwelling areas, while radiolarians dominate in surrounding areas, the diatom:radiolarian ratio can be used to map upwelling intensity (e.g. Molina-Cruz 1977; Thiede & Junger 1992). Another approach has been to identify the species composition of eutrophic-adapted diatom assemblages and use these to define a 'transfer function' which is then used to plot palaeoproductivity estimates. This transfer function is based on an equation that incorporates multiple regression of the core-top diatom assemblages against modern productivity rates calculated for each site. Schrader (1992, fig. 9) has used this method, for example, to infer transitions from high palaeoproductivity

to lower values over the oxygen isotope stage boundaries of the last 200 ka. Interestingly, a significant fall in palaeoproductivity 120 ka ago, was coincident with presumed maxima in atmospheric $p\text{CO}_2$ (Fig. 2g). A similar kind of approach has been followed with radiolarians. In this case, assemblages characteristic of eutrophic water masses are used to derive an 'Upwelling Radiolarian Index' (URI) and trace upwelling history, as, for example, through the Quaternary off Somalia (e.g. Caulet *et al.* 1992, fig. 5).

Little has yet been done to estimate palaeoproductivity using biosiliceous remains prior to the appearance of diatoms in the Late Cretaceous. Radiolarian and siliceous sponge spicule cherts may provide indicators for silica-enriched bottom waters as far back as the Cambrian (e.g. Brasier 1992b).

Organic-walled phytoplankton An increase in phytoplankton biomass typically takes place during eutrophication events of various kinds (Table 5), such as upwelling (Powell *et al.* 1992) and river flow (Malone 1991). Fossilized organic-walled plankton, such as dinoflagellate cysts, might therefore be expected to have the potential to provide good indicators of past nutrient conditions. Upwelling is known to affect modern dinoflagellate cyst assemblages by causing enrichment of cooler water, peridiniacean (P) cysts compared to gonyaulacacean (G) cysts, as recorded from offshore Peru (Powell *et al.* 1992). Dominant P-cysts have been used as markers for palaeo-upwelling, along with high diatom concentrations and laminated sediments, in the late Miocene to Holocene of the Bering Sea and North Pacific (Bujak 1984), and in the Quaternary off Peru (Powell *et al.* 1992). The latter confirms a strong correspondence between increased upwelling and cooler, glacial climates, but P-cysts also predominate in cold arctic waters, where high nutrients are unrelated to upwelling (Powell *et al.* 1992).

Gonyaulacacean dinoflagellates are involved in the infamous 'red tide' eutrophication events, where nutrients are high but turbulence is lower than found in the west-coast upwelling (Margalef 1978). They also predominate in upwelling zones off SW Africa (Wall *et al.* 1977) where surface waters are not so cool as offshore Peru and the terrestrial flux is greater. Thus, it seems that dinoflagellates are as sensitive to the temperature of surface waters as they are to the nutrient level, and hence their use must be exercised with care.

Table 5. Fossil indicators of ocean eutrophication, e.g. from upwelling. Compiled from sources cited in the text

BIOLOGICAL

1. **Diatoms and radiolaria:** Maximal accumulation rates with maximal upwelling; diatom: radiolarian ratio increases towards core of upwelling zone; eutrophic-adapted diatom assemblages tend to be dwarf, thin-frustuled; transfer functions of eutrophic-adapted assemblages can be plotted to provide palaeoproductivity or upwelling estimates. **Sponge cherts** may have potential from Cambrian onward.
2. **Organic-walled phytoplankton.** Increase in ratio of P- to G-cysts.
3. **Organic matter.** Increase in TOC, often laminated, high in amorphogen.
4. **Phosphate skeletons (e.g. fish teeth, conodonts) and sediments.** General increase with nutrient availability.
5. **Barytic skeletons and sediments.** General increase with nutrient availability.
6. **Meroplanktonic larvae.** Abundant larval skeletons of benthic molluscs.
7. **Calcareous nannoplankton.** Coccolith oozes may form. Increase in *Helicopontosphaera*.
8. **Planktonic foraminifera.** Foraminiferal oozes may accumulate. Simpler smaller, forms (no spines or supplementary apertures, e.g. *Globigerina bulloides*) predominate, preferring cool or coastal waters. Endosymbionts facultative or lacking. Transfer functions or eutrophic-adapted assemblages are used to indicate upwelling intensity.
9. **Smaller benthic foraminifera.** Very small infaunal forms, especially buliminids, of low diversity, predominate under oxygen minima.

FOSSIL GEOCHEMISTRY

10. **Ba/Ca ratios in carbonate skeletons.** Barium increases under high nutrient conditions, especially noteworthy in plankton/surface dwellers/oligotrophs.
11. **Cd/Ca ratios in carbonate skeletons.** Cadmium increases under high nutrient conditions, especially noteworthy in plankton/surface dwellers/oligotrophs.
12. **Oxygen isotopes in carbonate skeletons.** $\delta^{18}\text{O}$ in plankton is more positive with upwelling of cooler waters.
13. **Carbon isotopes in carbonate skeletons.** More negative $\delta^{13}\text{C}$ of upwelling waters may be reflected in plankton: but complications arise in short term over vital fractionation and local effects.
14. **Ce anomaly.** Ratio with La and Nd is reduced under influence of nutrient-enriched, oxygen-depleted waters. Can be studied in fossil apatite.

Organic matter Regions of upwelling are, of course, characterized by laminated, organic-rich sediments, much of it composed of amorphous organic matter or 'amorphogen'. Molecular organic geochemistry indicates that most of this has a marine planktonic origin (Powell *et al.* 1992).

Off Peru amorphogen is accompanied by diverse dinoflagellate cysts and an absence of accompanying terrestrial organic matter. Interestingly, organic-rich, laminated horizons can also yield peaks in the abundance of foraminiferal test linings (Powell *et al.* 1992), but as yet little is known about the origins and interpretation of such tests. Ocean productivity estimates can be derived from the %C_{org} (percentage of organic matter) as described by Sarnthein *et al.* (1992). Such studies indicate that productivity in the late Quaternary has been greatest during cool, glacial phases (Fig. 2b).

Phosphatic skeletons and sediments Large numbers of small fish teeth are typical of upwelling areas off NW South America (Thiede & Junger 1992). In the early Palaeozoic, equivalent indicators include assemblages with diverse and abundant phosphatic skeletons (conodonts, small shelly fossils, inarticulate brachiopods; Jeppsson 1990; Brasier 1992b). Grainstone phosphorite sediments are often related to nutrient enrichment and upwelling zones (e.g. Cook & Shergold 1986; Notholt & Jarvis 1990), although nodular micritic phosphorites can also occur as condensed deposits formed during conditions of very slow sedimentation. Little has yet been done to derive quantitative estimates of palaeoproductivity from biogenic phosphatic deposits.

Barytic skeletons Barium is known to be a good tracer for upwelling zones in the Palaeogene to Recent oceans (see von Breymann *et al.* 1992). Biogenically secreted baryte (as, for example, in xenophyophorian foraminifera) has advantages as a productivity indicator because a large percentage is preserved in the sediment (von Breymann *et al.* 1992). Such Ba-secreting organisms may also be confined to a rather discrete zone within the upwelling productivity belt, seaward of the shelf break (Shimmield 1985). This may explain why nearshore organic-rich sediments receive little Ba, which somewhat reduces its potential as a productivity indicator. It seems that diagenetic mobilization of barium in anoxic sediments can also distort the record (von Breymann *et al.* 1992).

Phytoplankton and meroplanktonic larvae Plankton samples from modern upwelling zones are known to contain surprising numbers of benthos, such as ?epiplanktonic phytoplanktonic foraminifera (*Rosalina globularis*) and meroplanktonic larvae of benthic gastropods, bivalves, and echinoderms (Thiede & Junger 1992). These

have been little used as an index to date.

Calacareous nannoplankton Much has yet to be learned about the relationships between calcareous nannoplankton and the environment. Pujos (1992) has used transfer functions to estimate coccolithophorid productivity through Plio-Pleistocene deep-sea cores. This suggests that they flourish markedly at the beginning of both interglacial and glacial stages. According to Pujos (1992), sudden decreases of salinity and increases in productivity are indicated by increased proportions of *Helicopontosphaera*; unfortunately, these two factors are difficult to separate because the influx of river waters and increased productivity were sometimes synchronous.

Planktonic foraminifera Sediments beneath upwelling zones contain large numbers of both planktonic foraminifera and coccolithophorid nannoplankton (see also Murray this volume), though their numbers are known to drop sharply between seasonal upwelling episodes (e.g. Thiede & Junger 1992; Curry *et al.* 1992). Several pelagic gastropods, such as *Limacina bulimoides*, also thrive in upwelling conditions but their aragonitic skeletons leave little chance for preservation in the fossil record (Thiede & Junger 1992).

Planktonic foraminiferal taxa best adapted to upwelling conditions prefer cool waters and a diet of phytoplankton. They can be recognized by their coastal biogeographic distributions (Thiede & Junger 1992), by their lack of spines and an absence of supplementary apertures. Endosymbionts are either lacking (e.g. *Globigerina bulloides*) or facultative (e.g. *Neoglobobulimina dutertrei*; Hemleben *et al.* 1988). One simple metric, therefore, is to calculate the percentage of such forms within a planktonic foraminiferal assemblage. A good correlation is seen to exist, for example, between the percentage of *G. bulloides* and organic concentrations measured in surface waters, and both have been used to indicate upwelling of cool, eutrophic waters (Prell & Curry 1981).

Globigerinoides ruber and other species with spines and supplementary apertures prefer warm, oligotrophic 'central' water masses where copepods predominate (Hemleben *et al.* 1988). They are, therefore, not typical of main upwelling areas. *Globorotalia menardii* and *G. tumida* are warm-water species with keeled tests that prefer areas where no coastal upwelling occurs (Thiede & Junger 1992).

Seasonal mixing or upwelling can show successions of dominant planktonic species with different ecological requirements. In the Sar-

gasso Sea, for example, *Globigerinoides* spp., which are adapted to oligotrophic conditions, are replaced by forms adapted to a more eutrophic regime during the winter months, when phytoplankton blooms develop (Tolderlund & Be 1971). Off California *G. glutinata* and *G. aequilateralis* and *N. pachyderma* predominate in the upwelling interval. Upwelling in April brings phytoplankton blooms that are grazed by the symbiont-bearing *G. quinqueloba*. Upwelling in May and June encourages dominance of asymbiotic *G. bulloides* which probably also graze on plankton blooms. The subsequent dominance of *N. dutertrei* during the post-upwelling interval may reflect its preference for thermally stratified waters with a pronounced chlorophyll maximum (Thunnell & Sautter 1992).

In the fossil record, temporal changes in the percentage of relatively eutrophic-adapted forms (e.g. *G. bulloides*, *G. quinqueloba*) and forms more adapted to oligotrophic conditions (e.g. *Globigerinoides* spp.) may be used to indicate shifts in the upwelling centre, warm events or El Niño events (e.g. Ibaraki 1992). One method widely used to provide productivity estimates in ODP research is the 'standard transfer function technique' referred to above (Fig. 2c: e.g. Sarnthein *et al.* 1992).

Benthic foraminifera There are few direct fossil indications for oxygen minima beneath upwelling areas because very low oxygen levels inhibit much of the benthos. Infaunal species of the benthic foraminifera *Uvigerina*, *Bolivina*, *Bulimina*, and *Nonionella* are therefore important because they can tolerate oxygen concentrations as low as 0.1 ml/L⁻¹ (e.g. Phleger & Soutar 1973). These belong to the informal grouping known as 'smaller benthic' foraminifera, with simple, septate tests (mostly 1 mm; as opposed to the 'larger benthics' discussed in the accompanying chapter, which have larger and more complexly partitioned tests).

Smaller benthic foraminifera living beneath high productivity waters today mainly belong to the rotaliine superfamily Buliminacea, which have high trochospiral to biserial tests and comma-shaped apertures bearing a tooth plate. Buliminacea living in these conditions tend to be dwarfed in size, which may be due to low oxygen levels (e.g. Phleger & Soutar 1973) and/or to rapid reproduction (e.g. Murray 1963). The relative abundances of such 'quasi-anaerobic' assemblages have been used to trace broad scale changes in upwelling intensity through the Neogene and Quaternary (e.g. Hermelin & Shimmield 1989; Heinze & Wefer 1992; Herme-

lin 1992) and oxygen depletion in the Cretaceous (Koutsoukos *et al.* 1990). Buliminacean-dominated assemblages can also be used to map river-induced eutrophication and anoxia, as in the Adriatic and off the Orinoco and Mississippi deltas (van der Zwaan & Jorissen 1991).

Trace fossils Anaerobic sediments associated with the oxygen minimum zone beneath strong upwelling tend to be well-laminated and barren of macrofossils. As conditions become dysoxic (at oxygen concentrations of 0.1–1.0 ml/L⁻¹), dysaerobic biofacies appear, with a dense but low diversity fauna of polychaetes, oligochaete and nematode faunas (Arntz *et al.* 1991; Savrda & Bottjer 1991). Small, meiofaunal body size (< 1 mm) and high surface area-to-volume ratios are favoured under these conditions where calcareous skeletons (except buliminacean foraminifera) are still scarce. Dysaerobic conditions may therefore explain the narrow burrow diameters found in Mesozoic sediments dominated by the trace fossil *Chondrites* (e.g. Bromley 1990). Conditions of weaker upwelling result in stronger bioturbation and in larger burrows (e.g. Arntz *et al.* 1991). Further aspects of bioturbation and nutrients are discussed in an earlier section.

Fossil geochemistry

Ba/Ca ratio Barium is known to be a good tracer for high productivity and upwelling zones in the Palaeogene to Recent oceans (von Breymann *et al.* 1992), apparently being taken up by decaying organic matter in the water column, in constant proportion to phosphorus. Barium, where available, is also incorporated into the CaCO₃ of invertebrate biominerals. The Ba/Ca ratio of benthic foraminiferal test calcite has therefore been explored as an indicator of the nutrient content in deep-water masses of the glacial ocean (Lea & Boyle 1989), while Ba in aragonitic coral skeletons (Lea *et al.* 1989) has been used to indicate the nutrient levels and local upwelling intensity in surface waters.

Cd/Ca ratio Cadmium has a similar distribution to Ba and P in the water column, being depleted in surface waters and concentrated in the oxygen minimum zone or at depth (Broecker & Peng 1982). Cadmium may therefore be a useful marker for the influence of nutrient-rich waters in the past. Like Ba, it is bound into the crystal lattice of CaCO₃ biominerals. Thus lattice-bound Cd/Ca ratios can be measured in the aragonite of Recent corals, to indicate past episodes of upwelling (Shen *et al.* 1987). A

similar approach has been demonstrated with foraminifera, in which an increase in the Cd/Ca of test calcite may serve to indicate episodes of upwelling, especially when combined with a corresponding decrease in $\delta^{13}\text{C}$ (e.g. Delaney & Boyle 1987).

Stable isotopes The advection of cold, nutrient-rich waters into the upper water column should leave its imprint in the stable isotopic composition of fossils with CaCO₃ skeletons. For oxygen, this is because its two stable isotopes (¹⁶O, ¹⁸O) fractionate in relation to temperature (see Corfield this volume), so that deeper, colder waters tend to have more of the heavy isotope ¹⁸O, while shallow, warmer waters tend to have more of the light isotope ¹⁶O. Carbon has two stable isotopes (¹²C, ¹³C) which are distributed through the water column according to three main effects: (1) primary productivity at the surface (which preferentially incorporates the lighter isotope ¹²C into biomass, leaving surface waters relatively enriched in the heavier isotope ¹³C); (2) organic decomposition in mid waters (releasing ¹²C and nutrients from decaying organic matter back into the water column, as in the oxygen minimum zone); and (3) ventilation by polar bottom waters (in which the influence of different bottom waters returns the isotopic balance a little more towards positive values).

If these isotopes are incorporated into CaCO₃ skeletons in equilibrium with the environment then they should give some indication of the seawater chemistry in which they were secreted. Mass spectrometry of fossil skeletons can then yield the ratio of these stable isotopes, expressed as $\delta^{18}\text{O}\%$ or $\delta^{13}\text{C}\%$, relative to the PDB standard. It is clear from studies of modern skeletons that 'vital effects' can overprint the environmental signal, producing values that are much lighter than ambient sea water. These vital processes are little understood but appear to involve the utilization of metabolic carbon in the secretion of carbonate. Some groups of organisms are known to have large vital effects (e.g. echinoderms, some corals), whereas others are thought to incorporate stable isotopes into their carbonate skeletons largely in equilibrium with sea water (e.g. planktonic foraminifera and some molluscs; for general discussion see Hudson 1977; Lee & Anderson 1991; Murray 1991).

In living planktonic foraminifera, more positive $\delta^{18}\text{O}$ values (i.e. enrichment in the heavy isotope ¹⁸O) and more negative $\delta^{13}\text{C}$ values (i.e. enrichment in the light isotope ¹²C) would be predicted during episodes of upwelling, which bring cool, ¹⁸O- and ¹²C-rich waters to the

surface. While studies of $\delta^{18}\text{O}$ have largely borne this out, $\delta^{13}\text{C}$ values have often proved contradictory between taxa and between areas (e.g. Kroon & Ganssen 1989; Thunell & Sautter 1992). For example, $\delta^{13}\text{C}$ of *Globigerinoides ruber* becomes more positive towards the core of upwelling in the Arabian Sea and not more negative as expected (Curry *et al.* 1992). *Globigerina bulloides* is also paradoxical in recording a significant depletion in ^{18}O and ^{13}C during upwelling episodes off California (Thunell & Sautter 1992) but an enrichment in ^{13}C in the northern Indian Ocean (Kroon & Ganssen 1989). Year-to-year contrasts between values obtained during upwelling episodes can also exceed the total variation over a given year. The results may even be unrelated to ecological succession through the upwelling cycle (Curry *et al.* 1992; *con.* Kroon & Ganssen 1989).

Several explanations have been put forward to explain these anomalies. It seems that there is a kind of ecological succession during the upwelling cycle in which successive species of planktonic foraminifera migrate upwards or downwards through the water column. However, these patterns of species migration appear to differ between areas (e.g. Thunell & Sautter 1992), so that a given species may therefore give contrasting isotopic signals. Another explanation involves changes in the Redfield ratio (see above), in this case related to local variation in the ratio between organic detritus and nutrients at a given site. It is estimated that a 10% increase in the Redfield ratio would increase surface water $\delta^{13}\text{C}$ by *c.* 0.2‰ (Curry *et al.* 1992). Yet another factor may be the $\delta^{13}\text{C}$ of organic carbon produced by photosynthesis, which varies naturally between different groups of phytoplankton: a 10% change from -20‰ to -22‰ could enrich the surface water $\delta^{13}\text{C}$ of CO_2 by *c.* 0.2‰ (Curry *et al.* 1992). However, as yet, little account seems to have been taken of the role of symbionts in determining isotopic response to nutrient flux. The outcome, therefore, is that patterns of $\delta^{13}\text{C}$ change are complex and cannot easily be used to indicate the onset of upwelling on short time-scales. Over larger time-scales these anomalies may be diminished by time-averaged signals, relating to the generalized history of relatively large water masses.

One ratio that has proved useful in tracing the history of upwelling over geological time-scales involves the 'delta del' method. Within the water column one may compare the difference in $\delta^{18}\text{O}$ or $\delta^{13}\text{C}$ between plankton living below the thermocline (e.g. *N. dutertrei*) and in surface waters (e.g. *G. bulloides*; Steens *et al.* 1992). These differences (expressed as the 'delta del',

$\Delta\delta^{18}\text{O}$, $\Delta\delta^{13}\text{C}$) are found to be least over upwelling areas because the mixing of waters brings about greater homogenization. When applied to ODP Site 117 over the last half million years, for example, Steens *et al.* (1992) found indications that monsoonal upwelling was greatest during glacial climates until *c.* 374 ka ago, when maxima switched to interglacial climates.

Palaeoproductivity may also be estimated by comparing the difference between $\delta^{13}\text{C}$ values ($\Delta\delta^{13}\text{C}$) of a pair of benthic foraminifera which can record bottom waters at or above the sediment-water interface (SWI; e.g. epifaunal *Cibicidoides wuellerstorfi*) and in interstitial sediment pore-waters (e.g. infaunal *Uvigerina peregrina*; see Corliss 1985; McCorkle & Emerson 1988). In this situation decomposition of organic matter within the sediment releases lighter, respiratory ^{12}C into the interstitial pore-waters which becomes incorporated in the tests of *Uvigerina* living there (e.g. Altenbach & Sarnthein 1989). Since the ratio of ^{12}C to ^{13}C is greater than found at the SWI, where *Cibicidoides* lives, a gradient in $\delta^{13}\text{C}$ exists between deeper sediments and the SWI. This gradient can therefore be measured as $\Delta\delta^{13}\text{C}$ between these two species at a given site. The isotopic gradient also increases when surface waters are more fertile, since large amounts of organic matter reach the bottom to be oxidized within the sediment, releasing yet more light ^{12}C into pore waters. This method, for example, tends to confirm the greater fertility of surface waters during Quaternary glacial periods (Fig. 2f; Altenbach & Sarnthein 1989; Abrantes 1992).

A third method is to examine the difference in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ between planktonic and benthic foraminifera at a given site and trace this through time (e.g. Shackleton & Pisias 1985). With this approach, the isotopic contrasts between the surface waters (e.g. *G. bulloides*) and sediment pore-waters (e.g. *U. peregrina*) may be at their greatest. Studies of Quaternary cores show that maximal values in $\Delta\delta^{13}\text{C}$ were reached during the last glacial period (Fig. 2h; Shackleton & Pisias 1985). Most importantly, the curve obtained can be calibrated against changes in $p\text{CO}_2$ obtained from Vostok ice cores (Fig. 2g; Barnola *et al.* 1987). Similar results have been obtained using the reef-dwelling giant clam *Tridacna gigas* rather than planktonic foraminifera, to provide the surface-water signal. Here again, the $\Delta\delta^{13}\text{C}$ between the giant clam and *Uvigerina peregrina* yields maximal values during the glacial phases (Schidlowski & Aharon 1992).

The Cerium anomaly Normal marine sediments and associated biogenic apatite are both markedly deficient in the rare earth element Ce when compared with other rare earths La and Nd. In anoxic regions, such as the Black Sea, however, the Ce anomaly is reduced and the Ce_{anom} in apatite provides a useful measure of the oxidation–reduction system prevailing in surrounding waters (Holser *et al.* 1986). Evidence for widespread anoxia is indicated, for example, within Late Cambrian conodont apatite (Wright *et al.* 1986) and evidence for anoxia seems to have declined gradually through the Palaeozoic (Holser 1984; Holser *et al.* 1986). These results seem to be generally consistent with other evidence for widespread anoxia in late Precambrian–early Palaeozoic oceans (e.g. Brasier 1992a, b).

Temperature and productivity

Temperature is known to have a major effect on physiology, doubling the rate of reaction for every 10°C of temperature increase (Hochachka & Somero 1984). Assuming that an organism follows the same metabolic strategy, twice as much food will therefore be required to sustain it in tropical waters as compared to polar waters. Some have argued, therefore, that given rates of nutrient input would support different kinds of ecosystem at different temperatures: oligotrophic-adapted in warm waters; mesotrophic or even eutrophic-adapted, in cold waters (Hallock *et al.* 1991). These authors suggested that a four-fold (or greater) increase in food supply could occur with a temperature drop of only a few degrees, as during seasonal, low-latitude upwelling. This principle should be borne in mind when considering the relationship between nutrients, productivity, the carbon cycle and climate.

Discussion – the role of nutrients in climate change

As can be seen from Fig. 2, there is a good correlation between fossil indicators for eutrophication and the Milankovitch climatic cycles over the last 200 ka. Note how evidence for increasing levels of fossil atmospheric CO₂ (ppm) in the Vostok ice core from Antarctica (Fig. 2g) coincides with evidence for decreasing ice volume, obtained from $\delta^{18}O$ in deep-water epibenthic foraminifera (Fig. 2a; Barnola *et al.* 1987; Sarnthein *et al.* 1992). This is at least consistent with a link between this gas and global warming.

Since the ocean stores 60 times as much CO₂

as the atmosphere, small changes in dissolved oceanic CO₂ can bring about large changes in atmospheric CO₂. The most likely means of achieving this is by varying the rate of carbon fixation by primary productivity, under the influence of the biolimiting nutrients. Increased delivery of ‘new P’ from the land, faster recycling of P atoms via deep upwelling and changes in the amount of biologically ‘recycled P’ near the ocean surface could all be implicated (e.g. Broecker & Peng 1982; Shackleton & Pisias 1985), as could the effects of reduced temperature (discussed above).

The association between high organic carbon content levels in sediments, and glacial maxima from the $\delta^{18}O$ record (Fig. 2b), suggests a Quaternary scenario in which high wind stress brings about low latitude upwelling, advecting deep nutrients to the surface and raising primary productivity. The increased rate of carbon burial on the seafloor helps to reduce pCO_2 , raise the CCD and cool the atmosphere (Sarnthein *et al.* 1988). In considering these effects, however, it is important to distinguish between two different kinds of biological carbon pump in the oceans: the oceanic and the neritic pumps (Schrader 1992). The **neritic pump** will effectively remove CO₂ from the atmosphere by extracting carbon and lowering the partial pressure of CO₂ in surface waters via primary productivity. It will permanently store organic carbon on the shelf and upper slopes in hemipelagic sediments. The **oceanic pump**, on the other hand, is arguably less effective in permanently removing carbon from the atmosphere–ocean system. This is because organic carbon exported to the deep oceans will largely be oxidized and recycled. Coastal upwelling systems, such as those off NW South America, are therefore thought to play a major role in the global carbon cycle and climate change (Schrader 1992).

Understandably, much interest has therefore centred on the history of upwelling centres. Today, these are located in tropical and subtropical zones, where wind stress encourages neritic upwelling along the western margins of the Americas and Africa. Oceanic upwelling also occurs in the western Indian Ocean, associated with monsoonal winds. Conditions of high, but episodic flow, of new P into the ecosystem in these areas brings about very large standing stocks of plankton and nekton for brief periods in surface waters, associated with a drop in sea-surface temperature. Current evidence suggests that denitrification zones are extensive several hundred metres below the ocean surface, giving nitrate a major control on productivity of these planktonic ecosystems. Organic-rich sediments

accumulate where these oxygen minima impinge on the shelf and slope. Here, oxygen depletion brings about a marked reduction in benthic diversity. Shutting off the main nutrient supply (as in El Niño events) can have catastrophic effects for the end members of the food web, such as fish and birds. The very distinctive physico-chemical properties of these waters therefore brings about distinct ecological conditions that leave a strong palaeontological signal in the record of plankton blooms, nekton mass mortality and dysaerobic to anaerobic benthos.

Since the results obtained from isotopic studies of upwelling episodes may be equivocal, fossil species are clearly providing important criteria. It should be emphasized, however, that unravelling the relationship between upwelling, productivity and carbon burial is complex and controversial, even for the Quaternary.

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Fossil indicators of nutrient levels. 2: Evolution and extinction in relation to oligotrophy

M. D. BRASIER

Department of Earth Sciences, Parks Road, Oxford OX1 3PR, UK

Abstract: An overview of hypotheses on the impact of nutrients on biosphere history reveals the need for quantitative fossil indices for oligotrophy. Emphasis is given to indicators for endosymbiosis in relation to oligotrophic regimes, and a middle Eocene case history is selected for closer examination. Quantitative data, relating to changes in cellular integration in foraminifera are consistent with a catastrophic shift from highly oligotrophic towards eutrophic conditions, associated with global cooling near the end of the middle Eocene.

In an accompanying paper (Brasier this volume) the potential of fossils to indicate a regime of high nutrient level has been discussed, and it has been shown that such eutrophic conditions are closely linked to climate change during the Quaternary. This review explores the way in which low levels of nutrient availability may be recognized from the fossil record, and considers the wider implications for biosphere evolution.

Some useful working definitions relating to nutrients, oligotrophy and eutrophy are given by Hallock (1987) and Brasier (this volume). In this paper, the term 'nutrients' refers particularly to inorganic, 'biolimiting nutrients' (e.g. dissolved nitrate and phosphate in sea water) rather than to organic, 'preformed nutrients'. The terms 'oligotrophic' and 'eutrophic' are qualitative terms used to refer, respectively, to regimes of low and high biolimiting nutrient availability, and their associated levels of primary productivity.

The last few decades have seen many attempts to examine the effects of nutrient supply and feeding regime upon evolution. By the late 1960s much data had accumulated on the diversity of fossil plankton. It was tempting, therefore, for micropalaeontologists to make deductions about ocean productivity in the past. In the pioneering model of Tappan (1968), for example, low diversity of fossil plankton was equated with low productivity.

Modern marine ecologists, however, were beginning to show that diversity is actually higher under conditions of low nutrient supply (e.g. Margalef 1968), and palaeobiologists were forced to reconsider. Valentine (1971) predicted, therefore, that evolutionary diversifications should be associated with oligotrophy and extinctions with higher productivity. A further, palaeoceanographic, dimension was introduced

by Fischer & Arthur (1977) who related series-to system-length changes in diversity to sea level, rates of deep ocean circulation and nutrient recycling.

Levinton (1972, 1974) was one of the first to document the contrasting evolutionary histories of trophic groups, through a comparative study of suspension and deposit-feeding bivalves. The latter, he suggested, have depended on relatively stable bacterial populations whereas the former have depended on fluctuating plankton populations. Levinton therefore surmized that suspension feeders should arise and become extinct at higher rates than deposit feeders. Survivorship curves of suspension- vs deposit-feeding taxa have given some support to this view (Levinton 1974; Kauffman 1977).

Over the last decade it has become increasingly possible to relate evolutionary events to oceanographic data. A number of researchers have argued that certain suspension feeders and nektonic carnivores/planktivores have diversified under conditions of high nutrient and food availability, only to decline when that supply was reduced in various ways. For example, a decline is recorded in the diversity of American suspension feeding molluscs after the Miocene, perhaps related to reductions in phytoplankton productivity following emergence of the Panamanian isthmus (Vermeij 1990; Allmon 1992). High rates of extinction are also recorded in suspension-feeding marine invertebrates across the Cretaceous-Tertiary boundary, when plankton productivity collapsed (Sheehan & Hansen 1986). Much further back in time, the diversity of extinct conodont animals (which are presumed to have been nektonic carnivores, high in the food chain) is thought to have fallen in response to lowered levels of nutrient supply around Baltica during the Silurian (Jeppson

1990). Even the global rise and fall of suspension-feeding archaeocyathan sponges in the early Cambrian (Debrenne 1991; Brasier 1992b) raises similar questions.

Table 1. *Nutrient-related factors which may bring about the demise of oligotrophic-adapted reefs and reduce carbonate production rates (from sources in the text, especially Hallock & Schlager 1986 and Hallock 1988a).*

1. **Plankton blooms** reduce water transparency, or bring about toxicity, slowing the growth of corals, larger foraminifera and lowering the rate of carbonate production.
2. **Freely available nutrients** encourage symbiotic protists to escape and lead a free planktonic life.
3. **Phosphates** may act directly as crystal poisons to calcification.
4. **Biotic disruption and bacterial blooms** may result from overfeeding because it encourages mucus secretion which ultimately kills corals.
5. **Oxygen-depletion, or sulphide-poisoning**, on the seafloor, from decomposing plankton or mucus, kills benthic stages in the life cycle.
6. **Genetic variety** of forms largely produced by asexual reproduction is low, reducing the potential range of response to changing conditions.
7. **Competitors to corals and larger foraminifera**, such as coralline algae, fleshy algae, homotrematids, barnacles and bryozoans, the crown-of-thorns starfish, and forms with planktivorous larvae (i.e. many polychaetes, bivalves, echinoids, fish) may be favoured by higher nutrients and plankton production.
8. **Bioeroders**, such as endolithic algae and fungi, clionid sponges, boring bivalves and echinoids may flourish, weakening the reef framework.

Invertebrates with autotrophic protistan endosymbionts ('photosymbionts') may provide another useful index to nutrient levels. As discussed below, these are particularly associated with reefal communities. In the case of larger foraminifera, for instance, photosymbionts are associated with complex endoskeletal architecture. Hottinger (1987) examined this architecture in the foraminiferal fossil record and inferred that it may take at least 5–10 Ma for such photosymbiosis to develop from an asymptotic ancestral stock. Once symbiosis is established, diversity appears to be favoured by prolonged, stable, oligotrophic conditions (Hallock & Schlager 1986). This implies that an increase in nutrient levels could bring about the decline and extinction of oligotrophs and reefal communities, for a variety of reasons (Table 1). For example, in forms with a meroplanktonic life cycle, summer eutrophication can cause catastrophic hypoxia of the seafloor, wiping out the benthic phase of the life cycle (e.g.

modern hydromedusans of the Adriatic; Justic 1991). In forms with endosymbiotic protists, such as larger foraminifera and corals, eutrophication can have several adverse effects (Table 1; e.g. Hallock & Schlager 1986; Hallock 1988a). Indeed, these authors have suggested that the major cause of past reefal destruction should be sought in climatic cooling and regression, leading to increased rates of oceanic circulation, greater nutrient flux and reduced water clarity. Such ecological collapse may be viewed as the predictable demise of a highly interdependent, self-organized system that evolved under conditions which had remained stable for long periods prior to the calamity. This is rather elegantly suggested by recent computer models (e.g. Plotnick & McKinney 1993; Bak *et al.* 1994) and this problem will be returned to below.

Although nutrient changes have been implicated qualitatively, both in series- to system-length changes in diversity (e.g. Fischer & Arthur 1977) and in shorter scale oscillations (e.g. Jeppson 1990), there has been little rigorous testing of these ideas in the fossil record. A more quantitative approach to these questions of nutrients and evolution is urgently required.

Photosymbiosis

Although some photosymbiotic associations occur in nutrient-rich habitats (for example, those between *Chlorella* and invertebrates or protists in ponds and streams; Smith & Douglas 1987), most are found in nutrient-poor conditions or in hosts which depend on a nutrient-poor diet (Muscatine & Porter 1977). There is a strong relationship, for example, between protistan endosymbionts and low nutrient levels in reef-building corals of tropical to subtropical seas (Cowen 1983; Coates & Jackson 1987), or in larger foraminifera from similar habitats (Hallock & Schlager 1986; Lee & Hallock 1986).

Scarcity of nutrients brings advantages to photosymbiosis, since it allows internal cycling of P, N, CO₂ and O₂, and organic compounds between host and symbiont (Hallock 1981). This symbiotic relationship probably accounts for the high gross primary productivity to be found in coral reefs, despite the low levels of nutrients in surrounding waters and low net primary productivity (Hallock & Schlager 1986). Palaeontologists have therefore considered the possibility that ancient reefal growth was accelerated under oligotrophic conditions that stimulated photosymbiotic relationships with microbes (e.g. Cowen 1983, 1988; Talent 1988; Kuznetsov 1990).

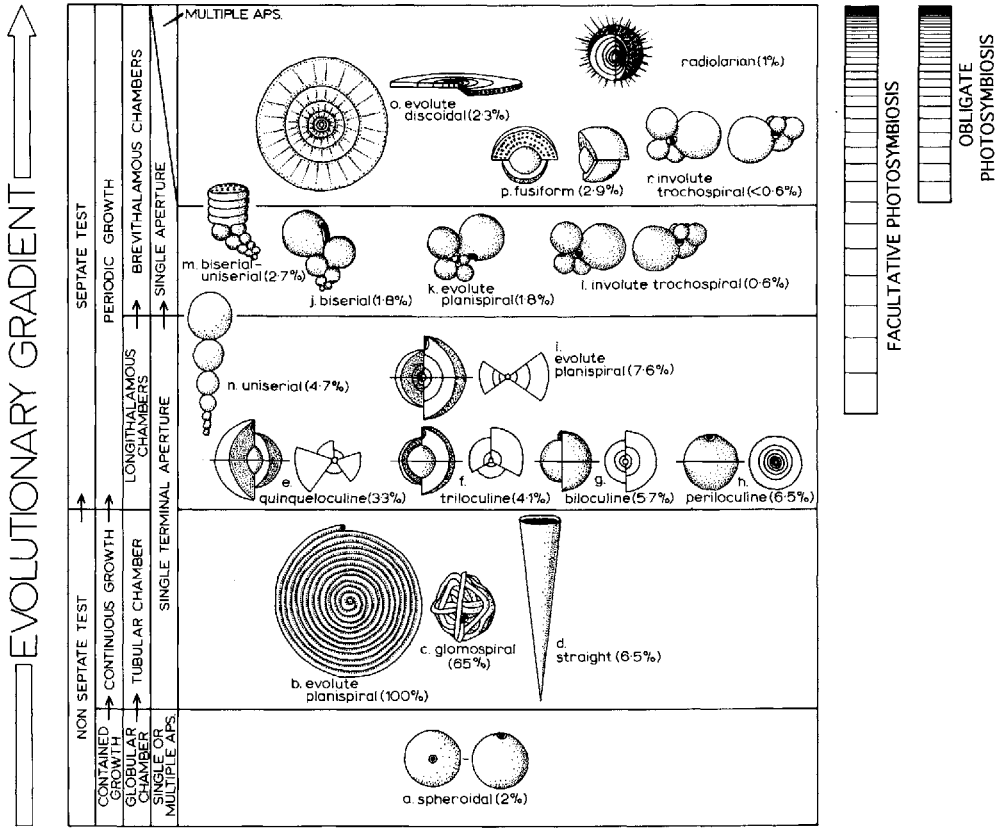


Fig. 1. The evolutionary gradient in foraminiferid test architecture, from 'primitive' (below) to 'advanced' (above). Models of unit volume after Brasier (1982a) are used to compute the minimum line of communication (MinLOC), here given as a standardized percentage in brackets, relative to the evolute planispiral form 'b'. Forms with obligate photosymbiosis have relatively short lines of communication within the test. Adapted from Brasier (1986).

To test these ideas there is a need for quantifiable criteria, firstly to indicate photosymbiosis in a group of fossil organisms from a deposit and secondly to provide independent evidence for oligotrophic conditions. Five approaches for the recognition of photosymbiosis are discussed below: (1)–(3) symbiotic skeletal architecture in larger benthic and planktonic foraminifera, and in corals and archaeocyathan sponges; (4) bioerosion and lithology; and (5) skeletal geochemistry, by carbon isotopes.

Symbiotic skeletal architecture

Since the internal photosymbionts reside in the soft tissues of invertebrates, and leave no direct record in the skeleton, their presence must be inferred indirectly, from aspects of preserved skeletal architecture consistent with this kind

of symbiosis. Foraminifera are used below to provide an example of this approach.

Foraminifera are single-celled rhizopod protists that protect their cytoplasm within an agglutinated or secreted skeleton (the test) that provides for a long and useful fossil record. In primitive forms this test typically comprises a single globular chamber, or a tubular chamber, often spirally wound (Fig. 1b, e.g. *Cornuspira*). Most smaller benthic foraminifera appear to have evolved from the latter by periodic development of septa during growth, to form chambers which are rather elongate ('longithalamous') in many primitive septate forms, such as the miliolid *Quinqueloculina* (Fig. 1e) Shorter ('brevithalamous') chambers characterize many modern 'smaller' benthic and planktonic foraminifera, and the latter often have globular chambers (e.g. *Globigerina*, Fig. 11).

Table 2. Morphological comparison between larger benthic foraminifera (symbiont-bearers) and smaller benthic foraminifera (generalized, symbiotic)

	Symbiotic larger benthics	Asymbiotic smaller benthics
Size	> 3 mm ³	< 3 mm ³
Test shape	Changes with light level and turbulence	?Little change
Surface area: volume	Maximized, especially with depth	Little change
Complex internal morph	Well developed	Rare
Dimorphic tests	Microspheric tests, larger than megalospheric, tests	Similar size
Sexual reproduction	Relatively suppressed	Relatively common
Upper wall/side walls	Thinner upper wall	Similar thickness
MinLOC	Approaches minimum	Medial to maximal
Facies	Shallow carbonates	Many facies

The most advanced architectural character involves the acquisition of multiple apertures, as seen in some planktonic foraminifera (e.g. *Globigerinoides*, Fig. 1r) and alongside the development of more complex, 'larger benthic'-foraminiferid architecture (e.g. Fig. 1o & p). Research has indicated that it is in these architecturally advanced forms in which photosymbiosis is best developed and reaches its most interdependent or 'obligate' condition (Fig. 1).

Larger benthic foraminifera Here, chambers of the test tend towards further subdivision into chamberlets by means of skeletal partitions (e.g. Fig. 1o). Chambers (or chamberlets where developed) bear openings (foramina) that allow communication within the test and with the outside environment, where they appear on the surface as multiple apertures.

Such skeletal complexity in the larger foraminifera makes them a potential vehicle for the study of symbiosis in evolution. They also have a wide geological occurrence in neritic marine sediments, a long time range (Devonian–Recent), and most have skeletons of relatively stable calcite (rather than metastable aragonite, as in scleractinian corals). A number of studies have examined the complex tests of modern taxa in relation to the needs of endosymbiotic algae, which thrive in well-illuminated and low-nutrient habitats (Table 2; e.g. Brasier 1986; Hallock *et al.* 1991; Lee & Anderson 1991).

Recent work suggests that the depth of habitat in the foraminiferid host is closely related to those wavelengths of light required by specific symbionts: red and violet light favours chlorophyte symbionts in shallow water (<20 m); yellow, green and blue light favours rhodophytes or dinoflagellates at intermediate depths (<70 m); and green and blue light favours

chrysophyte diatom symbionts in deeper waters (<130 m; e.g. Leutenegger 1984). Although these symbionts leave no trace, their light requirements are widely thought to provide a primary control on larger foraminiferid test shape and chamber arrangement, which may be expected to optimize the surface area needed for photosynthesis (Haynes 1965).

Figure 2 shows some typical forms of larger foraminiferid tests generated by modelling (Brasier 1986). Each model is of unit volume and provides evidence on maximum cross-sectional area (the maximum surface for illumination from above). As can be seen, relatively globular to rounded fusiform tests of alveolinid miliolines (Fig. 2a & b), fabulariid miliolines with involute chambers (Fig. 2c) and conical tests of rhyphydioninid miliolines (Fig. 2e) may have low surface areas relative to volume when compared with the form of ancestral milioline *Quinqueloculina* (Fig. 2d). Given that the relative surface area decreases in relation to volume as the test size increases, these contrasts would be multiplied in many real examples. The model predicts that forms with such lowered relative surface area would be best adapted to shallow water carbonate substrates where white carbonate sands bring about 'back-lighting' and UV light levels are high. This is broadly consistent with evidence for the occurrence of fossil alveolines, fabulariids and rhyphydioninids in shallow water 'miliolid' carbonate facies.

The more-flattened discoidal tests of soritoid miliolines (Fig. 2h & g) greatly increase the relative surface area, which not only allows them to attach to vegetation but permits a wider depth range, close to the limits of tolerance in their endosymbionts (typically *c.* 40 m). In larger rotaliids with discoidal tests the translucent test and diatom symbionts permit a greater depth

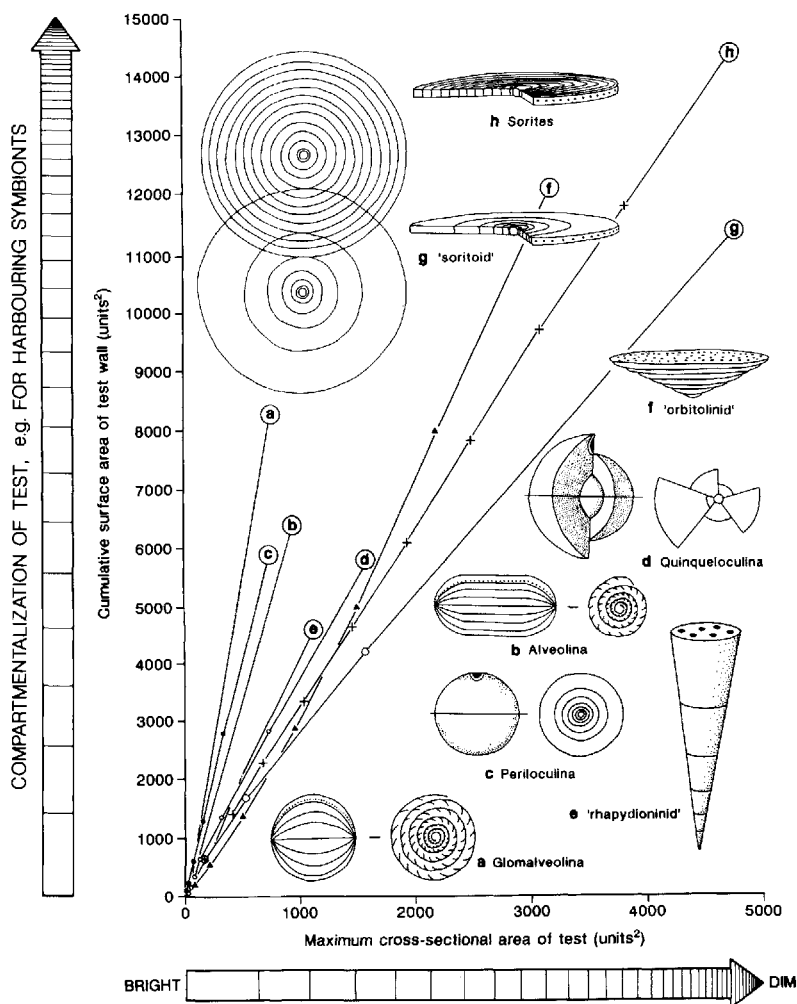


Fig. 2. Larger foraminiferid test architecture, expressed in terms of surface area. Models of unit volume after Brasier (1986) are used to compute the maximum cross-sectional area (related to illumination) and cumulative surface area (related to compartmentalization). Forms with photosymbionts living in dim light tend towards an increase in their surface area-to-volume ratio.

range (< 130 m; Leutenegger 1984). As might be expected, there is a clear relationship between depth of habitat and flattening of the test (see Hallock 1988b, c).

Another feature typical of larger foraminifera is a tendency to increase the cumulative surface area of the test wall (Fig. 2). Such a trend is further enhanced by compartmentalization of the chambers into small chamberlets (not modelled here). It has been suggested that this structural modification may encourage the farming of endosymbionts (Hottinger 1982). Not all living 'larger' foraminifera have been

shown to contain endosymbionts, however. In some cases this could be due to lack of study, but others dwell far below the photic zone (e.g. *Discospirina*), and may even have opaque tests (e.g. *Cyclammina*, which is agglutinated with an iron oxide cement). Possible explanations for this paradox involve the loss of photosymbionts through progressive migration into deeper waters or the presence of moneran symbionts as yet unrecognized.

Symbionts are also known from smaller benthic foraminifera. For example, *Elphidium* spp. and *Haynesina germanica* living in brackish

marshes and embayments often have green cytoplasm containing abundant symbiotic chlorophytes or diatoms (Lee & Anderson 1991) but the relationship does not appear to be obligate. Many simple miliolines living in tropical lagoons may also have green cytoplasm, but it is not yet clear whether these are symbionts or ingested food. In Fig. 1 it is suggested that facultative photosymbiosis has appeared in simple septate forms, with the relationship becoming more interdependent and obligate as more advanced forms of test architecture are reached. Cytological and geochemical data are needed to test this hypothesis (see below).

Quantitative features which deserve to be more thoroughly studied in time and space include the following.

1. **Maximum diameter of the test.** A large test size is characteristic of symbiont-bearing forms (Table 2) and the largest examples were among the world's largest cells, approaching 150 μm in diameter (e.g. *Nummulites millecaput*, middle Eocene; *Lepidocyclina gigas*, late Oligocene). These giant cells arguably provide the most spectacular examples of 'K-strategy' known from the fossil record (Hottinger 1982) and a progressive increase in cell size can be traced in most fossil lineages (Brasier 1986).
This increase in cell size brings with it major problems of internal communication, discussed below. Despite its obvious importance to community energetics, there is remarkably little documentation of foraminiferal test size in relation to environment. Since it is potentially one of the most available of all fossil biometrics, the dynamics deserves to be analysed more thoroughly.
2. **Test dimorphism.** The largest fossil forms exhibit great dimorphism between the sexual and asexual generations, with those produced sexually (the microspheric generation) generally reaching to greatest size (Blondeau 1972; Schaub 1981; Brasier & Green 1993). Much more needs to be known about the dynamics of such dimorphism. How does it vary in abundance and total biomass between highly oligotrophic and mesotrophic habitats? And how did this sexual strategy respond to stasis and change through time?
3. **Surface area:volume ratio.** As mentioned above, this increases directly with water depth and is inversely correlated with the degree of water agitation (Hallock *et al.*

1991). It also tends to increase with maximum test diameter, for there is an obvious need to maintain an adequate respiratory surface when there is only simple gaseous diffusion. Relative surface area appears to be one of three major determinants of test architecture in larger foraminifera, the others being substrate conditions and lines of communication (Brasier 1986).

A simple metric which acts as a proxy for relative surface area, and is often used on fossils in thin section, is the ratio of maximum:minimum cross-sectional diameter of the test (D/T; Fig. 4; e.g. Hottinger 1960; Blondeau 1972).

4. **Lines of communication within the test.**

Here the aim has been to compare the energetics of cytoplasmic pathways through the organism by means of simple geometry. Given a single-celled organization, increasing cell size, and a complex cytological metabolism, Brasier (1982*a, b*, 1984*a, b*, 1986) examined whether certain foraminifera minimize the energy expended on cytoplasmic streaming by streamlining their internal test architecture.

Geometrical models of foraminiferid tests were generated and the shortest line of communication between two adjacent foramina was computed for each chamber in each model. Two metrics were then used to compare the tests: MinLOC (the cumulative, minimum line of communication from the back of the proloculus to the most proximal aperture in the final chamber, standardized to test volume) and MaxLOC (the maximum line of communication across each chamber, between an aperture and the inner test wall, also standardized; Brasier 1982*a*, 1986). Another metric, the Parsimony or PI index (Brasier 1982*a*) provides a rough estimate of the relative parsimony of cytoplasmic pathways in fossil tests. This index allots a point score for various features of the aperture, chamber shape, and growth mode, which are then totalled. Long lines of communication have a PI of 3 (as in primitive foraminifera such as *Bathysiphon*), approaching a score of 10 as the architecture becomes more parsimonious, as in larger foraminifera.

Figure 1 gives the MinLOC for a variety of architectural forms, standardized relative to an archetypal evolute planispiral test (Fig. 1*b*). As can be seen, the lines of communication within the test become

shorter relative to test volume as more advanced architectures are reached. This shortening is brought about by changes in growth plan (e.g. tighter coiling), chamber shape (more flattened), apertural position (more umbilical) and apertural number. Multiple apertures provide an important means of optimizing shorter lines of communication, especially in flattened chambers.

These metrics provide clues to the metabolism of larger foraminifera, since all show MinLOC and MaxLOC values approaching the minimum for a given chamber and test shape. The MinLOC hypothesis of Brasier (1982*b*) suggested that this minimized the expenditure of energy on movement of symbionts through the test, e.g. in relation to diurnal changes in light. Theoretically, this might be taken to imply that more biomass has been reserved for reproduction and less 'wasted' upon respiration, though this has yet to be measured on living material. What is harder to explain is why larger foraminifera 'without symbionts' also show short MinLOC values (Brasier 1984*a*). Unfortunately, such living examples have been little studied and the presence of unrecognized moneran symbionts, such as cyanobacteria, cannot yet be discounted.

Using a combination of criteria, such as outlined above, it is possible to trace, provisionally, the multiple, iterative evolution and extinction of symbiotic associations in foraminiferal lineages, from the mid Devonian onwards (see below; Hottinger 1982; Brasier 1987).

Planktonic foraminifera These are much smaller than their benthic relatives, with tests variably adapted to maintain buoyancy in the water column (Brasier 1986). Planktonics inhabiting the upper 100 m of the water column at low to intermediate latitudes include several species which supplement their zooplankton diet with dinoflagellate or chrysophyte symbionts (Hemleben *et al.* 1988; Lee & Anderson 1991). Forms such as *Globigerinoides ruber* and *Orbulina universa*, with globular, spinose chambers and supplementary sutural apertures, contain dinoflagellate symbionts (e.g. *Gymnodinium beii*) and are well adapted to a warmer, oligotrophic habitat, as are their symbionts. Forms with facultative chrysophycophyte symbionts, such as *Neoglobobadrina dutertrei*, lack such spines and supplementary apertures. Those that are barren of symbionts may either be spinose (e.g.

Globigerina bulloides) or lack spines (e.g. *N. pachyderma*). Supplementary apertures are not present in such forms. Therefore, as discussed by Brasier (this volume), nutrient-rich waters tend to be dominated by facultative or symbiont-free forms adapted to cooler, high latitude waters.

Endosymbionts of planktonic foraminifera are moved outside the test each day to reside in the frothy ectoplasm on spines (Hemleben *et al.* 1988). The presence of spines may therefore be related to the maintenance of endosymbionts. Just as important for this diurnal migration are the apertures, which tend to be multiple and, like the foramina, placed to minimize lines of communication. Not surprisingly, then, it is the forms adapted to oligotrophic regimes, such as *Orbulina universa*, which approach minimal MinLOC and MaxLOC values (Fig. 1*r*; e.g. Brasier 1986). Again, this suggests less 'wastage' of the biomass on respiration and more reserved for reproduction, but the hypothesis has yet to be tested on living material.

Corals and archaeocyathan sponges. Modern scleractinian corals with zooxanthellae also have distinctive skeletal morphology that reflects their symbiotic mode of life (Table 3). These tend to be multiserial, colonial forms with small corallites and high (e.g. coenosteoid) tissue integration. Azooxanthellate forms are mainly uniserial, solitary, and only rarely colonial, with larger corallites and low (e.g. phaceloid to cerioid) tissue integration (Coates & Jackson 1987). Using such evidence these authors have inferred the presence of zooxanthellae in tabulate faunas of the Silurian and Devonian, and in scleractinian corals from the Jurassic onwards. According to their criteria rugose corals did not contain zooxanthellae.

Tissue integration between corallites might therefore seem to provide a useful index for the degree of 'networking' between individuals, and a rough guide to the presence of symbionts. But while this integration is consistent with the interdependence of invertebrate-protistan photosymbiosis it has not yet been explained in functional terms. Any extension of this approach to extinct fossil groups is therefore tenuous. In the early Cambrian, for example, where the main reef builders were archaeocyathan sponges, a strongly expressed individuality is suggested by aggressive tissue interactions between individuals that grew close together (Brasier 1976). This, and the low to intermediate levels of structural integration found within colonial archaeocyathans, have been taken to imply the probable absence of obligate symbiosis between archaeocyathans and protists (Wood *et al.*

Table 3. Morphological comparison (generalized) between zooxanthellate and azooxanthellate corals (based on Coates & Jackson 1987).

	Zooxanthellate	Azooxanthellate
Growth form	Multiserial, colonial	Uniserial, mostly solitary, few colonial
Corallite size (mm)	Median 1.8–3.3	7.3–8.0
Tissue integration	High, astreoid, aphroid, coenosteoid, thamnasterioid, meandroid	Low, cerioid or phaceloid

1992). But this verdict is necessarily very uncertain, and their conspicuously tropical, biothermal carbonate habitat must, for the present, keep the question open (e.g. Rowland & Gangloff 1988).

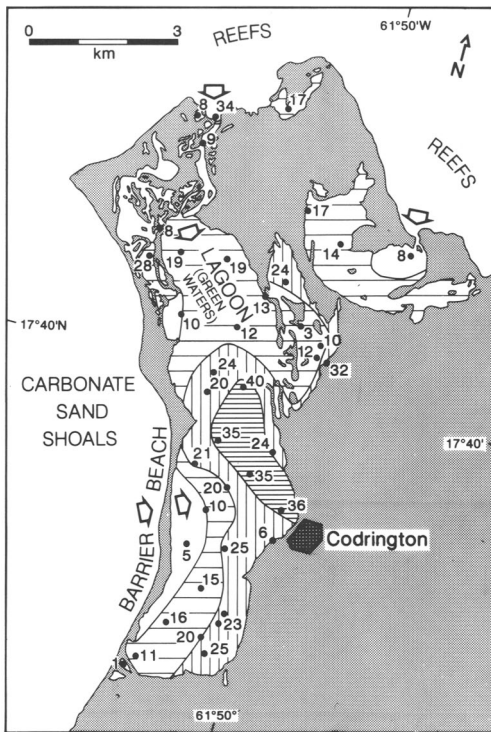


Fig. 3. Incidence of foraminiferal tests damaged by microboring and micritization, as a percentage of the total population in Codrington Lagoon, Barbuda (from Brasier 1972). The arrows show the influx and seepage of normal marine ('blue') waters into the mesotrophic ('green water'), hypersaline lagoon.

Bioerosion and lithology Borings and microborings into shells and reefal frameworks (e.g. by *Cliona* sponges, bivalves, regular echinoids) tend to increase under the influence of greater

pollution, nutrient supply and oxygen deficiency (Hallock & Schlager 1986). Figure 3 shows such an example in the mesotrophic, hypersaline lagoons of Barbuda, Lesser Antilles (Brasier 1972). Here, the percentage of microbored and micritized foraminiferid tests increases markedly away from marine influence and close to the only settlement, Codrington. The maxima here show little relationship with depth or salinity but are positively related to bimodal grain size, which probably reflects the influence of seagrass on the substrate (Brasier 1972, fig. 11). Hallock & Schlager (1986) suggested that such bioerosion may ultimately threaten the stability of reefal ecosystems through a fall in the rate of carbonate accumulation. Hottinger (1987), however, observed that it may be the fall in carbonate (e.g. foraminiferal, coral) production that suppresses carbonate accumulation when nutrient supply is increased.

According to Hallock (1988a), a range of criteria can be used to distinguish carbonates developed in such mesotrophic conditions from those formed under oligotrophic conditions (see Table 4). Although intense boring of carbonate substrates in the fossil record could be taken to indicate relative eutrophication (e.g. Kershaw 1993), or the potential effects of slower sedimentation rate (e.g. Hallock 1988a), it is clear that temperature-related oxygen-deficiency, depth and light limitation on bioerosion must also be considered (e.g. Vogel *et al.* 1987). In the case of corals, almost any factor that slows down their growth (including attack by predators such as *Acanthaster*) could lead to increased bioerosion. The problems of subsurface bioerosion and chemoerosion, and of subsequent reworking, are also difficult to assess. These stimulating ideas therefore require more quantitative documentation before they can be applied usefully to the fossil record.

Carbon isotopes In well-preserved carbonate skeletons, carbon isotopes can provide clues about the nature of the symbiotic relationship between host and symbiont. Two stable isotopes of carbon (^{12}C and ^{13}C) are incorporated by the

Table 4. Criteria for distinguishing carbonates developed under oligotrophic and mesotrophic nutrient regimes (adapted from data in Hallock 1988a)

	Oligotrophic	Mesotrophic
1% light level (tropics)	c. 130 m	c. 50 m
Reefs	Framestones	Bindstones, bafflestones, mudmounds
Larger foraminifera	Rotaliids flourish	Archaiads and soritids flourish
Coralline algae	Less important	May flourish
Halimeda	Plates preserved	Aragonite mud
Fleshy algae	Inconspicuous	Abundant
Seagrasses	Present	May flourish
Microbes, bacteria	Inconspicuous	Flourish, mats may develop
Micritized grains	Inconspicuous	Common
Bioeroders	Inconspicuous	Abundant
Carbonate sediments	Skeletal sands	Detrital sands, muds
Examples	Pacific atoll reefs	Florida Keys, backreef lagoons

Table 5. Comparison between larger foraminifera: archaiads and nummulitids (based on data in Brasier & Green 1993)

	Larger archaiads	Larger rotaliines
Symbionts	Chlorophytes, dinoflagellates	Chrysophytes
$\delta^{13}\text{C}$ test	Close to sea water, more negative with growth Locally very variable	Depleted in ^{13}C , more positive with growth Less local variation?
Ecology	More mesotrophic	More oligotrophic
Distribution	Thrive in Caribbean	Thrive in open Indo-Pacific

organism into skeletal carbonate and the ratio between these (expressed as ‰ $\delta^{13}\text{C}$, relative to the PDB standard; see Williams *et al.* 1989) can be compared with $\delta^{13}\text{C}$ occurring in standard marine water, or with other skeletal carbonate.

In larger foraminifera considerable ^{13}C and ^{18}O depletion is known to occur with increased light intensity in larger rotaliine foraminifera such as *Heterostegina* and *Amphistegina* (Williams *et al.* 1981; Zimmerman *et al.* 1983), but not in larger miliolines, such as *Archaias* and *Amphisorus* (Murray 1991; ter Kuile 1991). In some larger miliolines, the host appears to derive carbon for skeletal material not from the symbiont or food matter but from ambient sea water (e.g. ter Kuile 1991). This lesser nutritional role of the symbionts is perhaps related to less stable, more nutrient-enriched habitats (Hallock 1988b, c; Brasier & Green 1993).

The pattern is further complicated by growth-related vital effects. For example, Brasier & Green (1993) contrast the characteristics of archaiad miliolines and nummulitid rotaliines, as shown in Table 5. Today archaiads thrive in Caribbean seagrass habitats where nitrate fixation and nutrient regeneration can be high (Hallock & Peebles 1993); endosymbionts may even obtain some of their nutrients from the seagrass blades (Hallock *et al.* 1991). Such larger miliolines may also differ from larger rotaliines in obtaining more of their energy requirements

from pseudopodial feeding on algae (Lee & Anderson 1991). Experiments tend to confirm the more obligate nature of symbiosis in nummulitid rotaliines, since these grow much faster than miliolines when inorganic phosphate and nitrate are added to the cultures (ter Kuile *et al.* 1987). Today rotaliines thrive in more oligotrophic Indo-Pacific settings (Hallock 1988b, c). It follows that the contrast between archaiad-dominated Caribbean assemblages and rotaliine-dominated Indo-Pacific assemblages may well be explained by these different nutrient regimes, and by contrasting nutrient histories in the two areas (Hallock 1988c; Brasier & Green 1993). The smaller Caribbean Sea is ringed with major land masses and river systems supplying nutrient-rich surface waters across much of the region, whereas the larger Indo-Pacific Ocean provides many refugia in the form of atolls, where the oligotrophic state of mid-ocean surface waters can be exploited (e.g. Hallock *et al.* 1988).

Isotopic data on planktonic foraminifera are reviewed in an accompanying article (Brasier this volume). Little evidence exists to show that symbionts contribute carbon compounds to their hosts but foraminiferal growth rate is clearly enhanced and $\delta^{13}\text{C}$ of test calcite is made more positive under exposure to light (Hemleben *et al.* 1988).

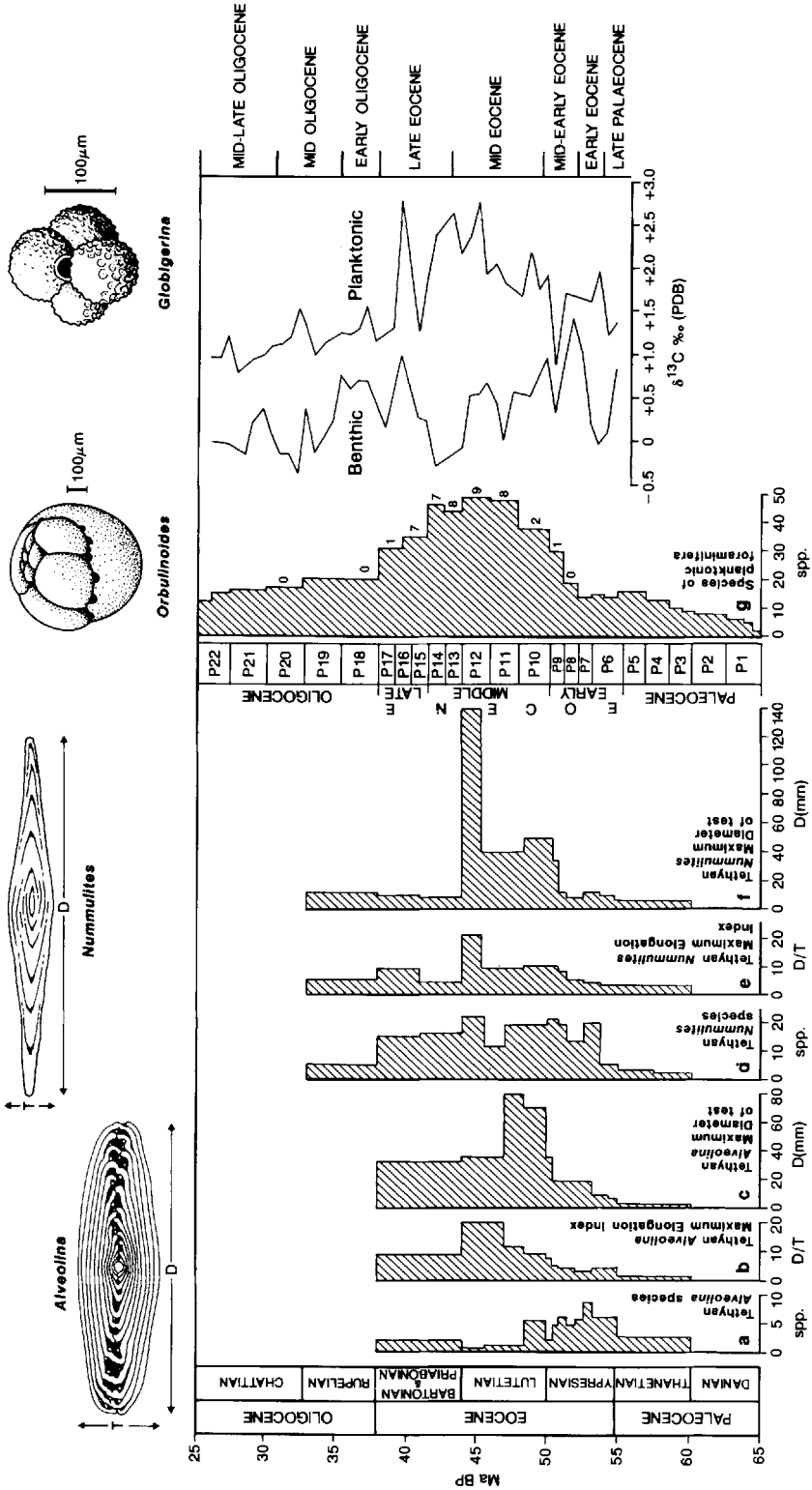


Fig. 4. Diversity and architectural changes in larger foraminifera (*Alveolina*, *Nummulites*) and planktonic foraminifera through the Palaeocene. Numbers beside the latter refer to planktonic species with supplementary sutural apertures. From sources in Brasier (1987). Carbon isotopic data from benthic foraminifera (left-hand side) and planktonic foraminifera (right-hand side) are from DSDP sites 277, 279 and 281 in the southwest Pacific, south of New Zealand, after Shackleton & Kennett (1975).

The Eocene event

This case history illustrates the fate of lineages that survived mass extinction across the Cretaceous–Tertiary boundary, when taxa adapted to oligotrophic nutrient regimes were largely exterminated (especially larger and planktonic foraminifera, rudistid bivalves and hermatypic corals; Hottinger 1987; Rosen & Tumsek 1989). At first the survivors appear to have been less specialized r-strategists without obligate symbiosis and it took c. 8–10 Ma for this adaptive zone to re-establish in Zone P4 of the Palaeocene, in the form of larger benthic alveolinids, nummulites, orbitolinids and some globigerinaceans (Fig. 4; Hottinger 1982; Hallock *et al.* 1991). Oligotrophic indicators, eutrophic indicators and geochemical and palaeoceanographic data are considered separately below.

Oligotrophic indicators

Alveolina Alveolinids are milioline larger foraminifera which today harbour diatoms in obligate symbiosis (Lee & Anderson 1991) and tend to thrive in unvegetated carbonate sand shoals (e.g. *Borelis*; Brasier 1974; *Alveolinella*; Severin & Lipps 1989). Their fusiform morphology elegantly combines shorter lines of communication with maximal surface area for photosynthesis (Brasier 1984*b*, 1986). Diversification in the late Paleocene–early Eocene was accompanied by a trend towards greatly increased maximum diameter and towards greater elongation of the test (Fig. 4; D/T; Hottinger 1960). This implies an increase in relative surface area (Brasier 1984*b*) consistent with occupation of deeper, clear water in highly oligotrophic conditions.

Decline in diversity and maximum size seems to have begun in the mid Lutetian (c. Zones P11–12), followed by a sharp loss of elongate forms after the Lutetian (c. Zone P13). No true Alveolinidae survived beyond the Eocene; later and living forms are homoeomorphs that evolved iteratively.

Nummulites. As mentioned above, Nummulitidae are rotaliine larger foraminifera which are obligate hosts to diatom symbionts (Lee & Anderson 1991). Today they prefer deeper, fore-reef substrates. In Eocene times species of *Nummulites* thrived widely on carbonate and siliclastic ramps from the Mediterranean to Indo-Pacific region, reaching a peak of diversity between the Ypresian and Lutetian (Fig. 4; Blondeau 1972; see also Hallock *et al.* 1991). A high diversity of large forms was certainly

present in Zone P12, when giant taxa with meandrine sutures thrived (e.g. *N. gizehensis* and *N. millecaput*). Maximum elongation at this time (Fig. 4) also suggests highly oligotrophic conditions. A large overturn of *Nummulites* in Zone P13 was followed by extinction of related *Assilina* spp. in Zone P14 (Hallock *et al.* 1991). Nummulite assemblages of the late Eocene are relatively impoverished and comprise small species with simple striate or reticulate sutures (Fig. 4; Blondeau 1972; Schaub 1981).

Planktonic foraminifera This same interval was also climactic for low latitude planktonic foraminifera (Fig. 4). Although total species diversity peaked in Zones P11–12, warm water indices actually peaked earlier, in Zone P8 (Hallock *et al.* 1991). It appears, therefore, that the middle Eocene peak largely reflects a secondary diversification of temperate assemblages.

It is less clear which of these may have been symbiont-bearing oligotrophs. Muricate forms such as *Morozovella* and *Acarinina* both appear to have been low latitude surface-dwellers (Corfield & Shackleton 1988). *Morozovella* sp. appeared in Zone P3 and reached a peak of diversity in Zones P6–P8, at a time of falling ocean productivity, then suffered extinction in Zone P11 (Corfield & Shackleton 1988; Hallock *et al.* 1991). There is little in their keeled morphology to suggest the presence of symbionts, nor do the stubby muricate spines resemble those found in modern forms. Muricate *Acarinina* spp. peaked in Zones P7–P9 and suffered a major decline after Zone P12. Their evolutionary pattern is close to that of alveolines and nummulitids (Hallock *et al.* 1991) and they might have contained symbionts.

It is suggested here that forms bearing supplementary sutural apertures (e.g. *Orbulinoides*) may have been symbiont-bearing oligotrophs occupying the deepest layers of the euphotic zone, much like living *Orbulina*. These 'orbuliniforms' reached a maximum in Zone P12, declined modestly in Zone P13 and abruptly in Zone P16, leading to extinction at the Eocene–Oligocene boundary (Fig. 4).

Eutrophic indicators

Diatoms and dinoflagellates Compared with the above, the data base for diatoms is less reliable, owing to a poor fossil record and fewer specialists. Baldauf (1992) highlights the importance of a 30% increase in diatom diversity some 43–41 Ma BP (nannoplankton Zone NP16 to lower NP17). Few diatom taxa became extinct at

this time and the increase has been related to greater floral provincialism. The timing of this expansion in phytoplankton adapted to relatively eutrophic conditions also coincided broadly with an expansion of biosiliceous sedimentation around the Pacific rim (Barron & Baldauf 1989; Baldauf 1992), and with the decline in foraminifera adapted to oligotrophic conditions, as discussed above.

Maximum diversity in dinoflagellate cysts occurs in the late Eocene (e.g. Bujak & Williams 1979). Although this appears consistent with more meso- to eutrophic conditions, more ecological data on the taxa themselves are needed to confirm this.

Isotope geochemistry and palaeoceanography

Data are available for $\delta^{13}\text{C}$ gradients through the water column in the Palaeocene–Oligocene interval (e.g. Fig. 4). Maximal gradients occurred during the late Palaeocene (Corfield & Shackleton 1988), best interpreted as indicating sluggish ocean circulation. This gradient declined to smaller values across the early to middle Eocene boundary interval and expanded again to a second maximum across the middle to late Eocene boundary interval.

Note the relative increase in benthic skeletal $\delta^{13}\text{C}$ in the late Eocene (Fig. 4). There was also a decline in the difference between benthic and planktonic $\delta^{13}\text{C}$ values. Both may be explained by increased rates of bottom-water circulation, broadly contemporaneous with high latitude cooling, increased rates of bottom-water formation and the advent of the psychrosphere (cool bottom water) biota, beginning as early as Zone P8 (e.g. Hallock *et al.* 1991). As mentioned above, an expansion of biosiliceous sediments also developed in response to coastal upwelling settings around the Pacific rim during the late middle Eocene (Zones P13 and P14; Barron & Baldauf 1989).

Summary of Eocene event

As summarized here, it is now widely accepted that high latitude cooling across the late middle to late Eocene interval increased the rate of oceanic circulation, raising nutrient resource in surface waters directly by upwelling, and perhaps indirectly by the reduced uptake of nutrients in cooler waters (e.g. Hallock *et al.* 1991). Protists adapted to more eutrophic conditions (e.g. diatoms and some dinoflagellates) diversified in response to increased provinciality brought about by greater latitudinal temperature gradients.

It appears that ecosystems with high levels of mutual interdependence between species (e.g. adapted to oligotrophic nutrient regimes) experienced an increase in extinction rate: (1) the shallowest benthic group (alveolinids) showed the first signs of decline, from about Zone P10 onwards; (2) the decline in giant, complex *Nummulites* spp. was very marked across Zones P12–P13, although the diversity drop was less sharp; (3) the decline in planktonic foraminifera was contemporaneous but relatively gradual; extinctions began to exceed originations in Zones P13 and P14, with the sharpest fall in orbuliniforms in Zone P16.

The early Oligocene appears to have been a cooler interval with a relatively well-circulated ocean and reduced oligotrophic-adapted communities (Hallock *et al.* 1991).

Towards a wider perspective

It seems likely that the pattern of evolution and extinction so clearly portrayed in the Eocene fossil record is not an isolated example. The larger foraminiferid fossil record shows comparable turnovers at some nine levels, and changes in nutrient flux may have been involved (e.g. Hallock 1982, 1985; Brasier 1987). Four of these turnovers are clearly associated with the spread of anoxic, nutrient-enriched waters on to shallow shelves (Frasnian/Fammenian, Triassic/Jurassic, Toarcian and Cenomanian/Turonian). Two are associated with the spread of upwelling-related diatomites and radiolarites (mid Eocene to Eocene/Oligocene boundary; early/mid Miocene). Even the K–T boundary event, with its meteorite impact scenario, must also have involved massive increases in the flux of nutrient into surface waters (Hallock 1988a).

Of these, the evolution of fusulinid larger foraminifera in the Permian is important because it yields classic examples of gradualistic evolution (e.g. Ozawa 1975) in a group which may have to be inferred to have contained photosymbionts on the basis of architecture (large, fusiform, short MinLOC, modified outer walls) and facies association (tropical carbonate sands). Their spectacular decline should be considered in the light of known evidence for massive phosphorite deposition during the middle to late Permian.

The mid Miocene event provides another case history, in which the size and diversity of Caribbean and Mediterranean larger foraminifera declines sharply during the Burdigalian (Brasier 1987), broadly coincident with nutrient-rich upwellings over the Florida Banks and the deposition of diatomite–phosphorite depos-

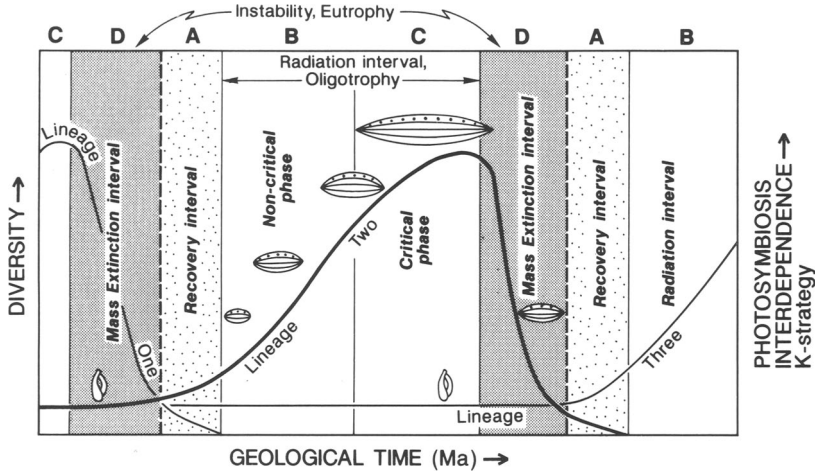


Fig. 5. A model for the evolution of organisms adapted to oligotrophic conditions (e.g. alveolinid foraminifera). The history of development towards photosymbiosis, interdependence and K-strategy is suggested for three separate lineages, through time. A–D refer to steps in evolution (see text for details).

its along the western Pacific seaboard (the 'Monterey Event', e.g. Compton *et al.* 1990).

Towards a model for larger foraminiferid evolution

The model discussed here (Fig. 5) is one in which oligotrophic ecosystems become progressively more 'self-organized' with time. A useful analogue can be found, for example, in a pile of sand in which each grain stands for a species and its ecological niche (Bak *et al.* 1994). The contact between grains, and their form of packing, resembles the interactions between species; the addition of more grains simulates the evolution of new species, with a corresponding increase in diversity. As the pile of sand rises and steepens the stability of each grain is more precariously linked to that of its neighbours. Eventually, a critical state is reached in which even a minor perturbation may cause a cascade of the sand pile. This serves as an analogue for an extinction event.

In the model outlined below examples of the ancestral stock are provided by simple miliolines of the Quinqueloculinidae. At present these thrive in shallow, tropical, mesotrophic conditions, associated with vegetated bays and lagoons (Brasier 1975*b*, Murray 1991), and this life habit is clearly traceable back through the Mesozoic. They are characterized by relatively long MinLOC and low PI values (Brasier 1982*a, b*). From the Cretaceous to Neogene, quinqueloculinid ancestors have evolved, iteratively, into homoemorphic larger foraminiferids 'lumped' together in the Alveolinidae (Loeblich & Tappan 1988). They are characterized by

relatively short MinLOC and high PI values (Brasier 1982*a, b*, 1984*b*) and, as discussed above, appear to have been adapted to sand shoal facies that developed in rather clear, tropical waters, i.e. consistent with oligotrophic conditions. These alveolinids typically suffered extinction during periods of major biological turnover. The main steps in the model (Fig. 5) are outlined below.

1. **Recovery interval.** Conditions begin to normalize after some interval of ecosystem collapse and recovery of the biota begins. Simple milioline survivors (e.g. *Quinqueloculina* spp.) flourish on shallow carbonate platforms, especially in the absence of competition from larger miliolines.
2. **Radiation interval: non-critical phase.** Benthic communities develop gradually, over millions of years, towards greater interdependence. Symbiosis, asexual cloning and greater colonial integration may all be associated with this trend. Small, relatively globular alveolinids (e.g. *Glom-alveolina* spp., *Borelis melo*, *B. pulchra*) evolve from simple milioline *Quinqueloculina*. Benthic calcareous algae and grazers begin to replace fleshy algae and suspension feeders. Symbiosis in this phase may have been mainly facultative so that environmental perturbations did not have a catastrophic impact.
3. **Radiation interval: critical phase.** Development towards greater interdependence and symbiosis continues. Large, elongate alveolinids appear (e.g. *Alveolina* spp., *Alveolinella* spp.) and the diversity of larger

foraminiferids continues to rise. Simpler forms such as *Quinqueloculina* continue to thrive, however, notably in more marginal habitats. Symbiosis in this phase may become more obligate. Some lineages advance markedly towards the K-strategy end of the spectrum, to the point where interdependence is high and their recovery from a physical perturbation becomes difficult.

4. **Mass extinction interval.** By this time, vulnerability of the biota is such that only a relatively minor perturbation may cause the collapse of specialized and interactive ecosystems, through the loss of a few key members (e.g. Plotnick & McKinney 1993; Bak *et al.* 1994). Large elongate alveolinids suffer preferential extinction during such intervals. Perturbations that could raise nutrient levels and bring about extinctions are listed in Table 2 of Brasier (this volume; see also Table 1 herein). In the model, forms adapted to more eutrophic conditions (e.g. diatoms, suspension feeders, planktivores, nektonic carnivores, grazers, fleshy benthic algae) thrive and diversify at this time.

Such extinctions left the larger foraminiferid adaptive zone vacant, to be filled at a later date by survivors with a less specialized and less interdependent life habit (such as *Quinqueloculina* spp.). The cycle is therefore poised to begin again.

Conclusion

Much interest has focused on the role of nutrients in evolution over the last few decades. These ideas now need to be tested objectively.

1. Factors that lead to lower nutrients in surface waters (Table 3 in Brasier this volume), and food availability through the water column, appear to be favourable to greater integration between organisms, as exemplified by endosymbiotic relationships between invertebrates and autotrophic protists. This raises questions about the relationship between the evolution of highly integrated cells, organs, organisms and communities and their associated levels of nutrient resource, that deserve to be tested in the fossil record.
2. The degree of integration can be quantitatively modelled in certain fossil skeletons, such as larger foraminifera (Brasier 1986). These are K-strategists that are mostly

known to contain autotrophic endosymbionts, whose architecture has evolved towards tests with minimal energetic pathways. The modulation of surface area in relation to water depth and turbulence is consistent with the illumination of these photosymbionts. A trend towards minimal energetic pathways is likewise inferred for planktonic foraminifera with photosymbionts (e.g. *Globigerinoides*, *Orbulina*). Furthermore, the increased 'networking' seen between hermatypic corallites shows a direct correlation with the presence of photosymbionts (e.g. astreoid and coenosteoid forms, Table 3; Coates & Jackson 1987). At present, these relationships between integration and photosymbiosis are little understood in terms of metabolism.

3. The value of bioerosion as an index of nutrient availability in the fossil record (Table 4; Hallock 1988a) is questionable. The potential effects of slower sedimentation rate, temperature-related oxygen deficiency, depth and light limitation must also be considered. The degree of subsurface bioerosion and chemoerosion, and of subsequent reworking, are also difficult to assess.
4. Stable isotopic data may provide indications of symbiont dependence in some groups (larger rotaline foraminifera) but not in others (larger milioline foraminifera, planktonic foraminifera). This dichotomy conceivably reflects differing balances in the source of carbon for biomineralization: e.g. largely from the symbionts in the former but from sea water in the latter.
5. Medium-term evolutionary cycles in the development and extinction of 'symbiotic architecture' in larger and planktonic foraminifera may have potential as a barometer of nutrient history in the oceans. Nine intervals of decline coincide with major intervals of biotic turnover (e.g. Brasier 1987), most of which are associated with indicators for increased eutrophication on marine platforms. This is most clearly documented for events in the Eocene, where metrics obtained from foraminifera indicate an abrupt decline in symbiotic associations across Zones P10-P16 (Fig. 4).
6. Much more needs to be learned about the impact of biological innovations upon nutrient cycles, particularly in the remote past. Table 6 provides a summary of some of the turning points.

Table 6. Some turning points in evolutionary biology relevant to nutrient and carbon cycles of the oceans.

Early Proterozoic: evolution of nitrogen-fixation in cyanobacteria, important in more oxidative, ammonia-free atmosphere; prevented N-limitation of shallow/surface waters.

Evolution of eukaryotes, by serial endosymbiosis (Margulis 1981), related to oxygen build-up and perhaps to oligotrophy.

Mid Proterozoic: evolution of denitrification, encouraged build-up of atmospheric oxygen. Ditto for evolution of sulphate-reduction (Lambert & Donnelly 1992).

Evolution of eukaryote plankton, increased export production of nutrients and C to deeper-sea sediments.

Late Proterozoic: giant acritarch phytoplankton (Knoll & Walter 1992), raised potential for nutrient and C burial in deeper sediments. Major glacial epoch (Knoll & Walter 1992) possibly accelerated nutrient flow.

Late Vendian: extinction of large acritarchs (Knoll & Walter 1992) meant potentially reduced export of nutrients and C to sediment; only very small forms survived (Brasier 1992a).

Evolution of multicellular metazoan heterotrophs, potentially improved nutrient and carbon regeneration (Brasier 1992a).

Cambrian: extensive bioturbation disturbed the balance of nitrate fixation encouraging more nitrate limitation, and hence potential for more phosphorus availability.

Deeper burrowing encouraged recycling of nutrients and C to sediment surface and overlying waters (Brasier 1992a).

Phosphatic, calcareous and siliceous skeletons had potential to remove nutrients, especially from nutrient-enriched waters (Brasier 1992a, b).

Tubular skeletons removed phosphate diagenetically from pore waters (Brasier 1990). Zooplankton grazing of phytoplankton reduced the potential for eutrophic-adapted algal blooms.

Zooplankton export of C, P, N, in faecal pellets, to

deeper seafloor implies greater potential for carbon burial and nutrient stratification (Brasier 1992a)

Devonian: land plants bring about higher nutrient input to deep sea (Calef & Bambach 1973).

Frasnian–Famennian extinction of acritarchs, lowers phytoplankton diversity through late Palaeozoic (Tappan 1968).

Carboniferous: coal swamp forests bring about massive carbon burial on land, with potential impact on atmosphere and climate.

P–T boundary: prolonged mass extinction, ending in rapidly falling productivity and/or lower carbon burial (Baud *et al.* 1989).

Triassic: dinoflagellates and coccolithophorids first appear, raising potential for C and nutrient burial in slope and ocean floor sediments.

Dinoflagellate–scleractinian coral symbiosis begins (Stanley 1981).

Jurassic: Coccolithic–globigerinid chalks notably accelerate the export of C and nutrients from surface to deep ocean (Kennett 1982).

Cretaceous: diatoms further accelerate the export of C and nutrients, even at high latitudes. Diatom–rotaliid and diatom–alveolinid foraminiferid symbiosis begins (Hallock 1988b).

Start of climatic cooling leading to glacial world.

Seagrasses and mangroves encourage mesotrophy in nearshore oligotrophic ecosystems (Brasier 1975).

K–T boundary: mass extinction of phytoplankton briefly lowers surface water productivity and carbonate production. Rapid recovery (Corfield & Shackleton 1988).

Palaeogene: diatoms displace radiolarians in competition for silica nutrients, and diversify at time of global cooling (Brasier 1980).

Neogene: seagrasses expand, potentially displacing oligotrophic by mesotrophic habitats nearshore (Brasier 1975).

Holocene: hominids bring about rapid eutrophication of many shelf seas.

7. A model is put forward (Fig. 5) in which an increasingly interdependent community structure (notably including specialized feeding adaptations such as photosymbiosis) develop under relatively stable, oligotrophic conditions. Organisms adapted to such regimes become increasingly vulnerable to physical perturbations, especially in the critical phase when fluctuations, including increased nutrient availability, may lead to ecosystem collapse. Extinctions then open up vacant adaptive zones, to be filled by survivors having a lower degree of interdependence. Forms adapted to more eutrophic conditions (e.g. diatoms, suspension feeders, planktivores, nektonic carnivores) appear to have thrived and diversified at this time.

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Organisms and the substrate: response and effect

ROLAND GOLDRING

*Postgraduate Research Institute for Sedimentology, University of Reading, Whiteknights,
PO Box 227, Reading RG6 2AB, UK*

Abstract. Benthic organisms are invaluable in the interpretation of ancient environments. The principles of animal behaviour at and below the substrate surface (e.g. encrustation, burrowing, boring, feeding) are well established. Three areas in particular are currently being developed: (1) Ichnofabrics are replacing ichnofacies in facies interpretation. The use of archetypal ichnofacies is abandoned in favour of an integrated approach (including palynology and geochemical analysis), using autecology followed by synecology and synthesis, and ichnofabric analysis; this provides greater resolution; (2) Comparisons of deep-sea studies with ancient bathyal sediments are leading to a better understanding of turbidite facies: the factors involved in the formation of the complex tiering of the pre-event ichnocoenoses and those involved in the colonization of the turbidite. The morphology and ethology of several shallow and deep-water ichnotaxa (e.g. *Zoophycos*, *Paleodictyon*) are still imperfectly understood; (3) The fabric of shell and skeletal concentrations reflects the dynamics of the final depositional environment, and the taphonomic signature, in the main, the environmental conditions under which the shells formed and accumulated. Together, these aspects, and their relative stratigraphic frequency, reflect regional patterns of hydraulics and basin dynamics. Advances in the appreciation of time-averaging should provide renewed interest in research into palaeocommunities.

The stratigraphical distribution of hardgrounds remains an enigma and their potential significance for basin analysis awaits full evaluation. Two groups of hardground are recognized: whether they formed under omission and wave bevelling, or solely under omission.

The substrate can provide a number of roles for organisms. For instance, the surface may permit attachment for an oyster, while for rock-boring bivalves the substrate provides, in addition, a protected situation, and for rapidly burrowing razor clams a favourable environment for rapid movement. For burrowing echinoderms the substrate also provides a food source as well as shelter. The nature of the substrate chiefly affects trophism, attachment and penetration of benthic organisms, though the role of organisms as clasts must also be appreciated. Dead shells, because of their distinctive standardized form accumulate in preferred ways under hydraulic action or leave characteristic impingement marks. The substrate may consist of organic, skeletal, siliceous, calcareous or phosphatic material, it may be primary or exhumed, and may be of a fluid, soft, loose, firm or hard consistency. Most organisms exhibit a degree of tolerance to the physical, chemical and biological limiting factors. These need to be evaluated so that the effects of an organism's actions can be evaluated and applied to environmental and facies interpretation.

Rhoads (1974, 1975), Aller (1982), Rhoads & Boyer (1982), Kidwell & Jablonski (1982)

reviewed the manner in which benthic organisms exert change on the physical and chemical properties of marine sediments. More recently biologists have emphasized the nature of the changes to benthic ecosystems due to bioturbation on all scales (Meadows & Meadows 1991).

This paper reviews recent work on the response of the sedimentological structures and fabrics that are produced by animals and used in environmental and facies interpretation. Conditions in the past are not necessarily represented by those of today and it is necessary to model anaactualistic conditions and to make deductions about extinct taxa.

Organism-sediment effects include:

1. Disruption of primary (hydraulic) sedimentary structures by burrowing and the production of new, biogenic structures (which may, in turn, become modified).
2. Conversion of fine-grained sediment into faecal pellets with hydraulically and chemically different properties. However, they are mostly destroyed by compaction unless frozen during early diagenesis or protected by umbrellar structures. The resulting fabric may then simulate a bioturbated

- mudrock. Pellet morphology varies between benthic and planktonic organisms (Cuomo & Bartholomew 1991) and can be used to define palaeo-oxygenation.
3. Burrowing modifies the geotechnical and geochemical properties of the sediment, including porosity and permeability (Meadows & Meadows 1991). Lined burrows can lead to channelling of fluid flow (Weaver & Schultheiss 1983). There is much scope for further research in this area.
 4. Discharge and resuspension of sediment by burrowers, whence it may be readily transported laterally.
 5. Faecal discharge by suspension feeders and selective feeding by deposit feeders can substantially alter the mass grain-size and its distribution.
 6. Mucus and organic films (e.g. wrinkle patterns on Solnhofen limestones; Seilacher *et al.* 1985), and mats (diatomaceous; Kemp & Baldauf 1993), affect physical properties and penetration of the substrate.
 7. Plants, animals and tube linings projecting upwards from the substrate surface increase sedimentation by reducing flow rate and trapping sediment (e.g. Allen 1965; Brasier 1975; Eckman & Nowell 1984; Gambi *et al.* 1990).
 8. Increased bed roughness due to bioturbation may lead to enhanced erosion.
 9. Changes in community structure may relate to change in the nature of the substrate, due to dead skeletal material,

and taphonomic feedback (Kidwell & Jablonski 1982; Kidwell 1991b).

This paper is divided into two sections. In the first the properties of the substrate in relation to the manner in which organisms cope with it are reviewed. The second section discusses the utilization of bioturbation in marine soft and hard substrates, and of shell concentrations in environment and facies interpretation.

Substrate properties

Substrate consistency

In the absence of bioturbation, primary structures must dominate. If primary structures are unresolvable (even with the use of X-radiography and similar methods) this does not necessarily mean that the sediment is bioturbated. A bioturbated fabric is generally distinct. The consistency of bioturbated sediment may be considered as five states: **soupground**, **softground**, **looseground**, **firmground** and **hardground** (Fig. 1). **Rockground** (with tectonic omission) and **shellground** (Dodd & Stanton 1990) refer to varieties of lithified hardground substrate. Criteria that can be used to recognize these states from the sediment fabric, and from associated autochthonous taxa, are:

1. **Soupground.** Incompetent, water-saturated sediment. Clay-rich sediment, with traces highly compressed and smeared, compaction extreme. (The role of different clay

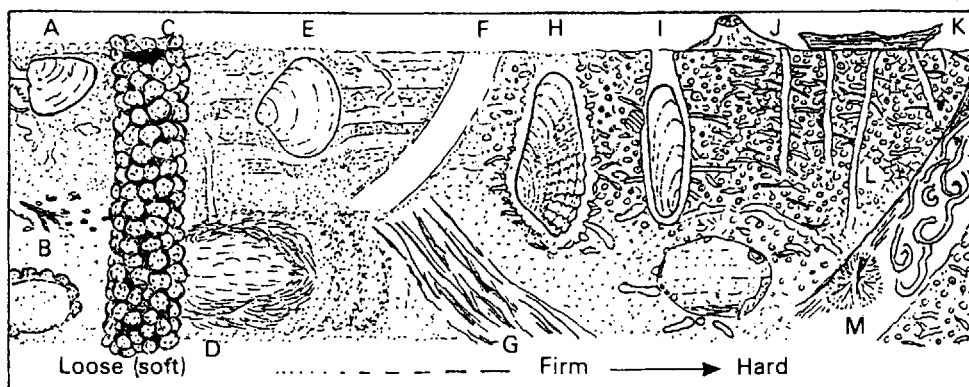


Fig. 1. Diagram to show types of biogenic response to loose (soft), firm and hard (lithified) substrates. (A) *Nucula*, (B) *Chondrites*, (C) *Ophiomorpha*, (D) *Echinocardium*, (E) *Mercenaria/Arctica*, (F) *Thalassinoides*, (G) *Spongiomorpha*, (H) *Petricola*, (I) *Lithophaga*, (J) crinoid holdfast, (K) oyster, (L) *Trypanites*, (M) encrusting bryozoan and serpulids on cemented burrow wall. (After Goldring 1991). B, C, F, G, L are trace fossils.

- minerals in the geotechnical properties has not yet been investigated.)
2. **Softground** is an ill-defined state: 'mud that can be squeezed through the fingers' (Ekdale *et al.* 1984). Burrows exhibit substantial compaction. Bioglyphs (scratches) indistinct or not preserved. Burrows indefinite with irregular outlines, adjustment or escape structures, also spreiten burrows (*Teichichnus*, *Diplocraterion*). It is useful to distinguish soft, muddy sediment from loose silty-sandy sediment (looseground) since the latter will normally have a greater cementation potential.
 3. **Looseground**. Loose well-sorted to moderately well-sorted silt or sand grade sediment. Penetration by intrusion and compression (below) is favoured if the sediment is thixotropic: dilatent properties assist excavation and back-filling. A supporting lining (e.g. pellet-stabilized wall of *Ophiomorpha*), or substantial mucus impregnation (e.g. echinoid burrows, *Scolicia*) to the burrow is typical of loose sediment. As grain size increases relative to burrow width (e.g. in oolites) so burrows become less regular. Rapidly deposited sediment, especially muddy sand in shelf depositional environments, is subject to syndimentary deformation.
 4. **Firmground**. Stiff substrate, recognized by minor burrow compaction. Burrow outlines sharp and sharp bioglyphs (e.g. *Spongeliomorpha paradoxa*, *Glyphichnus*). Encrusters include *Liostrea*.
 5. **Hardground, Rockground and Shellground**. These are best recognized by their encrusting and boring biota and, frequently, a mineralized crust. In carbonate sediment borings cut evenly across matrix and grains alike. Bivalves bore by mechanical or (mainly) chemical means (see also Seilacher 1992), producing *Gastrochaenolites* spp. (Kelly & Bromley 1984). Encrusters include oysters, serpulids, sponges, corals and certain crinoid holdfasts.

A more generalized approach to the nature of bioturbated substrates is covered by the terms **mixed**, **transition** and **historical layers** which are useful in muddy sediment, though less so for sandy sediment (Fig. 2). (They were originally used in description of deep-sea cores.) The mixed layer refers to total bioturbation of the sediment and uniform colour, beneath which the transition layer displays distinct burrows and marked colour contrasts associated with variable oxygenation of the sediment; in fact, a diagenetic effect

determined by bioturbation. The historical layer reverts to more uniform colour, since this is below the level to which most bioturbators reach. In the historical layer nearly all formerly open burrows will have become closed in muddy sediment. With increasing depth, and due to dewatering and/or pelletization, the consistency of the sediment shows increasing resistance to penetration. A **concealed junction** (within the transition layer), represents a fairly sharp change in sediment consistency, e.g. soft to firm, requiring different methods of penetration or behaviour and/or formation of different ichnotaxa. Such changes are a major factor in the tiering (vertical stratification of the bioturbators) of the substrate. Such boundaries must be particularly common in heterolithic sediment, fooling bioturbators.

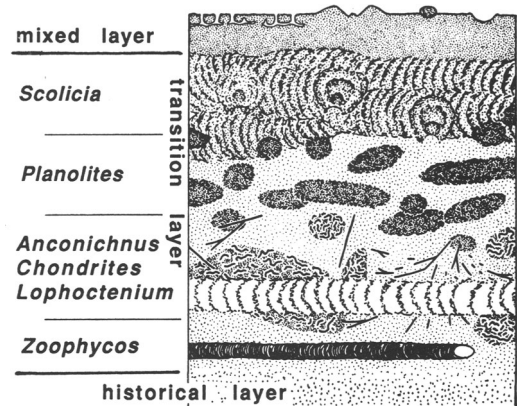


Fig. 2. Tiering diagram with distribution of mixed (homogenization), transition (excavation, back-fill and spreite) and historical (fossilized) layers. Surface trails and the open burrows of *Paleodictyon* are shown in the mixed layer. Modified after Bromley (1990; after Wetzel & Bromley, 1984).

As Rhoads & Boyer (1982) noted, pioneers may modify the physical and chemical properties of the sediment, facilitating later colonization (taphonomic feedback). Most ichnotaxa characterize a particular substrate state and level (see Bromley 1990 for discussion) or exhibit slight behavioural changes to cope, for instance, with increased firmness, as on the unlined floor of an *Ophiomorpha nodosa*. Maples & West (1990) noted how the locomotion trace associated with the bivalve resting trace (*Lockeia*) varied, reflecting a range of substrate conditions. The galleries of *Thalassinoides* show marked tolerance to substrate conditions as might be

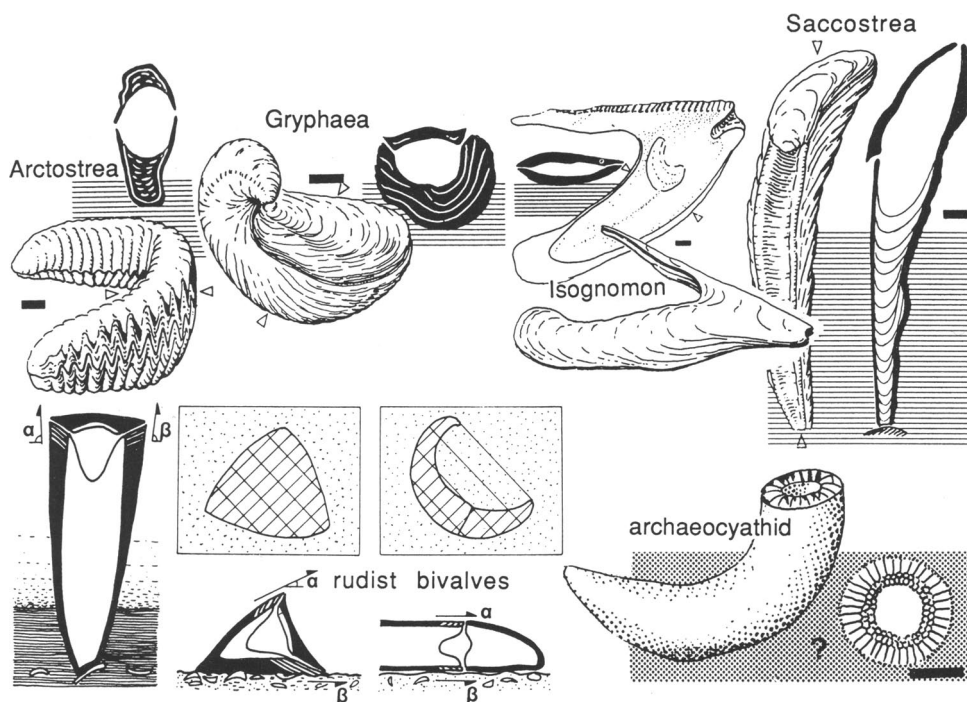


Fig. 3. A few bivalves and an archaeocyathid as indicators of soft substrates. Selected from Seilacher (1984) and Ross & Skelton (1993). Recliners: *Arctostrea*, *Gryphaea*, *Isognomon*, archaeocyathid (with self-righting 'Savazzi effect'); mud stickers: *Saccostrea*, hippuritid (bottom left). Position of sections indicated by open arrows. Scale bars: 10 mm.

expected for a deep domichnion. In relatively uniform lithologies, but with physical, chemical and trophic properties that change with depth, tiering can be complex and Bromley & Hanken (in Goldring & Pollard 1993) recorded at least five tiers in late Permian ichnofabrics from Svalbard (Norway).

For sessile organisms, mechanical stabilization on soft substrates is related to weight and size (Fig. 3). Seilacher (1984) determined the evolutionary pathways towards a soft substrate habitat of (mainly) bivalves, and Thayer (1975) presented a quantitative approach to some extant forms (see also Chinzei 1984). Recliners (including snowshoe adaptations) of various shapes and degrees of shell thickening (including iceberg strategy) are adapted to low sedimentation rate, whereas mud or sand stickers (with upright shells) probably relate to relatively high sedimentation rates. It should be possible to infer the density of ancient muds from the data from modern examples, and shell morphology provides clues about the contemporary hydraulics and sedimentation rate in ancient facies.

Ross & Skelton (1993) applied the same principles to the mode of life of rudists, though elevators (cf. stickers) are frequently clustered.

Mudrocks and muddy substrates

The relationships between mudrocks, preservation of laminae, the shelly biota and bioturbation, oxygenation and chemosymbiosis have received much attention over the last decade [see reviews by Savrda & Bottjer (1991); Tyson & Pearson (1991); Bottjer & Savrda (1993); Allison *et al.* (this volume); Bottjer *et al.* (this volume)]. Wignall (1990, 1993) considers that low oxygenation can be mistaken for softness. Both factors are frequently associated, but not always. Using autecological analysis it is the presence of shells adapted to a soft substrate that is most convincing (Fig. 4), though not without controversy. Wignall (1990, 1993) interpreted 'paper pectens' (very thin-shelled *Bivalvia*) as specially adapted to soft substrates, but Oschmann (1993) argued for a holopelagic mode of life. Bottjer & Savrda (1993) and Bottjer *et al.* (this volume)

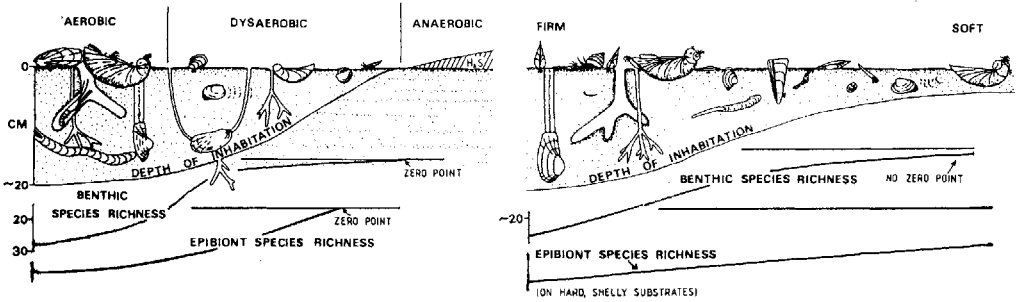


Fig. 4. Faunal changes (left) under a declining oxygen gradient and (right) in a fine-grained clastic substrate on transition from firm to soft conditions. (After Wignall 1993). Epifaunal taxa, left to right: *Chlamys*, *Gryphaea* with abundant epibionts including serpulids, *Parainoceramus*, small *Gryphaea*, procerithid gastropod; *Parainoceramus*, serpulid, trochid, *Gryphaea* with diverse epibionts, 'paper pecten', *Gryphaea*. Infaunal taxa, left to right: mecochirid crustacean, *Goniomya*, *Solemya* and associated *Chondrites*, *Palaeonucula*, *Protocardia*; *Goniomya*, *Nicanella*, *Pinna*, *Nucinella*, *Dentalium*, *Palaeonucula*.

integrated the characteristics of oxygen-related biofacies. The term *poikiloaerobic* (Oschmann 1991, 1993) defines a zone of fluctuating oxygenation, allowing colonization by a few opportunists to otherwise anaerobic conditions.

Substrate penetration

The ways in which marine sediments are penetrated by boring have been reviewed by Carriker *et al.* (1969), Bromley (1970), Golubic *et al.* (1975), Warme (1975) and Bromley & Asgaard (1993), and burrowing by Trueman (1975) and Bromley (1990). Bromley (1990) suggested ichnological terms related to the sedimentary properties rather than to burrowers' *modus operandi*. **Intrusion** indicates penetration of very loose sediment by pushing sediment aside and in very watery sediment by virtually swimming through it. The sediment collapses behind the intrusion. **Compression** is when an organism forces a passage through the sediment by pressing it aside. An open burrow results which may subsequently be back-filled. Numerous strategies are used to probe into the substrate taking advantage of thixotropic properties of the sediment for initial penetration and then to 'grip' the sediment. **Excavation** and removal of sediment elsewhere is a method used in various ways, by appendages and limbs or by mouth (reviewed by Atkinson & Taylor 1991) or by creating a strong irrigation current. (Excavation also includes grinding into the firm or lithified sediment.) **Back-filling** is less labour intensive when the sediment is moved to the rear

creating a **meniscus** back-fill, or sideways movement resulting in a **spreite** and akin to strip-mining the sediment.

Response to sudden (event) sedimentation can be more rapid if the organism is equipped to respond. Bivalves either invert and pull their way out or push their way out, aided by sand with dilatant properties. Juvenile *Mya arenaria* escapes more or less vertically; mature forms escape very slowly, if at all, and slightly obliquely. Few organisms can cope with the wash and backwash of a beach unless they can burrow fast and deep. The shallow burrowing *Mulinia* (Frey & Goldring 1992) can burrow rapidly and reacts readily to relocation. Ability to move upwards is also dependent on the nature of the smothering sediment, since mud-dwelling bivalves (such as *Nucula*) cannot escape through fine sand (Krantz 1974), though *Macoma nasuta*, living in silty fine sand, can cope. It is not surprising that escape structures have not been recorded from turbidites.

Other animals respond to incremental aggradation (or degradation) by producing spreite, best seen in retrusive (or protrusive) *Diplo-craterion parallelum*, or retrusive laminae as in *Lockeia* and *Conichmus* (Pemberton *et al.* 1988). Shinn (1968) showed that *Phyllactis* (burrowing anemone) can retract through 250 mm of sediments overnight. But the behaviour producing a spreite can serve other purposes, documented by Bromley (1990): for lateral extension for feeding while maintaining and ventilating galleries (*Rhizocorallium*), disposing of sediment on the floor of a burrow, e.g. in *Ophiomorpha*

and *Thalassinoides*, or irregular lateral displacement as in strip-mining (*Zoophycos*).

Why are sediments burrowed and bored?

When examining Phanerozoic sediments that are free of any bioturbation perhaps the right question to ask is: 'Why isn't the sediment bioturbated?' Rhoads (1975) outlined a model to express relative trace fossil abundance and environmental reconstruction. In sediment that was soft or loose, high rates of sedimentation (too high for colonization) are generally evident from the primary stratification. A few mobile animals can cope with high rates of sedimentation. In the Mesozoic *Macaronichnus* (Pollard *et al.* 1993) and *Anconichnus* (Goldring *et al.* 1991) were produced, respectively, by animals capable of colonizing mobile sand waves and ripples. In tempestite and storm stratification (see below) (Einsele & Seilacher 1991; Seilacher & Aigner 1991) the thickness of the unit is the critical factor determining depth of penetration by the post-event biota. But soupiness is also important as with centimetre to decimetre thick units of neritic, graded muddy sediments deposited from waning storm flows (Goldring 1971; Walker & Plint 1992), which are sometimes colonized (Goldring *et al.* 1991, figs 1 & 4). Heterolithic facies (millimetre to centimetre beds of sand and mud) are particularly common in the geological record and often are intensely bioturbated. Thick successions of virtually unbioturbated heterolithic facies are also common, particularly in deltaic and estuarine environments, though poorly described from modern sediments. When careful sample preparation shows that even the mud is unbioturbated, then factors other than sedimentation rate need to be addressed, including effects due to the **colonization window** (time available for colonization via larval settlement or relocation, Pollard *et al.* 1993), nutrient availability and oxygenation.

In uniform sediment, such as large thicknesses of muddy silts (often referred to as marls in the European literature), bioturbation and trace fossils are apparently missing. This is principally because of the uniformity of the lithology so that weathering does not differentiate soles or upper surfaces to expose the trace fossils. In every case the sediment needs to be slabbed and/or X-radiographed for mottling and fabric attributable to bioturbation (O'Brien 1987).

Sedimentary advection (the bulk redistribution of particles by bioturbation) affects the position of stratigraphically important microfossils and disperses geochemical marker horizons. In chalks, for instance, it would be unwise

to attach much biostratigraphical significance to sampling at less than *c.* 0.5 m intervals. A full study has not yet been carried out to quantify advective effects, but see Matisoff (1982). It will be necessary to determine the ichnofabric and the type of bioturbation present. Advection might be analysed in two stages: the effects of the relatively even upward migration of the mixed layer with sedimentation, and the very uneven effects due to open burrows penetrating through the transition layer (Smith 1992). Quantification of the latter will be particularly difficult. Wheatcroft & Jumars (1987) showed that deep-sea sediment mixing is size dependent. Tedesco & Wanless (1991) showed that open burrows pipe sediment downwards and completely change the nature of the sediment. The effects are as great as with sedimentary dykes.

Grain size

Warren & Sheldon (1967) and Wieser (1959) recognized that there was a close correlation between the grain-size distribution of sediment ingested by crustaceans (e.g. *Cumella*, 150–500 μm ; *Picrouma*, 150–350 μm) and that of feeding sites. This is of commercial significance in predicting fishery sites. The majority of edible fish are demersal, feeding at or close to the sedimentary surface. Geologically it may be possible to make inferences on the nature of bioturbators from the grain-size characteristics. Larval settlement on soft (loose) substrates is reviewed by Butman (1987). It is now clear that it is the hydraulic regime rather than the substrate factor *per se* that is important.

Oceanic bioturbation

A difficulty to be resolved is that modern biogenically reworked substrate surfaces do not much resemble ancient bedding surfaces, whereas modern hydraulically determined ones do. This is partly the result of current and wave-current action, and partly the result of the paucity of the photographic record of shoreface and shelf level-bottoms. Even beneath bentonites in sandy shelf sediments (L. Cretaceous) of southern England, the underlying sand was planed prior to bentonite deposition. Funnels infilled by tephra fall-out mark the only inhabited sites.

Where animals are present the deep-sea floor takes on an appearance quite different from the smooth floors of stagnant basins so that the substrate has a degree of irregularity as high as may be found in intertidal sediments, and with extensive and sharply defined surface trails

which often persist for a considerable period. This belies the softness of the surface because many animals have buoyant bodies that do not sink into the sediment. Nutrient levels in the deep ocean are invariably low and animals need to ingest much sediment, but the tight meanders and functionally similar patterns so often recorded from ancient turbidite soles and elsewhere are not that common. Sediment compaction will have been responsible for obscuring much of the detail, but Wheatcroft *et al.* (1989) suggest, perhaps surprisingly, that because of infaunal activity trace residence time is low.

Geologists may have a greater understanding of the nature and distribution of animal behaviour within deep-sea sediments than do biologists because of the deep-sea fossil record. However, this must be set against the conjectures made with often meagre biological input, and the acceptance that turbiditic facies are over-represented in the geological record relative to the amount of the modern seafloor that has been photographed. (This excludes, of course, the extensive areas mapped at small scale by sidescan sonar.) Ekdale (1980) pointed out that photographs of the ocean floor do not provide a true measure of the largely infaunal traces of the fossil record. This probably explains why observations (Kitchell 1979; Kitchell *et al.* 1978*a, b*, 1979) seem to contradict the Sanders (1968) time-stability model for deep-sea diversity. The deep sea, as reviewed by Gage & Tyler (1991), is not the stable and predictable environment envisaged by Sanders (1968), even though growth rates are lower and longevity greater in this environment.

The animals responsible for the much photographed deep-sea traces are gradually being recognized (Ohta 1984; Huggett 1987), but we are a long way from understanding what structures such as *Zoophycos* and *Paleodictyon* (Fig. 11) represent (Bromley 1991), and to what animals they are attributable. The environmental significance of both is important to geologists and marine biologists. The farming model for *Paleodictyon* (which seems to be most characteristic of distal turbidites) has yet to be confirmed from observations from modern sediments (Miller 1991*a*). The supply of nutrients to the ocean floor is clearly periodic (Bilett *et al.* 1983; Rice *et al.* 1986) and uneven, so that tightly spiralling feeding trails are likely on richer patches. This may be testable on ancient sediments.

The saga of *Zoophycos* seems to be unending. Following the work of Wetzel (1981, 1991) and Wetzel & Werner (1981), it is clear that *Zoophycos* is a deep-tier trace in modern deep-

sea sediments (Fig. 9). Kotake (1989, 1991) believes that the animal responsible for Pliocene examples in Japan carried material from a surface layer downwards, to be deposited in the complex spreite as pellets. The reason for this behaviour is uncertain. Bromley (1991) has reviewed the situation and proposed three models for what the pelleted sediment represents: (1) a back-filling derived from the surface and distinct from deposit feeding activity; (2) a food cache for future use or; (3) a more elaborate food cache to be subsequently farmed. Bromley (1991) admits that more than one behaviour pattern may be responsible for *Zoophycos* which ranges from the Cambrian. *Zoophycos* displays considerable variation, which is probably not simply a case of evolution over geological time (Bottjer & Jablonski 1988; Bottjer *et al.* 1988). Ekdale & Lewis (1991) and Ekdale (1992), following close examination of the giant *Zoophycos* from the Amuri Limestone Group (U. Cretaceous–L. Oligocene, New Zealand), argued that *Zoophycos* is a complex multi-systemed *Rhizocorallium*-like structure with a repeated shorter (overall) U-burrow rather than a single long U-burrow. Further studies by Gaillard & Olivero (1993) on Jurassic material indicate an upward coiling (retrusive) that is contrary to the traditional (protrusive) model of Seilacher (1967). This type of *Zoophycos* formed in cohesive sediment (by a J-tube), marking a period of reduced sedimentation following rapid sedimentation. While there can be no question about sediment stowage in the Japanese (Kotake 1989, 1991) and New Zealand materials (Tertiary), this is clearly by no means the general case. It may not be applicable to occurrences in the shallow marine Lower Limestone Group of the Scottish Dinantian (*Z. caudagalli*; Davies *et al.* 1986), or in lagoonal calcilitites in Lincolnshire, England (Bajocian) (G. Tegardine pers. comm. 1988). *Zoophycos* is in urgent need of a thorough taxonomic review.

Evolution of substrates

Evolution of the organic world means that environments (and therefore facies) have changed and evolved over geological time. Aspects of this relating to the substrate have been described and discussed by Goldring (1969), Droser & Bottjer (1988), Sepkoski *et al.* (1991) and Bottjer *et al.* (this volume). This is a field needing further investigation: for instance, the role of Palaeozoic encrinites (essentially the remains of camerate crinoids), and the appearance of marine grasses (Brasier 1975) and mangroves (Allen 1965; Plaziat this volume) must have had profound

effects on contemporary environments and their relationships.

The changes due to the evolution of the infauna that took place at the Proterozoic–Cambrian boundary interval when the inhibiting effect of the ‘Ediacara Garden’ (Seilacher 1992) were substantially reduced in shallow depths have still to be documented. Sepkoski *et al.* (1991) discussed five trends in the Phanerozoic due to expansion of the infauna: (1) decrease in the frequency of very thin storm layers (due to lower preservation potential); (2) increase in the degree of biogenic disruption of the upper portions of thicker tempestites; (3) increase in the abundance of poorly sorted sediments as a result of biogenic homogenization; (4) increase in the frequency of massive sedimentary units with only relict bedding; (5) decrease in the frequency of rapidly cemented layers, especially in heterolithic facies, as a result of increased burrow ventilation.

Sepkoski *et al.* (1991) mention several examples which do not fit the prediction. To test fully the changes expected it will be necessary to sample ancient environments where sediments were deposited under essentially similar physical and chemical conditions as well as palaeolatitude and sedimentological accommodation space.

Palaeoenvironmental uses of bioturbation and biogenic accumulations

Trace fossils and facies interpretation

Trace fossils have held an important role in facies interpretation for many years, and reviews of the ichnofacies concept typically look back to Seilacher’s (1964, 1967) English-language papers. Byers (1982) gave a critical assessment of the ichnofacies concept and showed that it was essentially a generalization, linking extensive experience of the rock record with a deductive explanation from current ideas on modern ocean sediments. Our understanding of marine processes and marine environments has been advanced by a further decade of research. Evidence from the sea-floor no longer supports the general model. As Byers (1982) pointed out, focus has been on the distribution patterns of the traces rather than the distribution of oceanic organisms. We are now beginning to understand the latter (Gage & Tyler 1991). Interpretation of sedimentary facies has also advanced and been refined. Byers (1982) posed the question, ‘Has the (ichnofacies) model reached the limits of

its resolution?’. There are still less than ten ichnofacies. The original bathymetric model has been extensively reviewed (Ekdale 1988, Bromley 1990) and superseded by a model based on a number of factors (Frey & Seilacher 1980; Frey *et al.* 1990; Bromley & Asgaard 1991; Pemberton *et al.* 1992b). In stratigraphic successions, relative bathymetry is still an important interpretative aspect, since coarsening-up and fining-up trends are frequently involved. Frey *et al.* (1990) recognized that substrate consistency defines the *Trypanites* ichnofacies in hardgrounds, rockgrounds, lithified clasts and bioclasts and the *Teredolites* ichnofacies in xylic (wood) substrates. The *Glossifungites* ichnofacies in firm, unlithified substrates and the *Trypanites* ichnofacies are typically associated with sedimentary discontinuities or omission surfaces. Frey & Pemberton (1987) proposed the *Psilonichnus* ichnofacies for marginal marine environments that include plant-root penetration structures as well as animal burrows. This low diversity ichnofacies is not readily associated with characteristic bed forms. Bromley & Asgaard (1991) defined the *Glossifungites* ichnofacies slightly differently, as reflecting firm to hard substrates. Ekdale (1980) pointed out that the softground ichnofacies (*Skolithos*, *Cruziana*, *Zoophycos* and *Nereites*), although often considered as being under only bathymetric control, are influenced by the nature of the substrate. Seilacher (1974) divided the *Nereites* ichnofacies into a more distal *Nereites* subfacies and proximal *Paleodictyon* subfacies. The *Scoyenia* ichnofacies was proposed by Seilacher (1967), formalizing earlier work (Seilacher 1963), as an attempt to discriminate between marine and non-marine trace fossil assemblages. This was an early generalization, and Pollard (1988; see also Goldring 1991, fig. 6.24) has refined the model distinguishing between the trace fossils associated with waterbodies, fluvial channel, floodplain and alluvial fans, aeolian dunes, and lagoonal and deltaic ichnofacies. Pickerill (1992) reviewed the present status of the *Scoyenia* ichnofacies and concluded that more studies are needed before universally applicable non-marine ichnofacies can be recognized. Other ichnofacies have been proposed by Bromley & Asgaard (1991) (*Arenicolites* ichnofacies) and Bromley & Asgaard (1993) (*Entobia* and *Gnathichnus* ichnofacies in hardgrounds).

It is the extensive *Skolithos*, *Cruziana*, *Zoophycos* and *Nereites* ichnofacies, under wide ecological control, that are of most concern to facies interpretation and sequence stratigraphy. The starting point of the latter is recognition of bounding surfaces (sequence boundary, marine

flooding surface, transgression surface, maximum flooding surface): represented by omission and condensation, particularly firmgrounds (Fig. 6). Seilacher (1954, 1955, 1958) recognized the immense distinction between turbidite-associated trace fossil assemblages and assemblages associated with shallow-marine sediments, and he noticed that these distinctions were related to behavioural aspects. These papers were almost contemporary with the beginnings of the modern approach to sedimentology: facies discrimination and the use of primary sedimentary structures in facies interpretation.

As the study of sedimentary facies has grown it is unfortunate that ichnological analysis has not always gone hand in hand with sedimentological analysis. Trace fossil studies have often preceded full sedimentological analysis and many detailed sedimentological studies have paid relatively little attention to the associated trace fossils. Since trace fossils are sedimentary structures this disparity in research effort has not assisted in refining facies interpretation as much as might have been expected. It might also explain why Bromley & Asgaard (1991) rejected the salinity factor and redistributed the putative freshwater assemblages (some of which are ichnocoenoses) amongst the marine ichnofacies according to their ethology. The shoreline is the most important environmental boundary, although it may be difficult to define, especially in tidal environments. In estuaries the salinity gradient may be more useful. Further confusion arises with Bromley & Asgaard's (1991) proposal of the *Arenicolites* ichnofacies for opportunistic occurrences of *Skolithos* in storm deposits. Frey & Goldring (1992) criticized this because: (1) all previous ichnofacies have been named on the basis of a representative ichnogenus and *Arenicolites* in general is hardly known as an indicator of opportunistic colonization, and (2) it ignores the considerable variation and diversity of ichnofossils known to occur in hummocky beds (Frey 1990).

The ichnofacies concept is flawed in respect of facies interpretation (Goldring 1993) because:

1. The resolution of ichnofacies is today insufficient. While there are still less than ten ichnofacies, this is at least an order of magnitude less than the number of facies (mainly lithofacies) described and currently in use.
2. The ichnofacies concept suggests that facies interpretation can be accomplished without first making autecological analysis, though this has been firmly rejected (Frey *et al.* 1984, 1990).
3. If by facies the whole aspect of a sediment is understood, then ichnofacies emphasizes only one aspect.
4. It includes, in most instances, only distinct and elite trace fossils, tending to ignore bioturbational mottlings of uncertain taxonomic assignment, but which are nevertheless important.
5. The environmental implications of several of the archetypal ichnofacies are sedimentologically misleading. Attempts to resolve the question of the primary sedimentary structures and other trace fossils associated with *Zoophycos* have not resulted in any way that is significantly useful in facies interpretation (Ekdale 1992; Goldring 1993). Bromley (1990) refers to the *Zoophycos* ichnofacies as the 'black sheep' of the family. Wetzel (1991) described deep-sea, deep-tier occurrences of *Zoophycos* as *Zoophycos* ichnofacies in a situation where shallow tier members of the *Nereites* ichnofacies have been lost taphonomically, by being obscured during sediment accumulation and tier replacement. The problem is with the terminology, not with the geology.
6. The aspect of scale is confusing for facies interpretation. Bromley & Asgaard (1991) discuss how a hardground can pass laterally into a nodular (concretion) horizon, but that if both are bored *Trypanites* ichnofacies can be applied only to the hardground.
7. By selecting a particular ichnotaxon to designate the ichnofacies it is somewhat illogical to carry the name when the eponymous ichnogenus is absent, such as the post-Palaeozoic occurrences of (marine) *Cruziana* ichnofacies though *Cruziana* (= *Isopodichnus*) is present in non-marine facies (see Magwood 1992).
8. In the Lower Palaeozoic *Cruziana* is not conspicuous in facies which, because of their shelly fauna and intensity of bioturbation, would be generally recognized as neritic. It is most characteristic of heterolithic facies where the Bioturbation Index is low (1–2), and where mudrock is not appreciably bioturbated. In neritic facies *Cruziana* is generally 'hidden' in intensely bioturbated ichnofabrics (Goldring 1985; Frey & Goldring 1992).
9. Applying archetypal ichnofacies to slabbed core is difficult because of the problems outlined by Bromley (1990), especially in that interstratal and bedding parallel traces

- are difficult to recognize, or are lost to investigation.
10. The ichnofacies concept does not readily take into account small but important facies changes, particularly where ichnofabrics overlap gradationally or by omission (Fig. 10). Bromley & Asgaard (1991) emphasize that *Chondrites* and *Zoophycos* do not necessarily indicate seafloors deficient in oxygen.
 11. It has been shown that several ichnogenera, previously considered of relatively little value in ichnofacies analysis, may be useful (e.g. *Chondrites* in the interpretation of substrate oxygenation levels and *Planolites* in near-shore facies).
 12. Sedimentologically important facies, especially deltaic, estuarine and lagoonal facies, are not readily recognized by the scheme. Deltaic facies are often characterized by opportunist traces. Ekdale (1980) mentioned that not all sedimentary environments might be distinguished by trace fossil analysis. This is not the point. Trace fossils help in interpretation and do not need to provide full answer alone.
 13. Ichnotaxa generally referred to as shallow-water forms are increasingly being found in association with turbidites (Kern & Warne 1974; Uchman 1991a, 1992), including thin-bedded (distal?) facies. Some 'deep-water' ichnotaxa are reported in shallow marine sediments (Archer & Maples 1984) or non-marine facies (Pickerill 1992). Some ichnotaxa restricted to Mesozoic and younger sediments occur (and originated) in shallow marine Lower Palaeozoic and Vendian environments (reviewed by Crimes & Fedonkin 1994; Vidal *et al.* 1994). This aspect is accepted in modern ichnofacies concept but does not offer much help in facies interpretation!

Not all authors have interpreted their ichnotaxa distributions in terms of archetypal ichnofacies, preferring to look for empirical associations. Clausen & Vilhjálmsson (1986) (Fig. 5) recognized four such associations in the Lower Cambrian of Bornholm (Denmark): *Skolithos*, *Diplocraterion*, *Rhizocorallium* and *Teichichnus-Buthotrephis* (*Phycodes*) associations. However, they related open burrows (passively filled) to the host sediment rather than to a colonization surface. If open burrows (dwelling, suspension feeding) are separated from actively filled burrows (mostly sediment eaters) and related to likely colonization surfaces then the distribution of the traces is substantially different, and

their significance for facies interpretation enhanced. Fürsich (1975) employed dynamically significant criteria to define Upper Jurassic neritic *Diplocraterion*, *Teichichnus* and *Rhizocorallium* associations. Crimes (1970) integrated ichnology with facies analysis in his analysis of Cruziana sandstone facies.

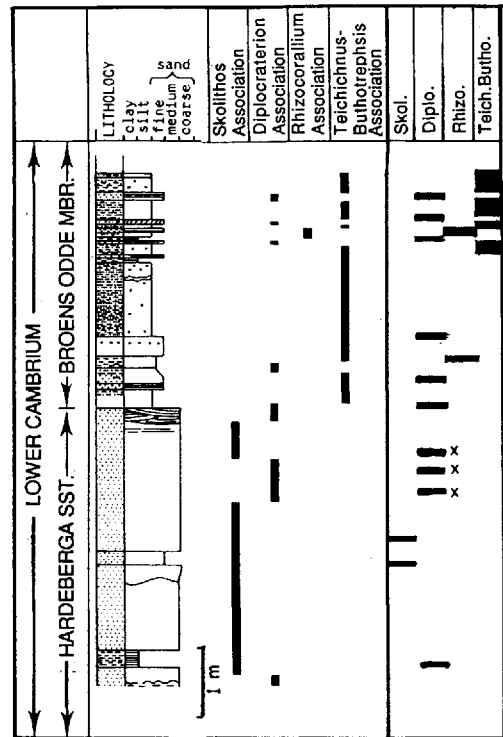


Fig. 5. Lower part of the generalized section of the Lower Cambrian sequence from Snogegaek Harbour, Denmark (modified from Clausen & Vilhjálmsson 1986), with relative abundances of trace fossils (left) after authors; (right) with tentative relationships to colonization surfaces (Frey & Goldring 1992) using distributions indicated by authors. x – in this section of uniform medium-grained sand the three levels of *Diplocraterion parallelum* are probably represented by only the lower part of the protrusive spreiten: the upper part and interval of muddy sediment having been eroded, penecontemporaneously. This sand unit would then represent at least four sand depositional events.

It is useful to pose the question, 'What information do sedimentologists want from trace fossils?': (1) Any information that will aid in the interpretation of sedimentary facies to as specific a degree as possible (including informa-

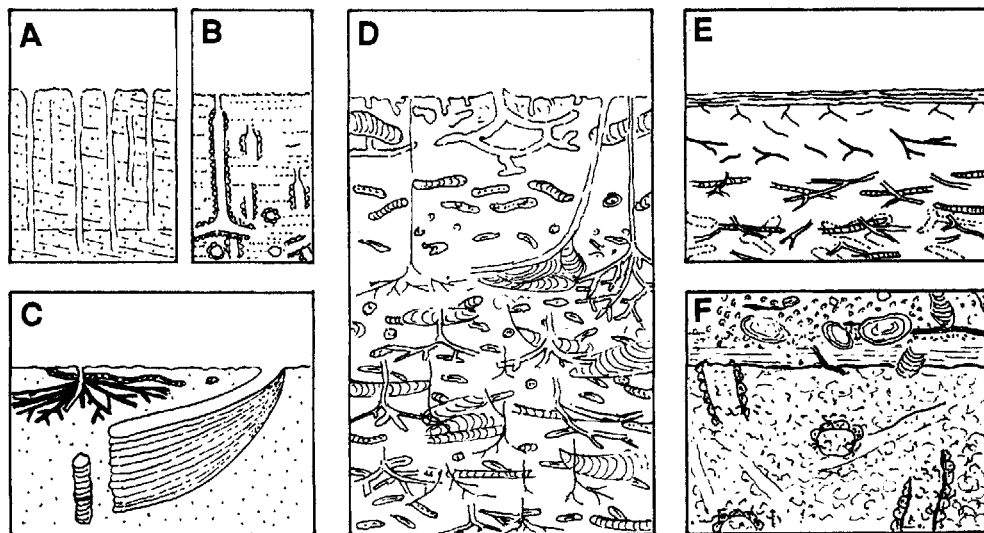


Fig. 6. Styles of tiering. (A) Single colonization produced by opportunists, e.g. *Skolithos* (after Droser 1991). (B) Single successive colonization of *Ophiomorpha* on aggrading beach (after Frey *et al.* 1978). (C) Simple tiering (frozen tier) as first colonization of an event unit (tempestite or turbidite, Fig. 11). (D) Complex tiering associated with aggradation and overprinting of the tiered suite in chalk (after Ekdale & Bromley 1991). (E) Gradational overlap reflects gradual changes in ecological parameters. This can involve the overall environment as, for instance, in a prograding sequence where shoreface zones overlap offshore facies. In a siliciclastic core such change usually accounts for an appreciable thickness. In mudrocks subtle changes in the intensity and duration of oxygenation fluctuations are recorded by relatively thin units. Savrda & Bottjer (1989*a, b*) related duration to the degree of cross-cutting and thickness of the bioturbated unit, and intensity of oxygenation to the diversity, size and penetration depth of the burrows. The figure shows (schematically after Savrda & Bottjer 1989*b*) deoxygenation of the substrate marking gradual environmental change. (F), Omission overlap, marking sharp facies change, e.g. Fig. 10A–F (after Taylor & Gawthorpe 1993).

tion on the chemical and hydraulic processes, and wave climate); (2) information relating to the nature of the original substrate and taphonomic and diagenetic changes that have occurred during burial history (including porosity and permeability); (3) information relating to sedimentational history on a small time-scale (penecontemporaneous erosion) and larger time scale (basin analysis, sedimentation and erosion rates); (4) stratigraphic correlation.

Such information is best obtained by analysing and assessing the ichnology with the physical sedimentology and invertebrate palaeontology: by integrating all aspects of the facies and its diagenesis, and by integrating studies of the bedding and slabbed surfaces [as Pemberton & Frey (1984) did for the *Cardium* Formation (U. Cret. Alberta), and successfully achieved by Wang (1993) in the Rhaetic of southern England]. Ichnological analysis must involve autecology (Ager 1963), followed by synecology

and synthesis, and with greater emphasis on slabbing, serial sectioning and the ichnofabrics than hitherto applied. Ichnofabrics (Ekdale & Bromley 1983; Taylor & Goldring 1993) result from all aspects of the texture and internal structure of a sediment that results from bioturbation at all scales. This includes discrete and elite trace fossils and the mottled to massive sediment where only negative features may indicate meaningfully the primary sedimentary structures. Analysis of the ichnofabric also means analysis of the ordering (introduction into the ichnofabric) of the different elements and the tiering (Fig. 6). Taylor & Goldring (1993) gave methods for the description and analysis of bioturbation, and also reviewed previously proposed schemes of assessing degree of bioturbation. The **Bioturbation Index** (Table 1) defines the grade of bioturbation in terms of bedding distinction, burrow density and overlap. The **Ichnofabric Constituent Diagram**

Table 1. Bioturbation Index (BI) where each grade is described in terms of the sharpness of the primary sedimentary fabric, burrow abundance and amount of burrow overlap. (After Taylor, in Taylor & Goldring 1993)

Grade	Bioturbated (%)	Classification
0	0	No bioturbation.
1	1-4	Sparse bioturbation, bedding distinct, few discrete traces and/or escape structures often common.
2	5-30	Low bioturbation, bedding distinct, low trace density, escape structures often common.
3	31-60	Moderate bioturbation, bedding boundaries sharp, traces discrete, overlap rare.
4	61-90	High bioturbation, bedding boundaries indistinct, high trace density with overlap common.
5	91-99	Intense bioturbation, bedding completely disturbed (just visible), limited reworking, later burrows discrete.
6	100	Complete bioturbation, sediment reworking due to repeated overprinting.

The percentage bioturbation values should be used as a guide and not an absolute class division.

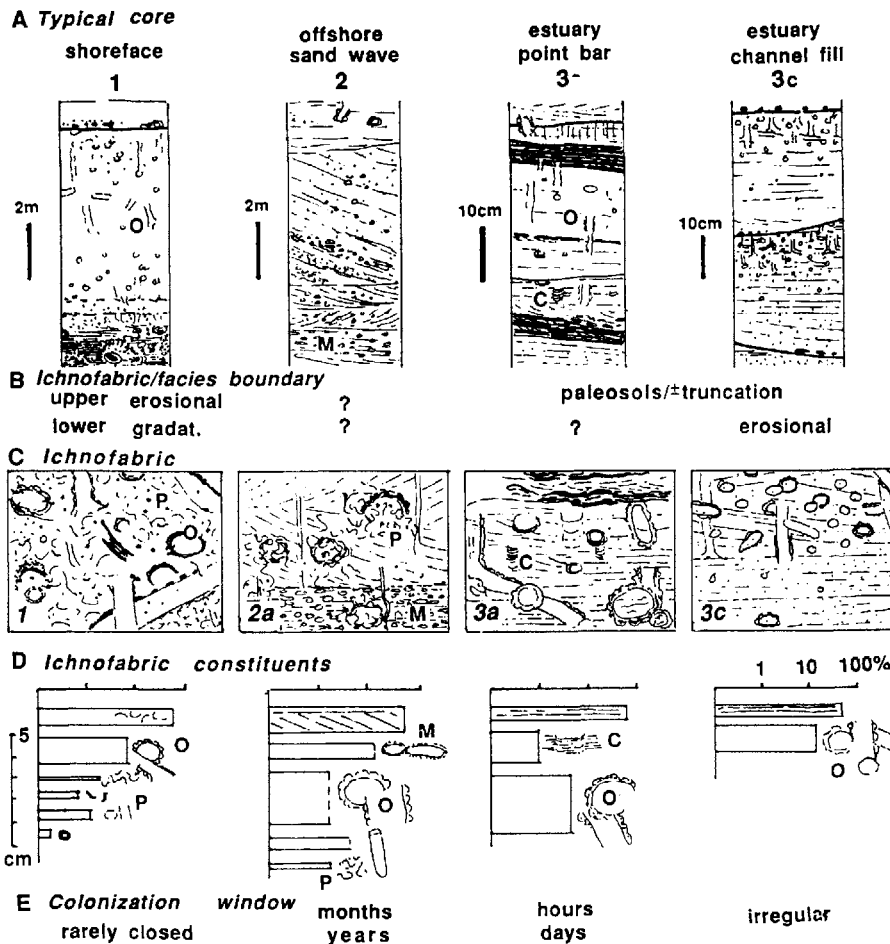


Fig. 7 Ichnofabrics with *Ophiomorpha* from estuarine, shoreface and offshore facies. Diagram to illustrate relationships between typical core expression, type of boundary between ichnofabrics/facies, typical ichnofabrics and their constituents (see Fig. 8) and nature of the colonization window. O, *Ophiomorpha*; P, *Planolites*; C, *Conichnus*; M, *Macaronichnus*; (after Pollard et al. 1993).

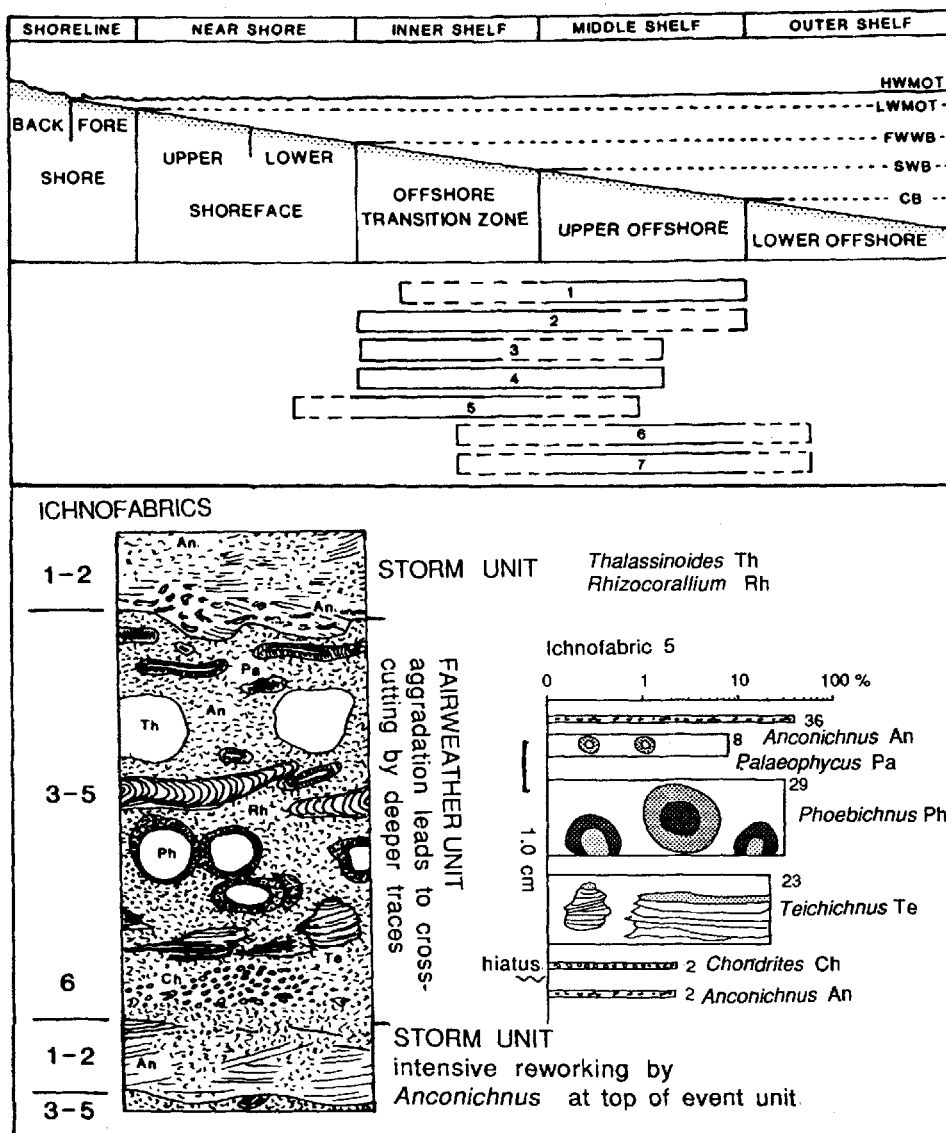


Fig. 8. (Upper) Inferred distribution of ichnofacies associated with *Anconichnus horizontalis*. The seven ichnofacies relate to sedimentation rate, substrate consistency, depth [as related to fair weather wave base (FWWB), storm wave base (SSB) and base of storm generated currents (CB)]. (Lower) schematic diagram of ichnofacies 1-6 in relation to event bed and fair weather (equilibrium) processes, with schematic ichnofacies constituent diagram of ichnofabric 5 (Bioturbation Index 6) (photographically illustrated in Taylor & Goldring 1993, fig. 1F), where *A. horizontalis* in muddy, fine-grained sandstone is partly obliterated by deeper burrows. On the horizontal axis the percentage area of the sedimentary structures and burrow types are plotted on a log scale. On the vertical axis, events (in order) from the initial sedimentation events (primary fabrics) to subsequent modification by bioturbation (secondary fabrics). After Goldring *et al.* (1991); Taylor & Goldring (1993). [Note: *A. horizontalis* should now be referred to *Phycosiphon incertum* (Wetzel & Bromley 1994).]

(Figs 7, 8 & 13) provides a visual means for describing and comparing ichnofabrics by: (1) assessing the extent and type of the remaining primary fabric; (2) unravelling the tiering and ordering of the ichnotaxa; (3) recognizing the type of bioturbational event: either opportunistic or tiered equilibrium. The ichnofabrics of event beds can be represented in a way similar to that applied to hardgrounds (Fig. 13).

An integrated approach to facies interpretation

Freeing ichnotaxa from their confined associations with ichnofacies allows greater advantage to be taken of the information about ancient environments they each carry. Some examples follow:

1. In the Mesozoic and Cenozoic *Ophiomorpha nodosa* is common in shallow marine sandy facies. Pollard *et al.* (1993) showed (Fig. 7) how the several ichnofabrics with *Ophiomorpha* can be used to discriminate between shoreface, estuarine and offshore sand-wave sedimentary environments. The citations from non-marine facies (e.g. Stewart 1978 and earlier citations) are misidentifications, or doubtful, rare occurrences related to marginal, up-estuary environments (e.g., Bown 1982; Merrill 1984; Hasiotis & Bown 1992). Intuitively, the *Ophiomorpha* behavioural morphology is likely to be uncommon in the firm substrates encountered in (partly vadose) river bank and shallow lake depositional environments where the highest preservation potential should be, though it is just foreseeable that the species responsible may have inhabited both marine and non-marine environments.
2. Within the Mesozoic the lower shoreface to upper offshore facies can be differentiated (Fig. 8) (Goldring *et al.* 1991).
3. *Chondrites* and *Planolites* are generally referred to as facies-crossing ichnotaxa. The relative depth and size of *Chondrites* in a black shale sequence is a useful indicator of oxygen level deterioration or amelioration (Bromley & Ekdale 1984; Savrda & Bottjer 1986; Bottjer & Savrda 1993) (Fig. 9). Situations of rising O₂ levels also provide the pioneers with sediment high in nutrients. It is not surprising that *Chondrites* is more common where food was abundant (Uchman 1990), and that the *Chondrites*-animal was able to penetrate

deeply to a zone of reduced oxygen content. However, Wignall (1990) sees the role of *Chondrites* differently in the Jurassic mudrocks of northwest Europe and as an indicator of rather higher oxygen levels.

4. *Diplocraterion parallelum*, especially where protrusive and retrusive forms are associated, seem to dominate marine flooding surfaces in the Mesozoic. It occurs widely at the unconformity surface marking the major transgression of the Rhaetic. In younger Jurassic sediments it also provides a useful indication of short-lived marine incursions (Taylor & Gawthorpe 1993; Fig. 10B), where the mud infills may contain marine dyncocysts. It is uncommon after the early Cretaceous and its distribution in late Cretaceous and Cenozoic sediments needs investigation. With respect to colonization surfaces *D. parallelum* does not occur typically with *Ophiomorpha* or *Skolithos* and is not a member of the *Skolithos* ichnocoenosis. In contrast, *D. habichi* (of Fürsich 1974) colonizes the top of storm event units in the Jurassic. *Arenicolites* and *Planolites* are pioneer traces in deltaic deposits.
5. Studies of turbiditic facies (Leszczynski 1991a,b, 1992, 1993; Miller 1991b, 1993; Powichrowski 1989; Uchman 1990, 1991a,b,c, 1992) now closely parallel oceanographic work (above). The separation of the **pre-event** (pelagic) ichnocoenosis from the **post-event** (turbidite) ichnocoenosis is well known, and it might reasonably be expected that the model developed by Wetzel (1991, following earlier papers) (Fig. 9), based on studies of modern deep-sea sediments, would apply to the background (pre-event) sediments. Siliciclastic turbidites do not lend themselves well to ichnofabric analysis since bioturbation structures are mostly distinct only on soles and upper surfaces, but calcareous turbidites may display good ichnofabrics (Powichrowski 1989). Miller (1993) showed that the differences between proximal and distal trace fossil distributions reflect original differences of the trace makers as much as preservational factors, though appreciating the importance of disturbance regime (Pickett & White 1985).
Post-event colonization was probably synchronous with the termination of the event, and resulted in a single (frozen) tier. Several environmental factors are involved: the biotic ones being subordinate to the abiotic. Penetration depth is obviously

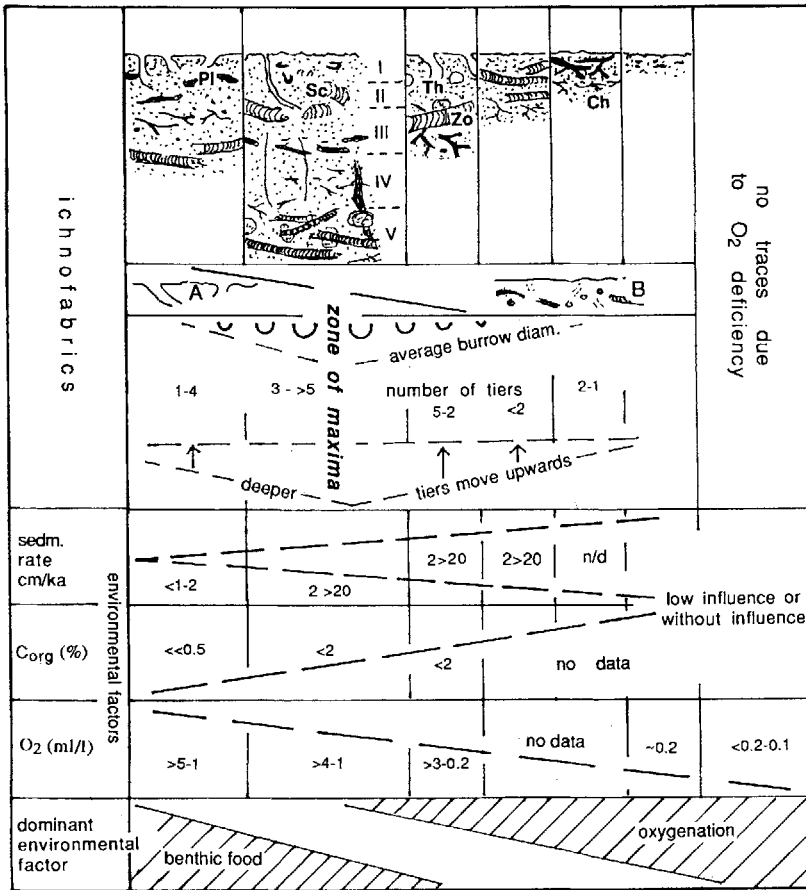


Fig. 9. Ichnofaunal response to environmental factors (oxygenation, benthic food availability and sedimentation rate), adapted from Wetzel (1991), and based mainly on observations on modern sediments off NW Africa at depths of 500–1000 m+. Roman numerals indicate tier: Sc, *Scolicia* (echinoid), Pl, *Planolites* (active fill), Th, *Thalassinoides* (crustacean), Ch, *Chondrites*, Zo, *Zoophycos*. (Note: Wetzel did not observe *Paleodictyon* in his cores.)

related to the particular trace producers, but also to the thickness of the structural divisions of the event unit, with feeding and grazing traces extending along organic-rich laminae of the T_d division (parallel laminated silt and mud) (Fig. 11). According to Leszczynski (1993) *Helminthoida* and *Scolicia* tend to be associated with grey sediment in Cretaceous Palaeogene turbidites in northern Spain. The nutrient level is reflected by the colour of the sediment and the level of oxygenation can be correlated with burrow diameter. Red muds display burrows with the most

blurred outlines suggesting particularly high fluidity. *Lophoctenium* seems to be present at sharp top surfaces, suggesting the absence of the T_e (pelitic) division, and a firmer substrate.

The background ichnocoenoses reflect several environmental parameters which include sedimentation rate and the time available between turbidite events, and also the sediment composition. The complex and variable tiering is not easy to unravel. Oxygenation (Leszczynski 1991a) is reflected in the variable nature of the present spectrum (Fig. 12) (allowing for

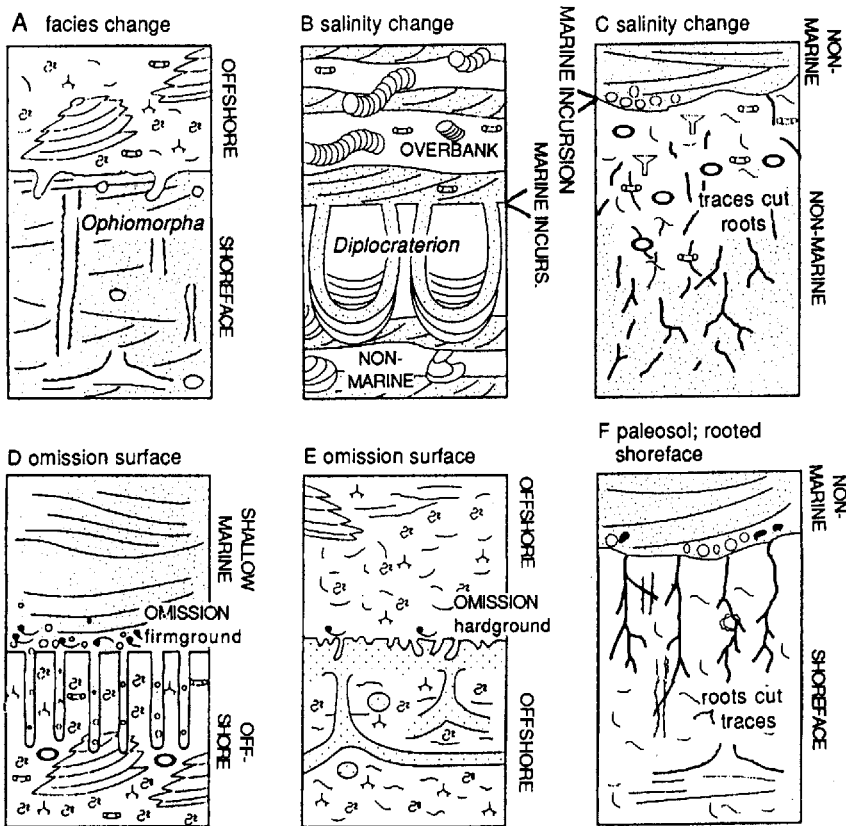


Fig. 10. Cartoons to illustrate how trace fossils can indicate key stratal surfaces, with examples from the Mesozoic of the North Sea and Yorkshire coast. (A) represents a marine flooding surface; (B & C) a marine incursion into non-marine sediments; (D & E) omission surfaces, (D) representing a change in lithification (transgressive surface), (E) condensed (long) interval; (F) sequence boundary. After Taylor & Gawthorpe (1993).

similarity of erosion), and on sediment colour, total organic carbon (TOC) and association with agglutinated/calcareous foraminifera. A problem still to be addressed is the manner in which the 'background' ichnocoenosis replaced the post-event suite. Leszczynski (pers. comm. 1992) considers that the graphoglyptid producers (e.g. creators of *Paleodictyon*) colonized the upper parts of event beds in dysaerobic situations. More intensely bioturbated background sediments are impoverished in graphoglyptid (open) burrows. Bromley & Asgaard (1991) make the pertinent observation that the soles of thinner turbidites, recording shallow tier traces, can be seen as ichnological examples of fossil ores (Fossil Lagerstätten).

6. Recognition of brackish water facies is an on-going problem. An integrated ap-

proach, using at least the shelly biota, trace fossils and palynology (e.g. Wightman *et al.* 1987), is essential. The problem is compounded in that shell preservation may be poor, identification of taxa difficult, and shell mixing and dissolution frequent. The topic is reviewed by Pemberton & Wightman (1992). Ruffell (1988) noted that in the lagoonal Lower Cretaceous (Wealden) of southern England marine shell beds (in part washovers) exhibit valve disarticulation and greater breakage than non-marine shell beds. *Diplocraterion* is a useful trace fossil marking marine incursions (above). Overall absence of marine trace fossils but an abundance of *Palaephycus* can be indicative (contrast with Wightman *et al.* 1987). Pemberton *et al.* (1992a, b) concluded that the ichnofacies represented a mixture of

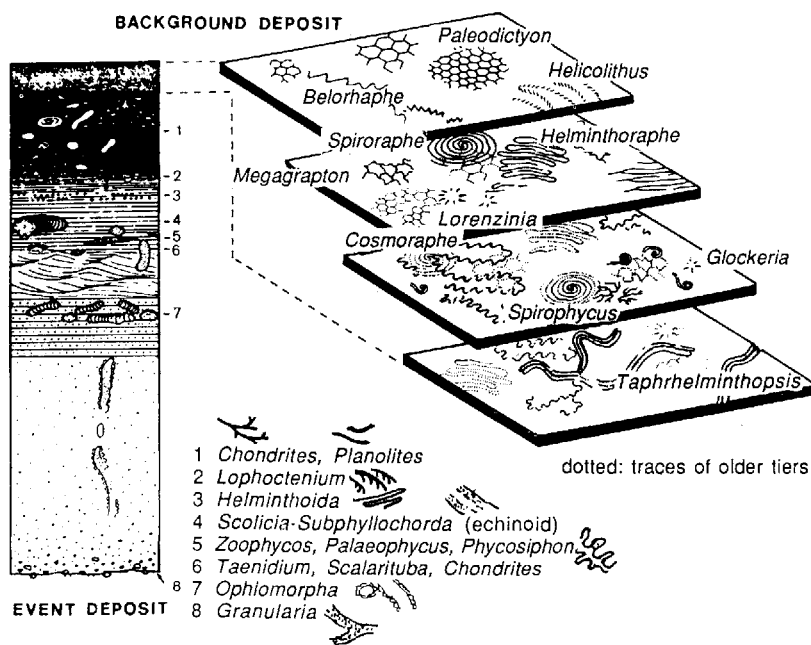


Fig. 11. Generalized trace-fossil tiering (frozen) within the turbidite (event) layer and complex tiering within the background sediment. Based on the Upper Cretaceous–Lower Eocene of northern Spain. Tiering in the turbidite layer is controlled by the textural and structural profile. Tiering of the background sediment (carbonate poor) reflects the ranges of penetration depth, nutrient and oxygenation levels. More intensively bioturbated sediments are impoverished in graptolites. After Leszczynski (1993).

units from the *Cruziana* and *Skolithos* ichnofacies, but this can be interpreted in different ways.

- Ichnofabrics from the Upper Cretaceous chalk were the first to be described (Ekdale & Bromley 1983; Bromley 1990), where application of light oil to a sawn surface (Bromley 1981) enhances burrow differentiation. Analysis of the ichnofabrics aid in distinguishing between allochthonous and autochthonous Chalk (Bromley & Ekdale 1987), between shelf and deep sea chalk (Ekdale & Bromley 1984), and in recognizing different states of the substrate during chalk deposition (Ekdale & Bromley 1991). It is useful to acknowledge the value of trace fossils associations for Upper Cretaceous correlation in northwest Europe (Mortimore & Pomeroy 1991).

Discussion The question may be posed: 'How do the shallow marine ichnofabrics that have been described correlate with what is presently

understood about modern neritic environments?'. Compared with the research that has been carried out on deep-sea substrates, relatively little has been done on modern siliciclastic (or carbonate) shelves. Areas of particular significance for ichnofabric study are shallow marine carbonates, deltaic and estuarine facies.

The question may also be posed: 'How do the trace fossil studies on turbidite facies link with modern views on the processes and products of turbidite deposition?'. The geological studies have been on relatively small basins, compared with, say, the Bengal Fan system (see Walker 1992), with accent on lateral change associated with oxygenation, type of substrate and nutrient values. Further studies will surely try to differentiate the many hydraulically determined facies (e.g. channel levee, lower fan, suprafan) and the allocyclic factors involved, notwithstanding the restrictions of outcrop scale.

Just as there are many sedimentary depositional environments and facies sequences, so there are far more ichnofabrics that are useful in

facies interpretation than the few so-called archaetypal ichnofacies. The value of the ichnofabric approach has been emphasized by Taylor & Gawthorpe (1993), who demonstrate its use in resolution of sequence stratigraphic framework (Fig. 10). When the sediment is intensely bioturbated (as is common in the Upper Jurassic of the North Sea) only the ichnofabric approach is suitable. No higher level of ichnofabric classification is required. Sedimentologists have found that terms other than the traditional broad environmental terms are unnecessary. For palaeobiological purposes *ichnocoenosis* is useful. At the large scale, Frey *et al.* (1990) have used *ichnocoenosis* interchangeably with *ichnofacies*.

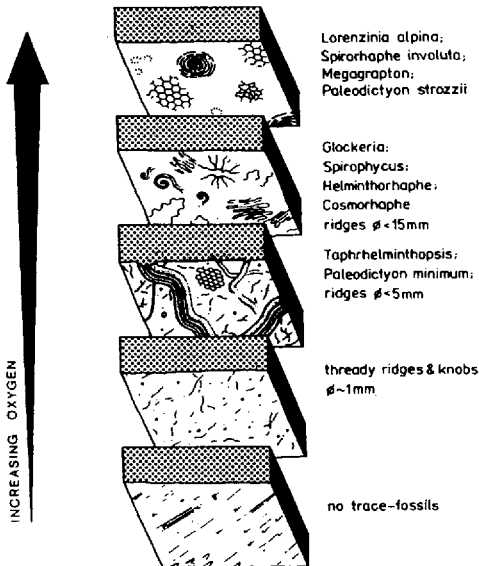


Fig. 12. Oxygen-related sequence of pre-turbidite trace fossils seen on turbidite soles (Cretaceous–Tertiary). The upper diagram represents optimum conditions for graphoglyptid producers. After Leszczynski (1991a).

Hardgrounds, encrusters and borers

The value of primary frame builders in build-ups (reefs) as indicators of water turbulence and illumination intensity is well documented. Martindale (1992) showed that (for Recent and Pleistocene reefs of the West Indies) the secondary frame elements (e.g. coralline algae, bryozoans), together with encrusting foraminifera and serpulids, also relate to environmental factors and, since they may continue to colonize

the substrates (until buried) after the demise of the primary frame builders they can indicate environmental changes, e.g. changes in water depth. This is likely to be a useful palaeoecological tool.

Hardground biotas and their distribution have now received much attention, as have the formation and diagenesis of hardgrounds (see reviews by Wilson & Palmer 1990, 1992). The more specific environmental distributions and relationships to basin development are less clear. Hardgrounds represent synsedimentary lithification of a carbonate seafloor or, occasionally, of mixed carbonate–siliciclastic sediment (Molenaar *et al.* 1988; Molenaar 1990; Martinius & Molenaar 1991). Without recognition of the boring and encrusting biota, it is more difficult to prove beyond doubt such synsedimentary lithification. However, this seldom means that **gradual ecological replacement** took place (Gruszczynski 1986; Miller 1986). In shallow marine environments small shifts in relative sea level can lead to emergence, frequently accompanied by incursions of meteoric water and rapid cementation. Wilson & Palmer (1992) discussed the formation of modern hardgrounds, cement minerals and the reasons for the observed changes over geological time. In modern situations it is generally found that a veneer of loose sediment overlies the cementing layer.

Unconformity surfaces and exhumed surfaces are rockgrounds: the biota colonized a surface following a (major) stratigraphical hiatus during which the sediment had become well lithified, and often tectonically disrupted, so that borings may penetrate and encrusters overlap cemented faults and fissures. Skeletal substrates also display such overlap: an encrusting oyster is itself encrusted and bored. Similarly, hiatus concretions can be encrusted *in situ*, and/or subsequently, when broken and incorporated into a conglomerate.

Fürsich (1979) classified Jurassic hardgrounds into nine types. The factors included degree of mechanical erosion, and whether the hardground surface reflects a primary bed form or structure (tepee structure). The relative degree to which erosional and biological processes (bioerosion and shell accumulation) acted determines the finer detail of the essentially planar hardground, which may record a complex history of aggradation and erosion. Hardgrounds are local, as on megaripple foresets, or of regional extent (Kendall & Schlager 1981). This is an important distinction, especially for basin analysis (Fürsich *et al.* 1992).

Although hardgrounds formed over a wide range of environments there seem to be two

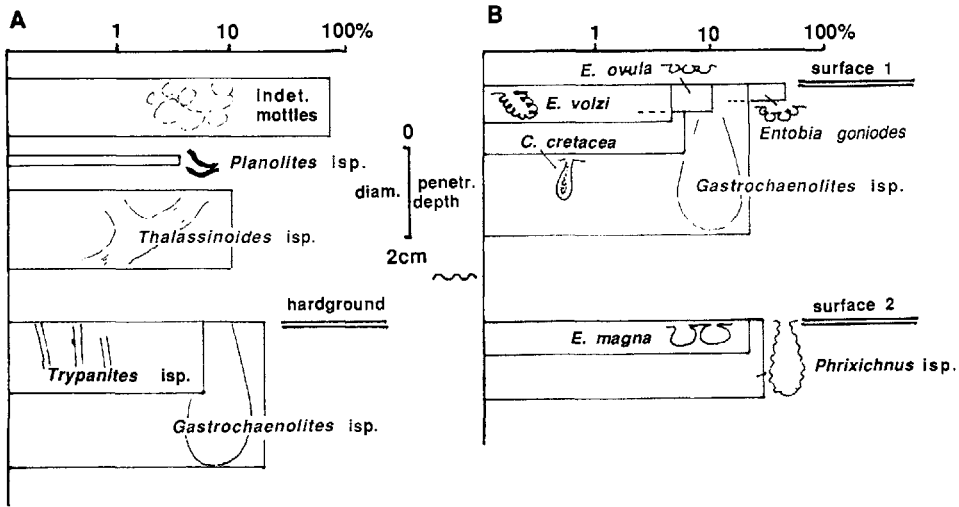


Fig. 13. Ichnofabric Constituent diagrams (schematic) for hardgrounds and rockgrounds. (A) Firmground to hardground, possibly representing gradual ecological replacement. (B) Rockground, displaying two ichnocoenoses reflecting an increase in bathymetry. Measurements in the vertical scale are to burrow diameter (top A) or to penetration depth of borers (and then related to successive hardground or rockground surfaces). For hardgrounds or rockgrounds the areas evaluated must be given. For small patches the 'cover' may account for up to c. 100%. Data based on Bromley & Asgaard (1993, fig. 13). (For further explanation see caption to Fig. 8.)

main hydraulic settings: (1) in shallow, warm epeiric seas, e.g. Ordovician, North America (Brett & Liddell 1978), Devonian, Russian Platform (Goldring & Kazmierczak 1974, with references to Russian literature), Jurassic, northwest Europe (Palmer & Fürsich 1974); Poland (Gruszczynski 1986); (2) in somewhat deeper offshore water, as in Cretaceous chalk of northwest Europe (Gale *et al.* 1987) and Tethyan Jurassic (Wendt 1971). In the first the hardground is typically abraded and planar, ground by the movement of sand-sized material under wave action, in the second it is irregular, due largely to the bioturbational topography produced in an environment of relatively low energy; a sediment-starved (abandoned) sedimentary surface. In the first, when pre-omission burrows of crustaceans and enteropneusts are present, excessive bioerosion led to situations resembling sediment starvation. The distribution of the biota is contrasting: in the first, abraded surfaces, in general, display one or more colonizations, often with evidence of several intermediate periods of planation. In the second, upper surfaces are sparsely encrusted and bored, possibly because of dustings of fine-grained sediment.

Many local, abraded hardgrounds formed above cross-stratified carbonate sands. Might

they represent very local cementation of a dune trough where cementation took place apparently at the same time as colonization and over the period represented by the local Colonization Window (Pollard *et al.* 1993)? Alternatively, the hardground may indicate a eustatic event or a change in sand supply. Hardgrounds are generally absent from depositional areas where current strength exceeded wave strength. It is agreed that micritic hardgrounds must have taken longer to form than those of sand grade sediment and it might be expected that they should be more likely to demonstrate gradual cementation and community replacement (Miller 1986) than hardgrounds developed on sand grade substrates. Of the many hardgrounds in the Polish Middle Jurassic hardgrounds discussed by Gruszczynski (1986), few show evidence for gradual cementation. Gradual lithification was probably more common in type-2 hardgrounds where cementation was slower, and only in certain cases proceeded to a fully cemented hardground. Of course, it is the biota that enable recognition of the states of lithification (Gruszczynski 1986), but the resolution is not as good as might be wished.

The reasons for the uneven distribution of hardgrounds over geological time are unclear, though latitude (tropicality) and the presence/

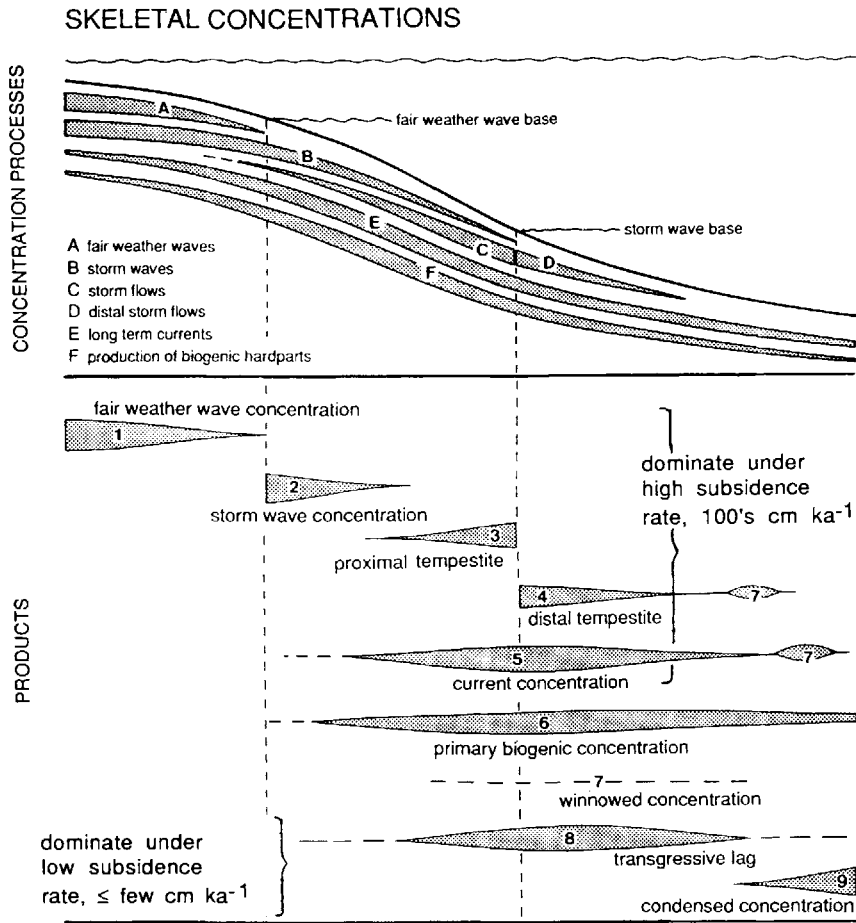


Fig. 14. Process-related classification of skeletal concentrations and their distribution along an onshore-offshore gradient, based on data from the Jurassic of Kachchh, western India (after Fürsich & Oschmann 1993). The types of concentration are grouped according to subsidence rate [after Kidwell 1993a, based on study of the Salton Trough (Neogene), Gulf of California (high rate) and Miocene sediments of the US Atlantic (passive) margin (low rate)].

absence of epeiric seas were likely significant factors. Hardgrounds are rare in the Dinantian (Mississippian), rare in the Pennsylvanian and unknown in the Permian. The sedimentary/tectonic settings for hardgrounds are also uncertain, but where current activity was dominant and erosion rates high, leading to thick successions, then hardgrounds are nearly absent. This applies to both times of calcite and aragonite regime (Sandberg 1983). Wilson & Palmer (1992) make the useful point that Ordovician hardgrounds are frequently asso-

ciated with echinoderm skeletal elements and 'that echinoderms promoted the rapid and widespread production of the very substrates on which they thrived and radiated' by syntaxial overgrowth by the marine calcite cement. Apparently, this does not hold for the Dinantian.

Most hardgrounds relate to either lowstand planation or transgressive and highstand flooding and planation (Fürsich *et al.* 1992; Fürsich & Oschmann 1993); many represent shallowing. Slightly deeper water hardgrounds formed

during transgression, just out of reach of wave/current activity.

The Ichnofabric Constituent diagram applied to softground ichnofabrics (above; Fig. 8) can be modified for the evaluation of the boring ichnocoenoses of hardgrounds and rockgrounds that may reflect changes in substrate consistency or depth (Fig. 13).

Table 2. *Attributes of shell concentrations*

1. **Final depositional biofabric.** Thickness of unit; geometry of unit; nature of sole of unit (e.g. erosive, \pm gutters); primary sedimentary structures (e.g. cross-lamination, \pm grading); nature of intraformational clasts; matrix (e.g. wackestone, packstone, grainstone, umbrella structure); close-packing of skeletal elements; size-sorting of skeletal elements (Kidwell & Holland 1991); orientation of skeletal elements (Kidwell *et al.* 1986).

Sum-up as plan and side view aspects.

(NOTE: Bed may be composite, when each layer must be separately analysed.)

2. **Preceding taphonomic history.** Disarticulation; abrasion; bioerosion (boring, biting); encrusting; relative abundances of taxa; diversity (species, genus); fragmentation; ecological spectrum (benthos, nekton); age spectrum.

Sum-up as likely succession of events between death and final burial.

3. **Succeeding history** (not considering compaction and metamorphic aspects). Bioturbation from top of bed, or from much higher (e.g. tubular tempestites), or from below bed.

Shell concentrations and biogenic substrates

Shell concentrations have been largely the preserve of palaeontologists for palaeocommunity analysis and in seeking morphological or stratigraphical information. The former aspect has provided some environmental information in terms of proximity and distality from a shoreline as in the study by Zeigler *et al.* (1971) of the Lower Silurian of Wales and the Welsh Borderland. Kidwell *et al.* (1986) showed how shell concentrations can be analysed sedimentologically and taphonomically, and this work has led to an appreciation of the information that shell beds can provide about depositional environment and basin development. Kidwell (1991a) reviewed classifications of shell accumulations. Fürsich & Oschmann (1993) took analysis of shell concentrations a step further, recognizing nine types of shell bed in the Upper Jurassic of Kachchh, each typical of a distinct depositional environment in a shore-offshore sequence (Fig. 14, Table 2). The fabric of a shell

Table 3. *Fabric and taphonomic features of shell beds.* (Drawn mainly from Fürsich & Oschmann 1993)

1. Fairweather wave concentrations

Fabric: bioclast supported; poor sorting; bimodal plan orientation.

Taphonomy: fragmentation high; encrusting, boring absent.

2. Storm wave concentrations

Fabric: erosive base; pack-grainstone; bimodal sorting (complete shells & comminuted debris); random orientation (plan); hummocky cross-stratification (shells in pods).

3. Proximal tempestites

Fabric: as for (2) but with indications of transport; packstone to wackestone; \pm grading; \pm cross-lamination/hummocky cross-stratification; flute casts.

Taphonomy: disarticulation general.

4. Distal tempestites

Fabric: thinner than (3); sorting better than (3); shells convex up; \pm grading.

Taphonomy: fragmented > complete valves; abrasion high.

5. Current concentrations

Fabric: cross-stratification; packstone matrix.

Taphonomy: abrasion and disarticulation high; \pm bioerosion.

6. Primary biogenic concentrations

High degree of autochthony (epifaunal, \pm nests), but local hydraulically determined patches; packstone to wackestone matrix; encrustation and boring; \pm compound/amalgamated units.

7. Winnowed concentrations

Fabric: generally <10 mm thick; stratification poor, sole \pm graded; \pm lateral passage to sharp sole.

Taphonomy: shell completeness often high (including thin shells); abrasion minor; \pm encrustation.

8. Transgressive lags

Fabric: often complex; \pm amalgamation & reworking; omission overlap bioturbation; incipient cementation; random orientation (overall); evidence of different hydraulic processes.

Taphonomy: disarticulation, fragmentation, abrasion variable through unit; encrustation, boring high.

9. Condensed concentrations

Fabric: as (8) but longer time involved, \pm mixed zonal fossils, but less overall transport; \pm evidence of early diagenesis & reworking of concretions; sole less regular than (7); pockets.

Taphonomy: time-averaging high: \pm shell dissolution.

bed reflects the dynamics of the final depositional process, and the taphonomic signature of the material (Table 3) the environmental conditions under which the shells formed and accumulated prior to incorporation in the shell bed. Fürsich & Oschmann (1993) distinguished

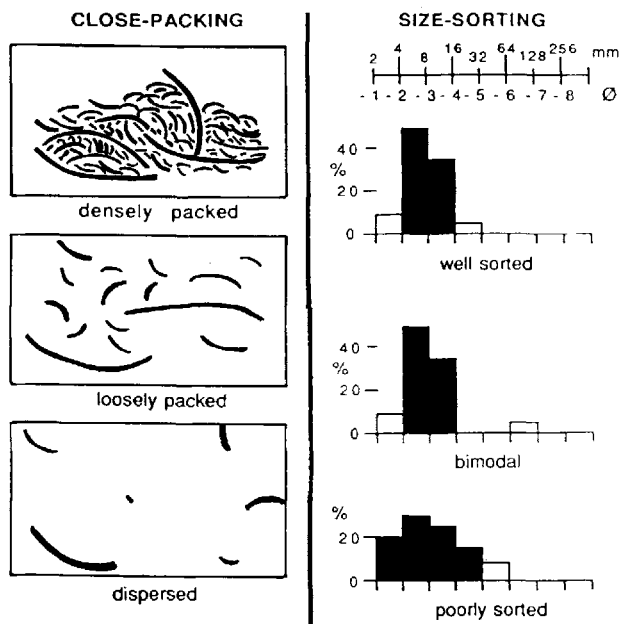


Fig. 15. Schematic illustration of categories of close-packing and size-sorting for bioclasts >2.0 mm. (After Kidwell & Holland 1991). Well-sorted: 80% lie within one or two adjacent (ϕ) size-classes. Bimodal: well-sorted but with distinct second mode. Poorly-sorted: over 80% lie within three or more size classes. Nine combinations can be used, e.g. loosely packed and well-sorted.

between **storm beds**, representing insignificant lateral transport, and **tempestites** which have involved lateral transport. [Einsele & Seilacher (1991) recognize only tempestites, where no significant lateral transport has taken place.] For analysing fabric, Kidwell & Holland (1991) introduced a useful classification for shell packing and size sorting (Fig. 15). The make-up of shell beds is also influenced by time-averaging (below), the input of exotic shells and biological processes, including mass mortality, gregarious settlement, population maturity (pioneer or specialist) and the effects of taphonomic feedback (Kidwell 1991b).

Subsidence and sediment accumulation rates during deposition of the Jurassic of Kachchh might be described as average. Kidwell (1991a, 1993a, b) presented a general model for lower and higher rates of sedimentation which can be used to modify Fürsich & Oschmann's (1993) scheme (Fig. 14).

Time-averaging (Figure 16) Time-averaging is reviewed by Kidwell & Bosence (1991). Though few shells are retained in life position they conclude that the effect of time-averaging on

the composition of level-bottom shelf, shelly assemblages appears to be minor, and that out-of-habitat movement is minor, thus justifying analysis of ancient shell beds for community reconstruction and community evolution. This appears contrary to the inferred dynamics of tempestites, as understood by Fürsich & Oschmann (1993). In studies on modern shell assemblages, Bosence (1979) noticed that species represented by dead material are of low abundance though relatively high in diversity. The dead-only species provide useful information about adjacent environments. In Mannin Bay (Eire) the dead-only species were those derived from the rocky shoreline. In ancient examples this sort of information can be valuable, for instance, in providing information about the nature of a type-1 sequence boundary.

Palaeocommunities The community concept is important for facies interpretation since each community is often representative of a particular environment. In terrestrial environments communities tend to be relatively sharply delimited, spatially and energetically. In the marine realm the widespread nature of nearly all the primary

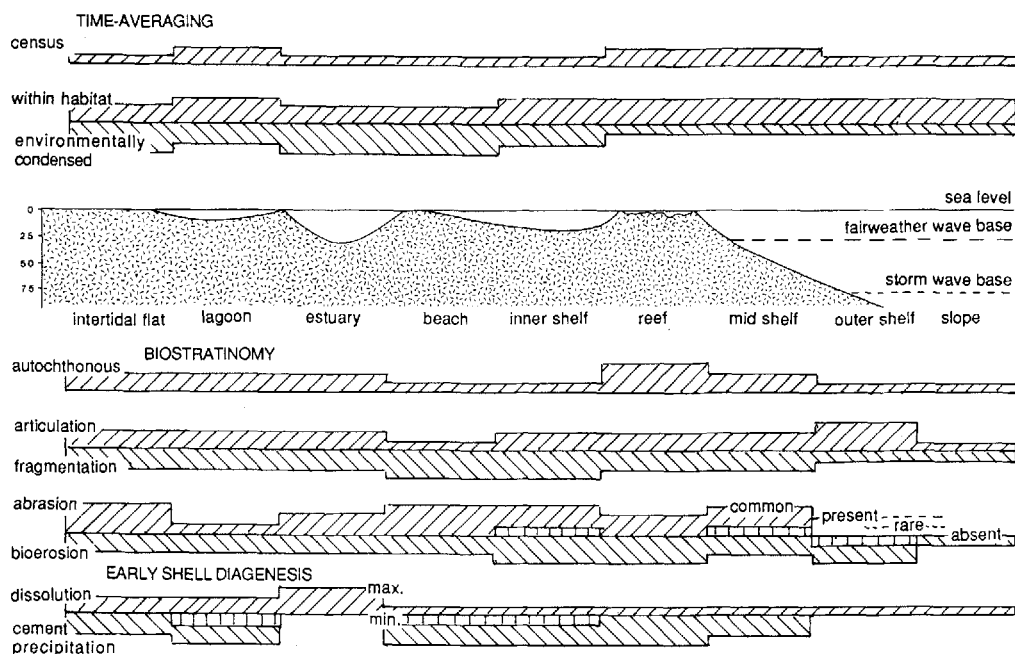


Fig. 16. Trends in taphonomy related to bathymetry and time-averaging. Census: a near perfect record of live, shelled taxa. Within habitat: modified record due to post-mortem disturbance and/or time-averaging. Autochthonous: in position of life. (After Kidwell & Bosence 1991).

production means that discrimination on the basis of energetics is fraught with difficulty and discrimination spatially is akin to the problems of facies analysis. Marine associations tend to be habitat communities where some degree of trophic interactions may be present. Full and detailed analysis of the palaeoecology of ancient communities is probably restricted to the rather rare instance of a substrate where an ecological succession has been preserved almost intact; such as in mudstone (Bray 1972) and in calcareous hardgrounds (Gruszczynski 1986), and the meticulous analysis of the palaeoenergetics of individual species (Powell & Stanton 1985).

Three developments should promote further studies: (1) the results of studies on time-averaging (above); (2) the integration of ichnology and ichnofabric analysis with analysis of the shelly biota; and (3) recognition of the type of skeletal concentration present (above). (It is likely that some of the palaeocommunities described in the literature will be found to be invalid since little regard was given to these three considerations.)

Four criteria are necessary for community

recognition in marine sediments: (1) the group of ichnotaxa is predictable; (2) the group of shelly taxa is predictable; (3) the taxa are representative of a limited area; which (4), has a single facies association. Although such a community will be far removed from an energetically closed system it will always be useful to determine what trophic levels and what stages of ecological succession are present.

In muddy sediments most autochthonous marine assemblages were preserved as such because of changes in water chemistry rather than by physical smothering (obruition), though many examples of the latter have been described from a range of habitats (Brett & Seilacher 1991; Seilacher *et al.* 1985). Growth rates in corals (e.g. Ali 1984) give a guide to sedimentation rate in depositional environments where turbidity was probably high.

Pioneers Opportunistic colonizers are probably over-represented in the fossil record. At the end of an abiotic interval, represented by a thick or thin sedimentary unit, the pioneering stage of substrate recolonization follows the gradual amelioration. Following an event which wiped

out or devastated the biota, the features by which pioneers may be recognized include dense tube and burrow aggregations (which may affect micro-topography and bed roughness), dense, often monospecific assemblages of deposit and suspension feeders. Pioneers must be distinguished from the biota of a stressful environment, e.g. beach with dense *Mulinia* (Frey & Goldring 1992, fig. 3), though this may not be easy. The geographical extent (ecologic field) of the abiotic event is a factor that needs investigation. For instance, in the Lower Greensand (Aptian, Lower Cretaceous) at Baulking, east of Oxford, the upper of two Ca-bentonites shows a gradual return to equilibrium conditions over an appreciable thickness of sediment. This contrasts with the rapid recovery of the biota following storm event beds elsewhere in the succession, as outlined by Einsele & Seilacher (1991) and Seilacher (1991). The ecology of natural disturbances is also a topic of concern to biologists (Pickett & White 1985).

Conclusions and prospects

The analysis of facies and fossil species shares common characteristics: both are difficult to discriminate, describe and relate to other facies/fossils. Indeed, one's worth as a sedimentologist or palaeontologist depends much on the success with which one's proposals are received. Facies analysis is particularly difficult because it encompasses every aspect of the sediment, including getting the palaeontological taxa right, and extending to the facies geometry and to the geographical situation (including latitudinal aspects) and relationships with adjacent facies. Facies analysis is best carried out by considering each factor in turn and then synthesizing in the traditional manner of palaeoecological analysis.

The application of ichnofabrics in an integrated manner to facies interpretation is already showing exciting advances and is enhancing the resolution previously available. The approach is also significant for basin analysis and sequence stratigraphy; in the recognition of key stratal surfaces and shallowing up parasequences (Taylor & Gawthorpe 1993). Since bioturbation modifies primary fabric, analysis in the interpretation of porosity and permeability should be rewarding; an area in which the acoustic properties of the sediment will be revealing.

The classification of shell concentrations by fabric and taphonomic signature (Fürsich & Oschmann 1993) represents a breakthrough in this field, but awaits testing in other basins and whether or not storm and tempestite concentra-

tions can be separated.

The growth of links between oceanographers and sedimentologists concerned with pelagic sediments is particularly encouraging and of mutual benefit. Techniques are now available for recognizing the culprits of many deep sea traces and their ecology and ethology. There is a special need for renewed research on the ichnology of modern shelf sediments.

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Quantitative approaches to palaeozonation and palaeobathymetry of corals and coralline algae in Cenozoic reefs

CHRISTINE PERRIN,^{1,2} DAN BOSENCE¹ & BRIAN ROSEN²

¹*Department of Geology, Royal Holloway University of London, Egham, Surrey, TW20 0EX, UK*

²*Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*

Abstract: The value of quantitative surveys of ancient reef slopes for palaeobathymetric analysis is reviewed. Reefs are selected for palaeobathymetric analysis because they are characterized by *in situ* preservation of benthic communities which are often depth related. In addition, if the reef crest and slope are preserved then ancient water depths can be measured.

The zonation of living reefs has been measured using semi-quantitative phytosociological methods as well as a range of plot and plotless techniques, but there is little agreement as to a single best method. For this study a modified line intercept transect method is selected as it may be used on both living reefs and on various types of outcrops of fossil reefs. This method minimizes problems arising from outcrop conditions, is faster than quadrat methods, can be used to assess different frame-building taxa, matrix, cement and porosity along ancient reef surfaces, and is also frequently used in studies of living reefs.

The zonation of corals and coralline algae on living and fossil reefs can be characterized by three parameters: framework density, diversity and species abundance. The framework density of reef corals is normally greatest on external reef slopes between 1 and 30 m and decreases into shallow reef crest environments, and towards shorelines. Coralline algal frameworks are highest in reef crest environments and may also replace coral frameworks in deeper reef-slope environments. Variations in diversity are complex and relate to biogeographical constraints as well as local variations of physical factors and biological factors. The distribution of reef-building assemblages is often expressed as a zonation which may relate to depth but also to hydraulic energy. Examples of coral and coralline algal zonation are presented and discussed from Indo-Pacific and Caribbean reefs.

Three case studies are presented based on the authors' work on reef zonation. The Seychelles reefs (Indian Ocean) are used to illustrate depth and water energy related zonation of present-day living corals. Coralline algal zonation is illustrated from present-day St Croix reefs (Caribbean), together with preserved zones in sections through these reefs. Coral and coralline algal zonation on fossil reefs are characterized using our modified line intercept transect technique on exposures from late Miocene reefs of Mallorca (Spain).

This review of reef zonation and introduction of a new technique for surveying ancient reef communities to establish depth related zones has important advantages over previous qualitative approaches. Direct measurements of palaeodepths in the field make subjective palaeobathymetric interpretations unnecessary and avoids the problems of assuming uniformitarianism. *In situ* organism assemblages are sampled which minimizes the effects of taphonomic changes on community composition. The technique allows the quantification of framework density, diversity, species abundance and zonation to be compared between different fossil reefs and between living and fossil reefs for the first time.

The establishment of palaeobathymetry is fundamentally important for palaeoenvironmental interpretations, for reconstruction of the internal structure of ancient shelves, and for identification of sea level changes in sequence stratigraphy and basin analysis. Determination of palaeo-

depth is generally based on palaeoenvironmental facies interpretations using indicators derived from biological or sedimentological criteria. When this information is combined with stratigraphic and geometric data it can be used to establish models like onshore-offshore trends or

proximity trends (Ziegler 1965; Allen 1967; Seilacher 1967; Broadhurst & Simpson 1973; Benedict & Walker 1978; Aigner & Reineck 1982; Baarli 1985, 1988; Brett *et al.* 1993). Palaeodepths derived from this approach can only be relative, however, because there are neither biological nor sedimentological criteria for precise and absolute water depth. For organisms, the primary reason for this is that there are no taxa whose distribution is directly controlled by depth, largely because depth itself does not influence them directly. Rather it is other factors like light, temperature, salinity, concentrations of nutrients, quantity of dissolved gases like oxygen, and water turbulence which vary with depth and actually influence organisms, but none of these has a consistent relationship with depth. Their depth relationship varies locally, regionally and temporally. The only a priori depth indication comes from light dependent taxa since these are confined to the photic zone (i.e. down to *c.* 100 m). For plants, the depth limit is usually the compensation depth for light but red algae, whose maximum depth appears to be 250 m, can exceed this (see Dodd & Stanton 1990). In any case, it is dangerous to assume that the ecological requirements, and consequently the environmental preferences of organisms have remained constant through time (Bottjer & Jablonski 1988; Bottjer *et al.* this volume). Rigid application of information from living organisms ('transferred ecology' of Lawrence 1971) can lead to false or problematic palaeoecological reconstructions.

One way of tackling these problems is to use an autecological approach based on depth-related changes in the morphology of a particular taxon, but these are often a response to light or energy gradients (Dodd & Stanton 1990, table 2.5.). Biotic assemblages and community structure (i.e. a synecological approach) can also be informative in palaeobathymetric analysis, as these may be related to depth zones, especially if they are defined along onshore-offshore trends (Ziegler 1965; Broadhurst & Simpson 1973; Fortey 1975; Fortey & Owens 1978; Benedict & Walker 1978; Petersen 1986; Brett *et al.* 1993). Moreover, statistical techniques can be used to provide information on depth gradients. For example, the most common parameter used in investigations of fossil foraminiferal assemblages is the ratio of planktonic to benthonic individuals (Grimsdale & Van Morkhoven 1955; Smith 1955) but faunal dominance and faunal diversity (Walton 1964; Gibson 1966) are also useful. Using assemblages of 'ahermatypic' (i.e. azooxanthellate) corals from a single stratigraphic formation, Wells

(1967) combined the indications of his groups' modern counterparts to obtain palaeodepth (and palaeosalinity) ranges (see also Barta-Calmus 1977). Rosen (1977) developed this method for a Lower Cretaceous example, by combining it with the diversity indications of contemporaneous zooxanthellate-like corals. This was based on a diversity-depth compilation of Recent zooxanthellate genera from eight modern regions.

Sedimentological criteria are also commonly used as indicators of relative palaeodepth or of sea level. Five common categories can be used to provide depth criteria: (1) facies – calcrite or caliche, beach rock, storm deposit, turbidite, etc. (Aigner & Reineck 1982; Aigner 1985; Hopley 1986; Roep 1986); (2) sedimentary structures – mudcracks, bird-eyes, ripples, cross-bedding, burrows, etc. (Allen 1967); (3) grain types – ooids, micrite envelopes, etc. (Bathurst 1967; Kump & Hine 1986); (4) mineralogy – evaporite pseudomorphs, phosphate, zeolites, etc. (e.g. Benedict & Walker 1978); and (5) particular features of early diagenesis – vadose cements and internal sediments or diagenetic sequences which enable the palaeo-water table to be identified (Purser 1969, 1980; Longman 1980; Aissaoui & Purser 1983; Montaggioni & Pirazzoli 1984; Coudray & Montaggioni 1986).

These limitations to most approaches to palaeobathymetry have led many authors to emphasize the need for integrated studies in making palaeobathymetric interpretations, based on comparison of independent biological and sedimentological criteria and on a good understanding of the geometry of the various deposits on platform or basin scale. As already mentioned, this kind of approach provides information on relative palaeodepths in a lateral succession of biofacies (e.g. Laporte 1969). Comparison of facies within a finely-defined time-interval may give information about the palaeotopography, and the depth patterns across a platform or basin at a given time (Benedict & Walker 1978). Comparison of biofacies in vertical sections at the platform or basin scale enables relative sea-level changes to be reconstructed. Such an analysis could lead to the distinction of tectonic controls (subsidence or uplift) from eustatic controls of sea level (e.g. Benedict & Walker 1978). Clearly, the finer the time resolution, the more precise the interpretation. These kinds of facies-based studies are clearly constrained by the taphonomic factors affecting shelf faunas and floras and by transport of skeletons and grain types (Kidwell & Bosence 1991). Seilacher (1967) emphasized the advantages of trace fossils from this point of view.

In general, palaeobathymetric precision also depends on the physical scale of a study. Indications of major sea-level changes or of large bathymetric zones (within a range of tens to hundreds of metres) from littoral to abyssal for whole basins contrasts with the finer scale approach in this paper, based on coral reefs. Coral reefs are chosen here for palaeobathymetric analysis for several reasons:

1. They are characterized by biological and sedimentological zonations which are partly related to depth gradients;
2. They commonly consist of preserved bioconstructional facies with numerous organisms in growth position (i.e. strictly autochthonous *sensu* Seilacher 1967), so it is easier to be sure of obtaining data from life-assemblages;
3. Their rigid reef framework, frequently subjected to early lithification, favours the preservation of the original reef morphology, hence relative depth information;
4. Their external palaeoslopes are more often preserved intact in the geologic record than in other kinds of environments and this makes direct quantitative estimates of depth possible;
5. It is possible to carry out fine-scale quantitative studies on such preserved reefs, yielding precise palaeobathymetric information (from several metres to tens of metres) suitable for inferring high frequency sea-level changes (*c.* 10^3 – 10^4 years).

Preservation of external palaeoslopes of reefs (4) is particularly important, because the uppermost points of such slopes provide a consistent reference 'marker' from which relative depth of *in situ* organisms on the slope can be measured. Moreover, there may be evidence for the top of the reef slope being at or very close to contemporaneous sea level, which then provides a marker for absolute depth measurements for the slope organisms. Note that use of reef slopes therefore provides direct data for depth distributions of organisms, so making a priori ecological assumptions of those organisms unnecessary. This also provides a sound basis for studies of palaeoecological zonation.

The main pitfall of using coral reefs is that they are subject to erosion. Reef crests and ledges are especially susceptible. In particular, the reef top is commonly truncated because of its location in the zone of wave action. In addition it can often be affected by erosion during a later sea level low-stand. Reefs also consist of

heterogeneous biologic material, often of massive aspect, and rarely show clear internal stratification (clear internal fine-scale discontinuities), so making it difficult to be confident of working on a single time plane. Consequently, palaeobathymetric analyses of ancient reefs require detailed prior understanding of their particular geological setting, reef geometry and internal structure. Moreover, because reef zonation consists of overlapping communities, both qualitative and quantitative data are needed for a detailed understanding and definition of reefal biotic assemblages.

Aim and scope of the paper

The aim of this paper is to present a new quantitative method which can be used for recording the palaeozonation of fossil reefs and its relationship to palaeobathymetry. However, because palaeozonation of fossil reefs has not previously been established quantitatively, and also because of the complexity of reef zonation, it is necessary to review and discuss previous ecological studies of living reefs. This is the basis on which present field methods have been developed for assessing zonation of fossil reefs – specifically, the selection and definition of parameters which can be measured both on present-day and fossil reefs. The new approach discussed here has the particular advantage of allowing quantitative comparison of results obtained both from present-day and fossil reef zonation. Analysis of field data and their interpretation are beyond the scope of this paper.

This paper is organized into four main parts. The first deals with the environmental controls on reef growth and zonation and considers the various effects of environmental factors on different scales in space and through time. The second part of the paper discusses the choice of a suitable quantitative technique for establishing palaeozonation and palaeobathymetry of fossil reefs. Techniques which are currently used, or which could be used on present-day reefs, are firstly reviewed; their reliability, suitability and potentiality for fossil reef analysis are then discussed and the selection and development of a new method are explained. The third part considers the various parameters for characterizing reef zonation and their relationship to depth on present-day reefs. Finally, three case studies are presented giving details of coral and coralline algal zonations, two of them from present-day reef environments and the third one from late Miocene reefs of Mallorca (Spain).

Environmental controls of reef growth and zonation

Many factors affect coral reef growth and their respective controls act on a variety of scales:

1. individual organisms: recruitment, growth rate, size, growth forms, reproduction, mortality (i.e. life histories);
2. populations: abundance and distribution of individual taxa;
3. communities and at the ecosystem level: habitats, differing composition of communities; ecological zonation;
4. reef dimensions and geometry;
5. global distribution of coral reefs;
6. reef growth through time.

(See also Miller 1991 for a similar hierarchical scheme.)

Abiotic influences on reef growth, which correspond to environmental physical and chemical conditions, are related both to global conditions (climate, oceanography) and to local geographical characteristics. On the global scale, light and temperature are the major controls of coral reef distribution (Rosen 1984; Achituv & Dubinsky 1990). The influence of temperature on reef-builders on individual reefs is mostly confined to the uppermost levels of reefs, especially reef-flats. The major factors controlling reef zonation, such as light intensity and hydrodynamics (Done 1983), are partly related to depth. Increase of nutrient-flux can act as an important control on community zonation and may affect reef growth by increasing bioerosion in relation to carbonate production rate and bioerosion (Hallock & Schlager 1986; Brasier this volume). Edaphic factors (occurrence and extent of substrates, local substrate morphology and sedimentation rate) depend on characteristics peculiar to the site, and therefore these factors are not depth related (but see below).

Biotic factors which affect reef growth concern the different types of interactions between organisms: predation, grazing, symbiosis, parasitism and competition for limiting resources like nutrients, light and space. Each species has its own characteristics: ecological requirements, behaviour, growth and other life history characteristics. The influence of biotic factors on reef zonation is important but highly complex, and does not have any simple relation to bathymetry. Historical biogeography also has an indirect influence on reef zonation since it controls the global and regional pool of species at a particular time.

Interactions between different ecological factors are numerous and complex. For example, an increase in nutrient supply is thought to have at least three effects (Hallock & Schlager 1986). It favours phytoplankton development, whose proliferation reduces light intensity. It stimulates the growth of fleshy algae which increases their spatial competition with reef-builders and reduces available substrate for the latter. It also favours infaunal suspension-feeding molluscs and hence increases bioerosion. Bioconstructors like corals modify their own substrates in an apparently self-perpetuating way, as in the 'facilitative taphonomic feedback' of Kidwell & Jablonski (1983). As the distribution of corals is partly depth controlled, a relationship between substrate factors and depth may therefore develop in more mature reefs. Despite the development and improvement of experimental studies, such as effects of sedimentation rates (Babcock & Davies 1991), it still remains difficult to establish simple relationships of cause and effect from ecological studies of present-day reefs. Moreover, these various factors, especially biotic ones, are difficult to quantify on living reefs. Such investigations require a considerable amount of data, in general collected at various periods of the year, and the use of extensive resources.

For fossil reefs there is no direct evidence of most ecological factors. A certain amount of information may be obtained from the studies of sediments: granulometry, grain abrasion, geometry of deposits, mineralogy, early diagenesis, boring organisms and so on. Geochemical and isotope techniques enable palaeotemperature (Weber 1977; Druffel 1985; Aharon & Chappell 1986; Carriquiry *et al.* 1988; Aharon 1991), palaeosalinity, irradiance (Weber *et al.* 1976; Weil *et al.* 1981; Pätzold *et al.* 1991), influence of nutrients and changes in ocean circulation (Shen & Boyle 1988; Shen *et al.* 1991, Brasier this volume) to be evaluated, but they can only be applied to relatively recent reefs (Holocene and Pleistocene) that still contain components whose original mineralogy and structure has not been modified by diagenesis. While some ecological factors like light intensity and hydrodynamics are partly and indirectly linked to a bathymetric gradient, the relationship of biotic factors and sedimentation rate to depth is not so clear.

Most ecological studies of present-day reef zonation attempt to establish patterns in relation to a selected environmental gradient, e.g. variations of distribution and abundance of individual taxa, or change in composition and structure of assemblages or communities along this gradient. Broadly, two approaches to

Table 1. *Coefficients of abundance-dominance used in phytosociological methods, from Scheer (1972, 1974, 1978), Molinier & Picard (1953) and Vasseur (1964)*

Abundance-dominance (from Scheer 1972, 1974, 1978)	Abundance-dominance (from Molinier & Picard 1953; Vasseur 1964)
r A few isolated specimens, cover negligible	+ A few isolated specimens
+ Sparsely present, cover low 0.25% cover	1 Cover < 1/20 total area
1 More frequently present covering < 5% of the sample plot (i.e. 1.25 m ²) or only isolated with the same cover 2.50% cover	2 Cover 1/20–1/4 of total area
2 Abundant or covering 5–25% of sample plot (1.25–6 m ²) 15% cover	3 Cover 1/4–1/2 of total area
3 Any number of specimens covering 25–50% of sample plot 37.5% cover	4 Cover 1/2–3/4 of total area
4 Any number, covering 50–75% 62.5% cover	5 Cover > 3/4 of total area
5 Any number, covering 75–100% 87.5% cover	

zonation studies are used. In the first, an environmental gradient is defined from prior knowledge or study of the spatial variation of a selected ecological factor (or a combination of factors): light, water energy, sedimentation rate, salinity, etc. Distributions of taxa are studied at pre-defined sites or localities along such a gradient. These kinds of studies can be called factor-specific zonation schemes. In the second, the patterns of occurrence of taxa are determined in their own right in relation to a neutral spatial scheme (e.g. a grid, a transect or a topographically defined set of sites). The distributions are then analysed with respect to ecological factors, these being either previously known, or investigated at the same time, and correlations sought and established. Gradients and zonations can be extracted from such correlations, e.g. by selecting an appropriate transect related, say, to bathymetry, distance from the shore, or distance from a detrital source. In the case of synecological studies, assemblage or community patterns may emerge whether or not there is clear correlation with one or more particular environmental variables. These patterns can be called 'general' zonation schemes and as is widely recognized, they are the net expression of numerous factors, both biotic and abiotic. In practical terms, the zones identified in a study are generally characterized and named by the dominant organisms in each zone, or according to the organisms which are apparently restricted to each zone. The first can easily be studied semi-quantitatively (e.g. the

Seychelles case study in this paper). The second lends itself to multivariate techniques (e.g. Done 1982). As restricted species may also be relatively rare or inconspicuous, some kind of abundance weighting might also be required. For a fuller discussion see Done (1983).

Since depth as a controlling factor consists of numerous variables, depth zonation patterns are likely to vary considerably both locally and regionally, making it difficult to establish a satisfactory generalized zonation scheme which also has a constant absolute relationship with particular depth values. At best one might obtain a scheme in which depths of zones are relative and in which the zones themselves may be condensed or attenuated according to conditions in different places and regions.

In order to discuss further how communities and other characteristics change along a selected gradient it is first necessary to define some distributional parameters of reef organisms which can be evaluated quantitatively or semi-quantitatively.

Selection and development of new quantitative methods for assessing fossil reef zonation

Quantitative and semi-quantitative methods used in ecological studies of living coral reefs

There has been an intensive development of semi-quantitative and quantitative techniques of

Table 2. Coefficients of sociability or gregariousness and coefficients of presence-constancy in the phytosociological methods (from Scheer 1978).

Sociability-gregariousness	Presence-constancy
1 Small isolated colonies or isolated solitary corals	I Presence constancy of 1–20% (seldom present)
2 Small colonies or isolated corals growing in small groups or forming patches of the size of a hand (c. 10 × 20 cm or circles with 16 cm diameter)	II 21–40% (not often present)
3 Small colonies growing in troops or forming small hedges or patches of 0.2–0.4 m ² (up to 65 × 65 cm or 70 cm diameter), or bigger colonies of this size	III 41–60% (often present)
4 Colonies of 0.7–2 m diameter or hedges and patches of 0.4–4 m ²	IV 61–80% (mostly present)
5 Colonies larger than 2 m diameter or hedges and patches bigger than 4 m ²	V 81–100% (constantly present)

benthic marine community analysis since the 1970s, often through the application and adaptation of approaches and techniques used in terrestrial plant ecology (Greig-Smith 1964; Pielou 1969).

I. Semi-quantitative techniques: phytosociological methods This approach is derived from the original method of Braun-Blanquet (1964) used for the ecological study of plant communities and later adopted by several authors for studies of marine soft-bottom biotas (Molinier & Picard 1953; Laborel & Vacelet 1958; Perès & Picard 1958; Picard 1962, 1965) and coral reefs (Barnes *et al.* 1971; Rosen 1971, 1972; van den Hoek *et al.* 1975; Pichon 1978*a, b*; Scheer 1978; Vasseur 1981; Faure 1982; Faure & Laboute 1984).

The method is based on analysis of species composition with more detailed observations of limited areas or sample plots, usually quadrats, the position and size of which is carefully selected as representative. In Braun-Blanquet's (1964) method, analysis of species composition combines both abundance (number of individuals for a species) and dominance (based on areal cover for a species). Each species is recorded in the field with a semi-quantitative coefficient of abundance–dominance defined from the Braun-Blanquet scale (1964) or from those by Vasseur (1964) or Scheer (1972, 1974, 1978) (Table 1). Species cover is determined by geometrically projecting the plan of individual colonies on to a horizontal surface notionally corresponding to the substrate below them. Species cover percentages may then be estimated by taking the respective average of each coefficient and comparing it to the total cover (Scheer 1978). Similarly, other scales have been established to define sociability or gregariousness and presence-constancy (Table 2; Scheer 1978).

II. Fully quantitative techniques Two types of technique are used: (1) plot techniques using either a randomly or an arranged distribution of quadrats as sampling units; (2) plotless techniques using a measurement (length between points) from or along a sampling structure, usually a line transect of a predefined length.

(IIa) Plot techniques Quadrats may be arranged in a continuous belt along a line transect (Grassle 1973; van den Hoek *et al.* 1975; Bak 1977; Dodge *et al.* 1982; Chiappone & Sullivan 1991). They may also be distributed discontinuously along the transect either randomly, or placed at predefined intervals, e.g. depth intervals. Weinberg (1981) described a random point transect method using a photographic record of quadrats randomly placed along a 20 m long line parallel to isobaths. Bak & Lukhurst (1980) used a transect normal to the shoreline with quadrats sampled at predefined depths of 10, 20, 30 and 40 m while Titlyanov & Latypov (1991) sampled 3–5 quadrats per metre of depth along a transect. Individual quadrats may be studied at selected depths in different sites for comparison (Sheppard 1985; Bak & Povel 1989), or distributed randomly in a defined area (Grassle 1973).

Sampling within quadrats may consist of individual counts and cover estimates: (1) made *in situ* (Grassle 1973; Weinberg 1981; Bak & Povel 1989; Chiappone & Sullivan 1991; Titlyanov & Latypov 1991) using, for example, phytosociological methods (van den Hoek *et al.* 1975); or (2) obtained from photographic records (Dodge *et al.* 1982). Alternatively, a point intercept surface method is used to sample the quadrats (Bak & Lukhurst 1980; Weinberg 1981; Sheppard 1985). The parameters usually obtained from quadrat analysis are number of species, number of individuals for each species,

total cover, cover of each species (in cm² or as percentages), and density (number of species per m²).

(IIb) Plotless techniques Loya (1978) reviewed plotless techniques used in plant ecology and considered them valuable and with potential for coral reefs. Two types of plotless techniques may be distinguished:

1. the plotless distance-measuring methods;
2. the line transects.

(IIb-1) Plotless distance-measuring methods Two main approaches are used in plotless methods (Loya 1978):

1. individuals are selected at random in the whole population, and, for each of them, the distance to its nearest neighbour is measured (=nearest neighbour method and random pair method);
2. sampling points are selected at random and the distance from each such point to the nearest individuals is measured (=closest individual method, point centred quadrat method and wandering quarter method).

The point centred quadrat method has been applied to coral reefs and compared with other techniques for evaluation (Weinberg 1981; Dodge *et al.* 1982). However, only one group of organisms (e.g. corals) can be studied at once. Inclusion of several categories of organisms requires consecutive series of measurements to be made for each one, at the same site (Weinberg 1981; Dodge *et al.* 1982).

Parameters which can be obtained from this technique are numbers of species, estimates of cover of each species (cm² or percentage), estimates of total cover (cm² or percentage), number of individuals for each species, density, and mean area per individual. The mean of the distance measured from each sampling point has been shown empirically to be equal to the square root of the mean area per individual (Cottam *et al.* 1953).

(IIb-2) Line transect methods Loya (1978) distinguished two major kinds of line transect methods. **The equally spaced point transect** consists of dividing the line into contiguous equal sized units (blocks), subdivided into a fixed number of equally spaced points. Species are recorded at each sampling point and frequency of individuals is estimated for each block (Kershaw 1957). In addition, different groups of organisms, as well as the nature of the

substrate, can be included. However, only frequency and cover are generated, and these are based on the assumption that the total number of points recorded for one species divided by the total number of points recorded along the transect represents a valid measure of the species cover.

Among the **continuous transect recording techniques**, the line intercept transect has been widely used in coral reef ecology (Loya & Slobodkin 1971; Loya 1972, 1978; Weinberg 1981; Dodge *et al.* 1982; Sheppard 1985; Bak & Povel 1989; Hubbard *et al.* 1990; Chiappone & Sullivan 1991). Along a transect, the length of line intercepted by each individual or component (i.e. organisms, substrate-type, etc.) is recorded. The basic assumption of this method is that the ratio of total transect length being intercepted by organisms to the overall length of transect is equivalent to the ratio of the total area occupied by the living organisms to the overall area. The various parameters generated by this technique are mainly linear cover (in cm and percentage), number of species, number of individuals and abundance of different components. Another variant of this technique, the chain method, was introduced by Porter (1972*a, b*). The systematic distance method is a variant of the continuous transect recording technique (Westman 1971) and consists of measuring the distance from a line to all individuals within a predefined width. This width is derived from the mean distance of individuals to a single reference point. Adaptations of this technique have been used for coral reef surveys by counting coral colonies within 0.15–0.30 m on either side of the line (Done & Potts 1992).

Approaches used in palaeoecological studies of fossil reefs

I. Qualitative methods: reconstruction of reef zonation from inshore–offshore trends Reconstruction of fossil reef zonation is strongly based on palaeoenvironmental interpretations of reef facies, which may then be arranged in inshore–offshore gradients (i.e. on the scale of a single reef) in order to establish models of reef zonation. Data generally consist of taxonomic lists for particular facies or lithologies. Sometimes, inshore–offshore trends may be directly identified from field data based on morphological and geometrical relationships between facies. This classical approach has been used for numerous studies (Broadhurst & Simpson 1973; Frost 1981; Frost *et al.* 1983; Schaefersman

1983; Bloy *et al.* 1989; Copper & Fay 1989; Lehmann & Simo 1989; Stanley 1989; Bosellini & Russo 1992).

II. Quantitative methods: reconstruction of assemblages There have been very few quantitative studies of reef assemblages. The main field techniques consist of *in situ* mapping of coral colonies or reef builders from vertical faces or bedding surfaces or quadrats (Kissling & Lineback 1967; Königshof *et al.* 1991; Weidlich *et al.* 1993), point-counting from quadrats (Zankl 1969; Schäfer 1979; Budd *et al.* 1989; Stemmann & Johnson 1992), and transect point-counting along vertical sections (Collins 1988). These authors have used their data for improved distinction of reef facies and quantitative characterization of assemblage composition (e.g. Collins 1988; Budd *et al.* 1989; Stemmann & Johnson 1992) and not specifically for establishing patterns of reef zonation or palaeobathymetry.

Discussion

From the various studies of present-day reef ecology it appears that lists of species established from purely qualitative observations at different sites on the same reef are not sufficient to characterize communities and reef zonation, mainly because of the gradual variation of community composition, and the predominance of widely-distributed species. For fossil reefs, as for their living counterparts, it is therefore necessary to use quantitative or semi-quantitative methods to specify relative abundance and dominance of organisms, to identify biotic assemblages, and to establish zonation patterns from their distribution. Because skeletons are commonly reworked in the reef environment, reconstruction of reef zonation will be more accurate and reliable if the only organisms surveyed are those which are definitely in growth position. The bulk of these will mainly be the reef builders themselves.

I. Reliability of the various techniques for present-day reef studies. Reliability of the various techniques used on present-day reefs has been evaluated and discussed by several authors from comparative tests based either on computer simulation or on *in situ* applications. Weinberg (1981) usefully compared seven different coral reef survey methods, four plot techniques using quadrats and three plotless methods. Point-intercept techniques, whether on a surface using quadrats, or along a line transect with recording points 0.2 m apart, provided the poorest results

and had to be considered as unreliable. The equally spaced point transect was considered poor in estimating percentage cover and rather bad for recording the number of species. In addition, this technique does not provide values for population densities. Line intercept transect and point centred quadrat methods were of medium value. The latter had been regarded as rather slow and inaccurate for determination of the number of species but was reliable for estimation of population densities and percentage cover. On the other hand, Dodge *et al.* (1982) regarded the point centred quadrat as reliable and easy to apply but noted that density values, which were approximations from distance measurements, had high standard deviations. The length intercept transect yielded the lowest estimate of the species number and was very inaccurate for estimating population density and percentage cover. Weinberg (1981) also emphasized that the major weakness of this method was the reduction of the three-dimensional reef structure to a one-dimensional analysis. Transects with a much wider sampling band were therefore recommended, the survey consisting of a series of quadrats recorded along a line, and hence equivalent to a plot technique (Weinberg 1981). The three other plot techniques involving individual counting and cover estimate, photographic recording and mapping of quadrats, were good for estimates of relative cover of dominant species.

Comparing the line intercept transect with a line transect using metre-square quadrats applied on small patch reefs of the Bahamas, Chiappone & Sullivan (1991) found the first method too conservative in recording community composition and species distribution, particularly for small colonies, and obtained the best results with the second method. Dodge *et al.* (1982) tested three plotless methods (line intercept transect, point centred quarter and point record along line transect) and one plot method on Bermuda reefs. Results of these tests were similar for coral cover and diversity estimates, but they differed in terms of amount and quality of data produced, ease and speed of application, working time, and scope for assessing different groups of organisms.

Advantages of plotless techniques are that they minimize problems of bottom topography and are more time efficient than the more fastidious and time consuming quadrat sampling methods (Loya & Slobodkin 1971; Loya 1978). Hence larger reef areas can be surveyed in a given time. However, a comparison of plotless (line intercept transect and distance of nearest neighbour) and plot methods (quadrats with

coral counting, and with point counting) using computer simulations, showed that all methods tested were equally bad for estimating coral cover and consequently the faster methods are preferred because they allow larger survey coverage in a given time (Kinzie 1978; Kinzie & Snider 1978).

From the above discussion it is clear that there is no agreement on one technique for quantifying reef assemblages, therefore our selection of a suitable method is largely based on finding one applicable to both living and fossil reefs. This is discussed below.

II. Application and requirements for fossil reef studies. The range of techniques that can actually be applied to a given site on fossil reefs is much more restricted than those used for living reefs, especially because of difficulties related to the nature of the exposure. Thus quadrat mapping, or continuous quadrat series on a reef palaeosurface may only be used on outcrops with exceptional three-dimensional preservation and exposure, though it is generally not possible to establish zonation due to the limited size of such outcrops (c.g. Kissling & Lineback 1967). This approach is therefore best for comparison of different sites on the same reef or on distinct reef build-ups.

Surveys using quadrats on a vertical surface (e.g. Budd *et al.* 1989; Perrin & Bosellini 1993), or on surfaces of any orientation (Weidlich *et al.* 1993), can provide reliable information on coral assemblage composition and framework density. These methods, however, inevitably incorporate a strong element of time-averaging which may be difficult to estimate and take into account. Hence their results are not directly comparable with population densities and cover values established from present-day reefs, where it can readily be observed that surveyed organisms are living contemporaneously. In addition, these methods are very time consuming.

Some techniques are unsuitable for the analysis of all the reef builders occurring at a given site, regardless of their size. Plotless techniques using a point distance are usually applied to the study of a population of comparable sized organisms (scleractinians, gorgonians and hydrozoans, for example). Quadrat methods are similarly not amenable to measurement at the same time of different taxa with a large size range (e.g. coral colonies and thin encrusting organisms).

The line intercept transect requires precise reference to a time accretionary surface either parallel to the general stratigraphy (applicable in the case of horizontal strata) or, more precisely,

along an internal reef palaeosurface. With this reservation, this technique is good because it otherwise offers several advantages:

1. Reduction of the sample unit (i.e. transect) to a line minimizes problems arising from outcrop conditions, and therefore the same technique can be applied to a larger number of potential sites.
2. It is faster than quadrat methods and so allows more ground to be covered in the same time.
3. It allows a large variety of components (i.e. different reef-builders, matrix, micritic crusts, diagenetic products and porosity) to be included simultaneously.
4. Data derived are directly comparable with those obtained elsewhere from the same reef at the same level, or at different stratigraphic levels, and also from different reefs and build-ups elsewhere or even of different ages. Data may also be compared with those derived from living reefs for which this technique remains one of the most frequently used.

III. Methods used in present study The line intercept transect method has been extensively tried out, adapted and applied to various Mediterranean Cenozoic coral reefs. Several variants have been developed and adopted depending on outcrop conditions. The quality of outcrop influences the precision of estimates of linear cover of individual taxa, and of the total linear cover of all organisms, in both individuals and in percentages. Consequently, comparison of results obtained from distinct transects may be difficult and of dubious significance if outcrop quality is not taken into account. Amount of preservation along measured transects may be quantified by including non-identified and non-outcropping parts of substrate as a single component recorded as 'scree and unidentified'.

On two-dimensional outcrops parallel or slightly oblique to the reef-front, one metre horizontally-offset sampling lines are taken at 1 m intervals up previously logged geological sections (Fig. 1). The intersecting length of the different components along transect lines are measured to the nearest millimetre. The components measured are: organic reef-builders in growth position (corals, coralline algae, serpulids, bryozoans, etc.), micritic crusts (*sensu* Riding *et al.* 1991), matrix, diagenetic cements and infillings and present-day scree. The intercept length of reef-builders is taken as the distance between outer surfaces of the reef-

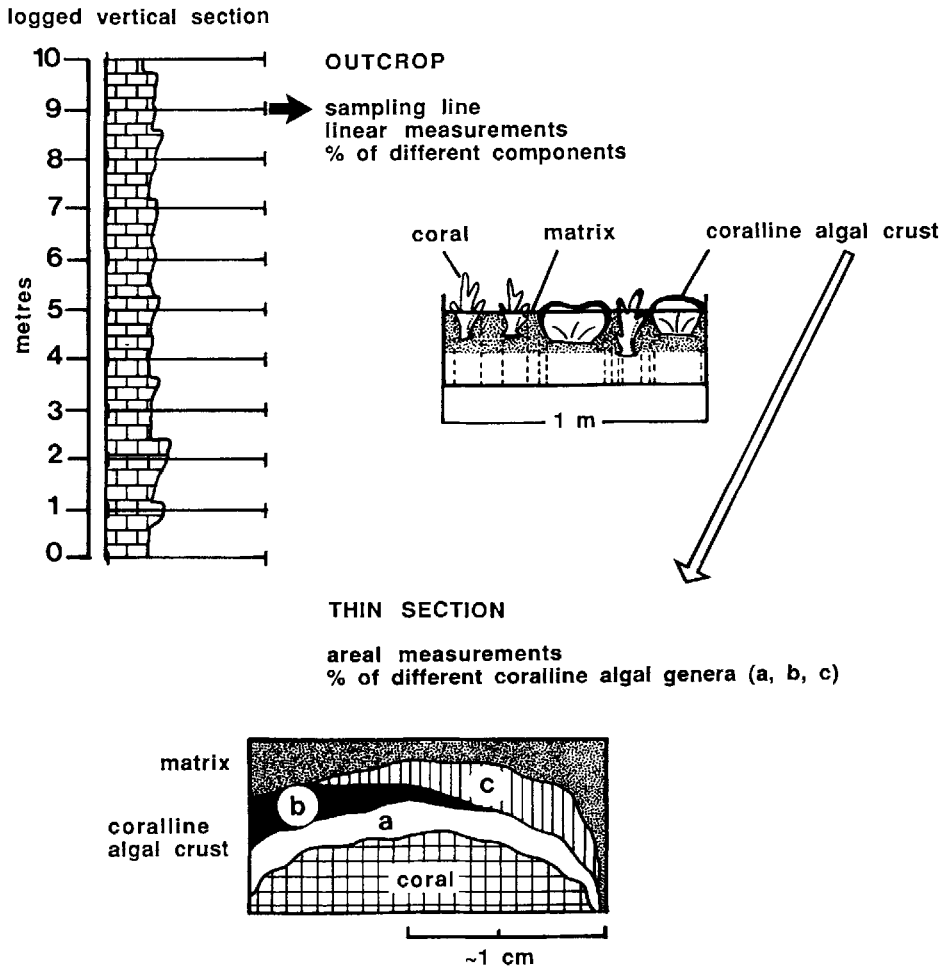


Fig. 1. Quantitative field technique used on vertical section of two-dimensional outcrops parallel or slightly oblique to the reef front. Technique used to measure the relative abundance of coralline algal genera (a, b, c) from thin sections.

building skeleton even if the interior has been dissolved or bored. Therefore, the secondary porosity of the skeleton resulting from borings by sponges and molluscs, or from dissolution, is not recorded. Corals are identified in the field according to their genus and growth form. Coralline algae are systematically sampled as hand specimens and then identified at generic level from thin sections. For each coralline crust in growth position, the cross-sectional areas occupied by different genera in these thin sections are measured and proportions calculated for each transect line. The quantitative data obtained from this method allows the sequence of reef-building communities through

time during reef growth to be characterized.

On two-dimensional outcrops, normal or oblique to the reef front, when the reef-slope surface can be seen in cross-section, the intercept length of the different components can be taken continuously along internal slope surfaces of the reef (Fig. 2). As the preserved reef slopes represent previous reef surfaces then the depth relations of the preserved *in situ* communities can be studied. Relative palaeodepths can be measured in the field from the profile top, which ideally is placed at the reef top if this is preserved.

On three-dimensional outcrops, normal or oblique to the reef front, the 1 m offset of

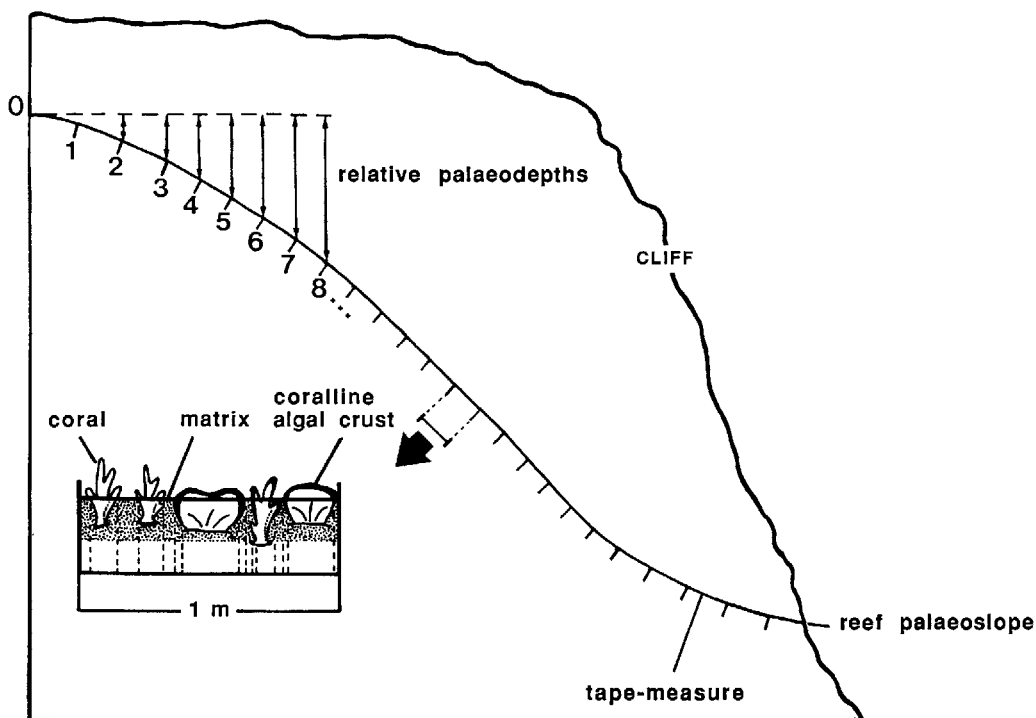


Fig. 2. Quantitative field technique used on two-dimensional outcrops normal or oblique to the reef front, when the reef palaeoslope can be seen in cross-section.

sampling lines is placed horizontally at 1 m intervals on the reef palaeo-surface. Relative palaeodepths are measured the same way as on two-dimensional palaeo-reef slopes (Fig. 3). Both latter methods allow the composition and the distribution of biotic assemblages to be characterized for a given time of reef development.

For these three types of transect, taphonomic bias is taken into account by directly recording along the line poorly or non-outcropping parts as an independent component, but also from qualitative observations of bioerosion along transects and study of skeletal diagenesis in thin sections. Relative palaeodepths measured in the field can be constrained from the relative position of the various transects measured on the same reef and from independent sedimentological and diagenetic criteria. Reliability and accuracy of these quantitative data obviously need to be tested before palaeoecological interpretation and comparison of reef zonation may be undertaken.

In evaluating the efficiency of quantitative techniques on present-day reefs, most authors

dwel on the time required for these investigations. For the study of fossil reefs, despite absence of constraints related to scuba diving, the use of the same techniques is slowed down by several factors:

1. The time needed for site selection and, in particular, for identification of internal reef palaeosurfaces which are generally hard to recognize and trace through outcrops.
2. The time required for palaeodepth measurement for each offset sampling line to the reef top along the line transect.
3. Identification and sampling of fossil taxa are especially time consuming in comparison with their living counterparts. Only a few, if any, coralline algal genera can be identified in the field, but, even in the most favourable cases, sampling, thin-sectioning and microscope study are necessary. For corals, identification of genera in the field is strongly dependent on preservation of skeletal structures but also on suitable orientation of skeletal sections visible at outcrop. For this reason, and also because

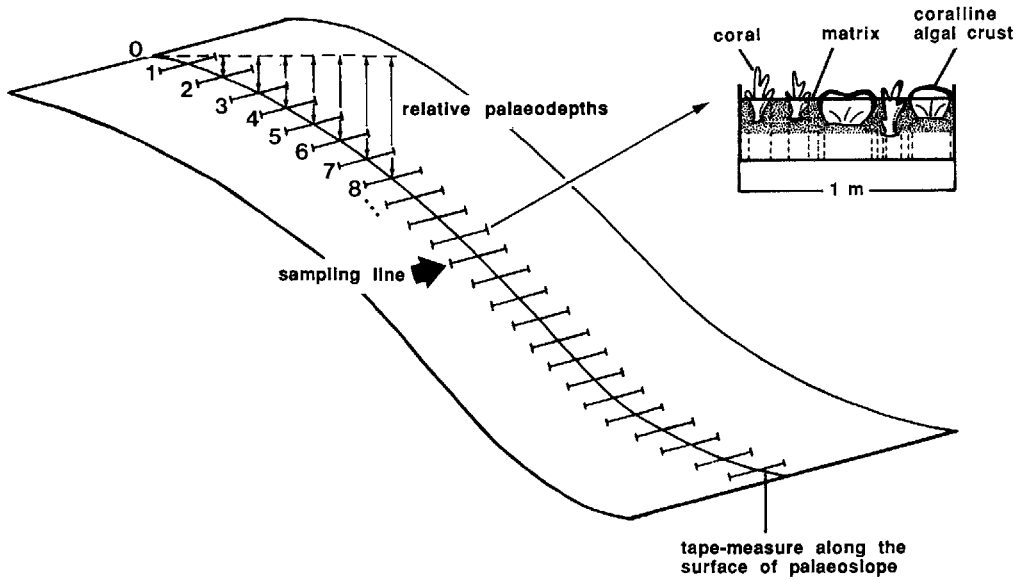


Fig. 3. Quantitative field technique used on three-dimensional outcrops normal or oblique to the reef front when reef palaeoslope is exposed in three dimensions.

of numerous taxonomic problems, the identification of corals to species level in the field was not considered as feasible.

For these various reasons the average time for the intercept-length transect method on a living reef which is estimated to be $20\text{--}30\text{ m h}^{-1}$ (Weinberg 1981; Dodge *et al.* 1982) is much longer when sampling and recording the same length of transect on a fossil reef, especially in the case of dense framework and diverse assemblages. Depending on the diversity of reef-builders, the population density and the accessibility of outcrops, this time can be estimated as $1.5\text{--}7\text{ m h}^{-1}$.

Quantitative characterization of coral reef zonation

Various parameters are used to assess reef zonation on present-day coral reefs. Only those which can be measured or estimated both on living and fossil reefs will be considered here. Emphasis is placed on measurements of reef-building organisms because of their *in situ* occurrence in both living and ancient reefs. Distribution and abundance of reef-builders can be characterized by three main parameters, quantitative or semi-quantitative values of

which are determined for each sample point of measurement (e.g. point on a grid or on a transect; point in a quadrat), generally along an environmental gradient:

1. framework density;
2. diversity of reef-builders;
3. composition of reef-building assemblages.

The following section reviews previous work on these parameters with respect to corals and coralline algae, the main reef-builders of the Cenozoic. Because of the different scales of their contribution (e.g. dominance of corals over coralline algae) and occurrence on reefs (e.g. high abundance of coralline algae on reef crests) the information obtained from these groups differs considerably. In particular, the information on coralline algae comes from the small number of local studies, which can be presented here, whereas data from corals is far larger and can only be reviewed in general terms.

Framework density

1. Definition The density of the organic framework is the quantity of reef building skeletal material preserved in growth position compared to the quantity of sediment, cement and primary porosity. In the case of sessile benthos like corals or coralline algae, there is a spectrum from

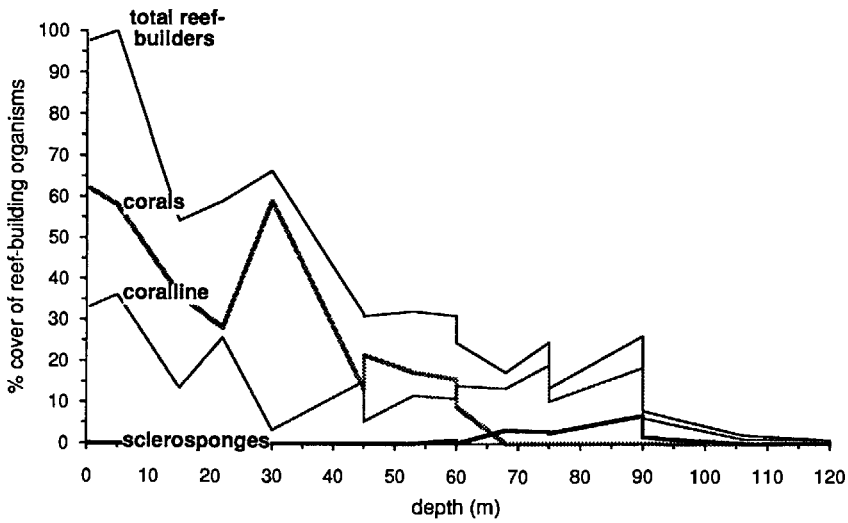


Fig. 4. Variation of cover of reef-builders with depth, northern Jamaica (data from Liddell & Ohlhorst 1988).

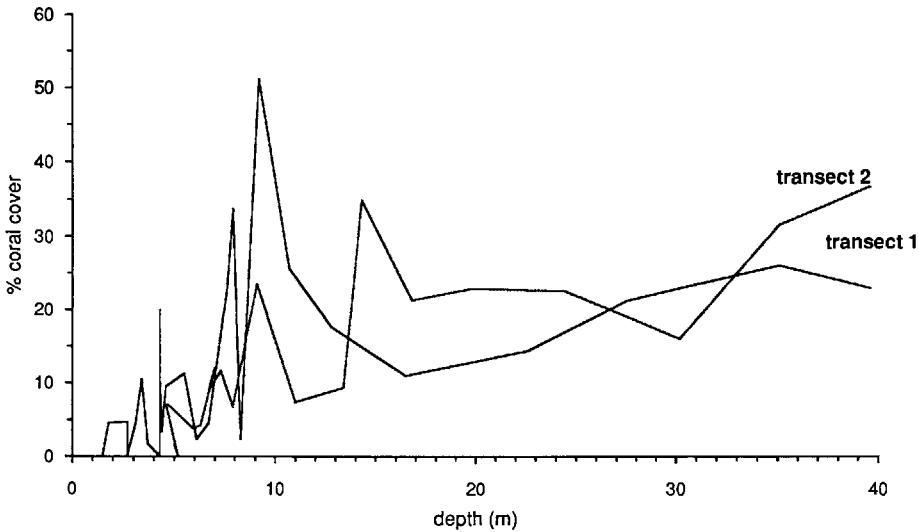


Fig. 5. Variation of coral cover with depth, St Croix reefs (data from Hubbard *et al.* 1990).

scattered colonies, or individuals, to a dense framework. Therefore, framework density varies both laterally and with depth on the same reef and may show large differences between individual reefs. Density reflects both the reef facies and reef community as it is closely dependent on the abundance (number of individuals or colonies), size and growth forms of the reef-builders. Size variation may be considerable because many reef-builders are colonial with

indeterminate growth. On present-day reefs framework density may be recorded by percentage cover or size-frequency distribution of reef-builders.

II. Lateral and depth-related patterns As a general trend, percentage cover of reef-builders initially increases with depth on the upper part of the reef slope, and then decreases at greater depths (Figs 4, 5; Wells 1957; Liddell & Ohlhorst

1988), though this is not a universal rule. In general, it also increases from the reef flat to the reef crest where corals are often replaced by coralline algae (Tracey *et al.* 1948; Wells 1957; Chevalier & Beauvais 1987; Hubbard *et al.* 1990; and see Fig. 18). On deep slopes, percentage cover of corals decreases rapidly and scleractinians can be gradually replaced by other organisms such as coralline algae (Minnery *et al.* 1985; Minnery 1990), sponges (Land & Moore 1977; Liddell & Ohlhorst 1988) or encrusting foraminifera (Reiss & Hottinger 1984; Perrin 1989, 1990, 1992), or by sediment.

Coral cover rarely reaches 100% and is often higher on external reef slopes than on reef flats, especially those emergent at low tide. On barrier reefs and atolls, especially in the Pacific, percentage coral cover is lower on the most exposed reef edges where coralline algal ridges are best developed (Emery *et al.* 1954, Wells 1957; Chevalier *et al.* 1969; Chevalier & Beauvais 1987). Decrease in coral cover with depth is widely attributed to gradual decrease in light intensity which reduces the photosynthetic enhancement of calcification by symbiotic algae, and hence calcification rate (Goreau 1959; Erez 1977; Chalker & Taylor 1978). Below a certain depth, colonies may decrease in size and exhibit transition to delicate foliaceous or platy shapes which give rise to lower density frameworks. These modifications in growth forms have been interpreted partly as a response to light decrease (Graus & Macintyre 1976; Chappell 1980; Fricke & Schuhmacher 1983; Chevalier & Beauvais 1987).

On the Discovery Bay reef, northern Jamaica (Fig. 4), coral cover is relatively high (28–62%) between 0.5 and 30 m depth, but down to 60 m, it decreases gradually to 10–15% cover, and disappears completely below 75 m (Liddell & Ohlhorst 1988). At St Croix, US Virgin Islands (Fig. 5), Hubbard *et al.* (1990) found a seaward increase in coral cover between 1 (51%) and 9–14 m depth (*c.* 7%) on the upper reef slope for the two measured transects, but on the lower reef slope the pattern of coral cover was more irregular. By contrast, inshore, the cover was less than 10%. The maximum coral cover on the reef front was considered to be controlled by a combination of terrigenous sedimentation, removal of biodegradable material by high water energy, and the proximity of the external reef slope to this zone (Hubbard *et al.* 1990).

Faure & Laboute (1984), using phytosociological methods for their study of coral faunas from Tikehau (Tuamotu Archipelago, French Polynesia), showed that cover percentage decreased from the reef periphery to the external

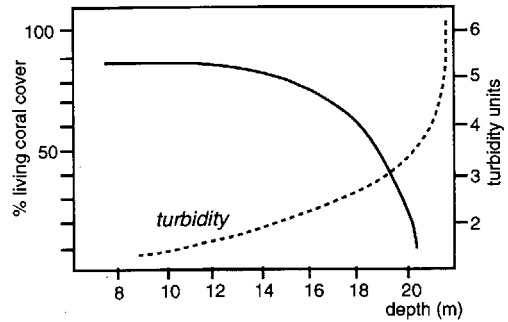


Fig. 6. Relationship between living coral cover, water turbidity and depth, Puerto Rico reef (from Loya 1976).

reef flat (1%) but reached *c.* 25% on the internal reef flat near the lagoon. On the algal ridge, coral cover is <10% in relatively sheltered areas (leeward side) and <2% in the high energy areas (windward side). The external reef slope is characterized by a general increase of coral cover with depth. Cover on the upper part of the slope is 5–25% between 0 and 4 m depth and 40–60% between 4 and 10 m. The slope break (10–25 m) cover is high (*c.* 60%) between 10 and 15 m, except in depressions where coral growth is limited by sedimentation. On the deeper reef slope (25–75 m deep), coral cover is always higher than 50% and reaches 60–75% in the deepest part of the slope below 60–70 m. In the lagoon, coral cover shows a high variability with values >10% on the internal slope (3–5 m depth). The geomorphological discontinuities, i.e. passes and 'hoas' (i.e. reef flat spillway, see Battistini *et al.* 1975 p. 50) have a strong effect on coral cover. The coral fauna can locally be prolific with 80% of cover on the raised features within the passes. By contrast, corals are poorly developed in the hoas and often found in their deepest parts, on the lagoon side. In addition, coral cover may vary laterally and vertically due to the influence of local factors such as turbidity. On a fringing reef of Puerto Rico, Loya (1976) showed a decrease in percentage cover with depth which is related to an increase in turbidity (Fig. 6). On Fanning Island (central Pacific), turbidity controls the framework density with a much lower scleractinian cover and an increase in proportions of branching forms in more turbid waters (Roy & Smith 1971).

On present-day reefs, percentage cover of coralline algae generally increases across the reef flat towards the reef crest where it reaches its maximum on the algal ridge (if present) and the

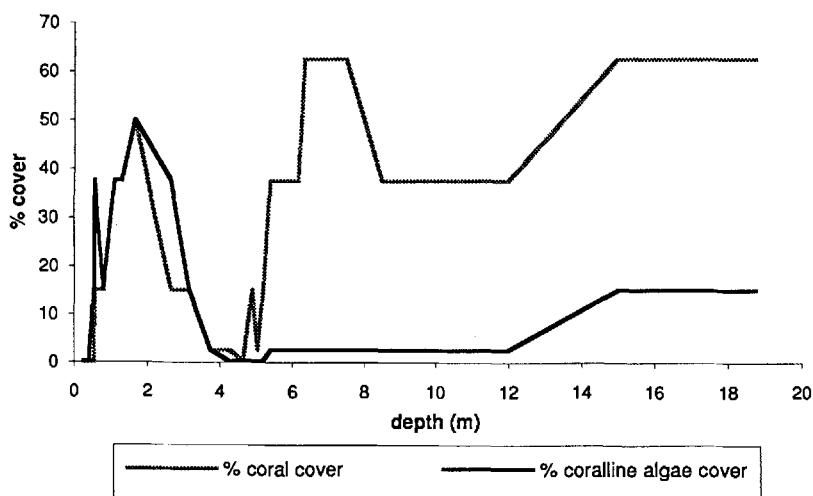


Fig. 7. Variation of coral and coralline cover with depth, Curaçao, Netherlands Antilles, estimates using the phytosociological method (data from van den Hoek *et al.* 1975).

upper reef slope. On the windward reef of Bikini Atoll (Marshall Islands), the algal ridge consists of 90–95% coralline algae and 5–10% corals (Tracey *et al.* 1948). In St Croix, too, the highest percentage cover of *Lithophyllum congestum* (<100%) is found on well-developed algal ridges subjected to continuously heavy wave action, while on less exposed reef fronts the percentage cover of this species remains < 25% (Steneck & Adey 1976).

However, the cover of coralline algae may also increase with depth. A deeper water study was undertaken by Minnery *et al.* (1985) on the Flower Garden Banks of the Gulf of Mexico where reefs sited on salt domes occur between depths of 20 and 110 m. Samples were collected by SCUBA, submersible, grab and dredge, and coralline abundance (from photographic transects) was found to vary from 10 to 15% in the Coral Reef zone (15–36 m), 50–90% cover of rhodoliths in the *Gypsina-Lithothamnium* zone (50–75 m), and 60–90% cover of crustose corallines in the Deep-Water Algal Reef zone. At Curaçao, van den Hoek *et al.* (1975) quantified the distribution and abundance of coralline communities along a transect perpendicular to the coastline (Fig. 7). The highest percentage cover of corallines (< 50%) occurs at shallow depths (0–3 m) where the coral cover is relatively reduced (< 25%) while the lowest coralline cover (< 5%) was observed between 5 and 13 m depth where the coral cover is 25–75%. In the deepest part of the transect (13–20 m depth), coralline and coral covers are 5–25 and

50–75%, respectively. In some Hawaiian reefs, crustose coralline algae have their maximum percentage cover (85%) at the reef edge in 0–5 m depth, where *Lithophyllum*, *Neogoniolithon* and *Porolithon* dominate down to 10 m (Adey & Macintyre 1973; Littler & Doty 1975; Littler & Littler 1984). On Discovery Bay reef, Jamaica, Liddell & Ohlhorst (1988) demonstrated a bimodal distribution of coralline algae with highest percentage cover (33–36%) between 0.5 and 5 m, and again between 75 and 90 m (18–19%), while on the fore-reef slope corallines constitute only 3–15% of the cover (Fig. 4).

Diversity of reef-building organisms

I. General remarks Diversity here refers only to taxonomic richness and more complex measures like the Shannon–Weaver index are not considered. Emphasis in this section is on taxon diversity patterns that are recorded from within reef systems, and methods used, rather than on the numerous theories used to explain diversity patterns. There is still no satisfactory consistent, universal explanation for diversity pattern (Brown 1988). A full review of reef diversity is beyond the present scope and purpose. Nevertheless, as reefs are widely associated in many people's minds with high diversity, a few remarks are appropriate.

Contrary to the impression of reefs always being rich in taxa, they are not all high diversity features. Indo-Pacific reefs are much richer in corals (over 70 genera and more than 500 species

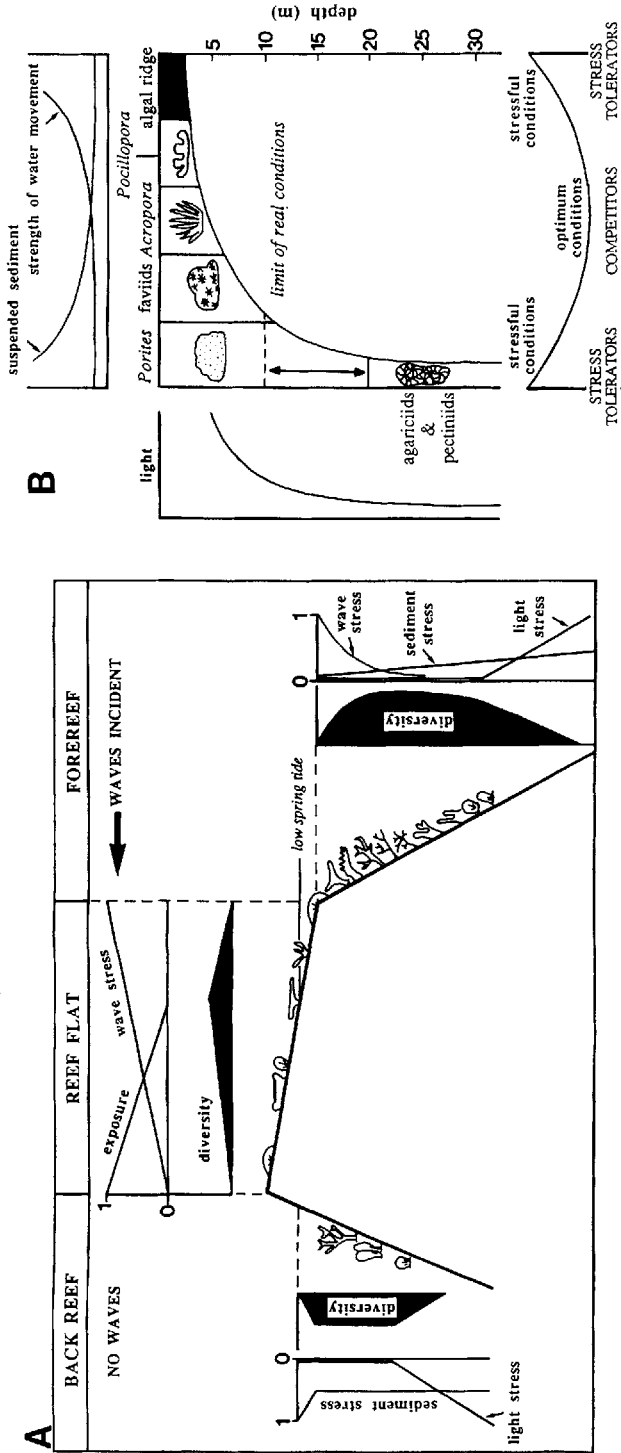


Fig. 8. Theoretical coral diversity and zonation. (A) Considering four stress factors: light, wave stress, sediment flux and subaerial exposure (from Chappell 1980). (B) Stress gradient control of ecological assemblages of Indopacific corals (from Rosen 1981).

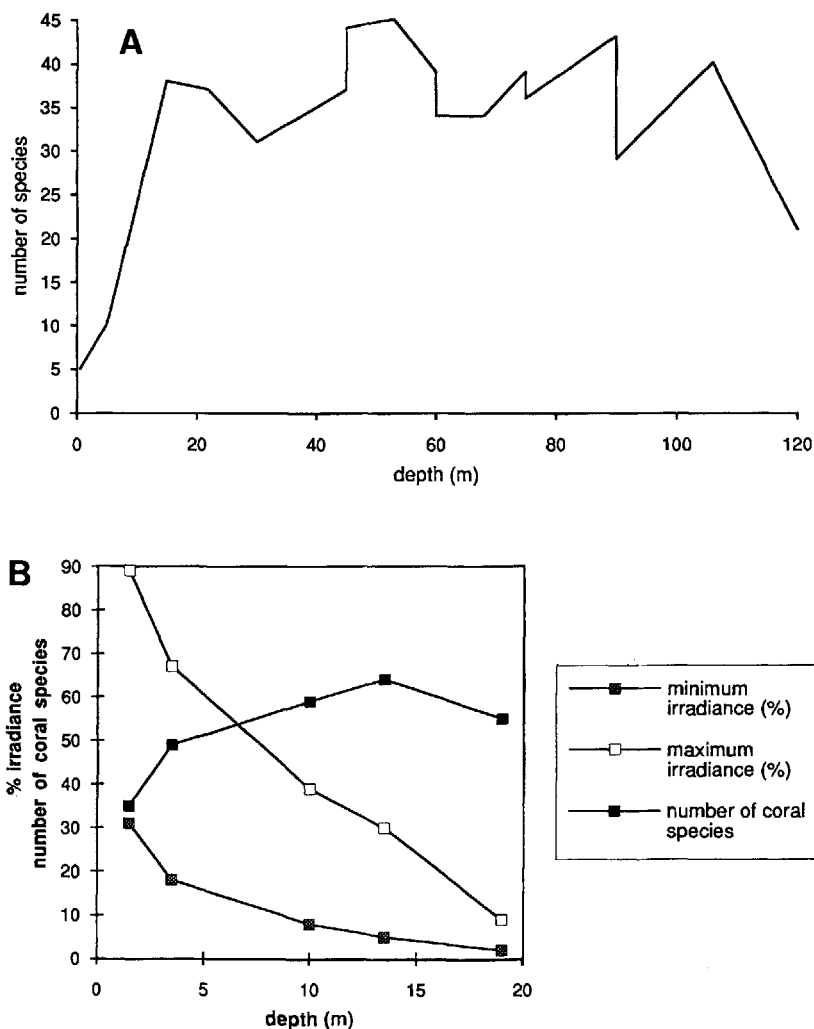


Fig. 9. Increase of coral diversity with depth in the uppermost part of the reef slope, due to a gradual decrease in the wave energy. (A) Northern Jamaica (data from Liddell & Ohlhorst 1988). (B) China Sea (data from Titlyanov & Latypov 1991).

on reefs of the richest areas) and many other reefal organisms than Caribbean reefs (*c.* 20 coral genera up to *c.* 70 species in the richest areas), while diversity within the Indo-Pacific markedly decreases eastward from the richest area in the Indo-West Pacific 'focus', as well as latitudinally. It is not satisfactory to explain such patterns simply in terms of 'stress' response since these patterns are both ecological and historical in origin (Rosen 1988; Jokiel & Martinelli 1992; Pandolfi 1992; Veron & Minchin 1992; Belasky 1993). Even allowing for the fact that the fossil record is incomplete, high

diversity is not universally true of ancient reefs: the coral fauna of the late Miocene Mallorca reefs (discussed below) consists of only five genera. It seems far more likely that reefs have an inherent potential, whether realized or not, to carry a large number of species rather than to cause high diversity endogenetically. Two of the most attractive explanations for this potential are: spatial (or habitat) heterogeneity and intermediate disturbance. It has also been widely argued that many reef species are specialists rather than generalists. Many of the problems associated with trying to explain taxonomic

diversity patterns, especially on a biogeographical scale, have been excellently reviewed by Brown (1988) and Williamson (1988), and are as applicable to reef systems as any other biotopes. For a recent discussion on diversity of reefs in particular see Done *et al.* (1995).

Within a single reef, diversity of reef-builders varies with many environmental factors but of prime consideration are the methods used and on the level of investigation in the studied region. In general, for a given area, generic and specific diversities increase with the intensity and periodicity over which a reef has been studied, independently of the methods used. This is particularly important for diversity estimations in the deepest parts of the reef slopes because of the difficulty and expense of working at these depths. Because of the numerous approaches used for characterization of coral reef communities, accuracy of diversity defined in an area is closely dependent on the methods used, some of which do not record the lateral variations which are particularly important in shallow waters (Faure 1982).

II. Variations of coral diversity Lateral and vertical variations of coral diversity on a reef result from the interaction of physical and biotic factors. Chappell (1980; see also Rosen 1981) constructed theoretical diversity curves assuming an inverse-linear relationship between stress and coral diversity and by considering four stress factors: light, hydrodynamics, sediment flux and subaerial exposure. He also pointed out the importance of biotic factors like predation and grazing, nutrients and especially spatial competition. Chappell's curves (Fig. 8) are constructed for an idealized simplified reef cross-section subdivided in three main topographic zones: back reef, reef flat and fore-reef. In the back reef, where hydrodynamic stress is reduced to its minimum, variation of coral diversity with depth shows first an increase in shallow water related to a decreasing influence of sediment flux; secondly, a depth range with constant diversity and then, in deeper water, a rapid decrease due to light reduction. On the reef flat the theoretical curve of diversity is characterized by a seaward increase associated with the decrease of subaerial exposure stress, and then a decrease toward the reef front resulting from the gradual influence of higher wave energy. The fore-reef shows a gradual increase of diversity in shallow water reaching a maximum at wave base. Down the slope, gradual increase in sediment flux and reduction of light intensity reduces coral diversity in deeper waters.

On external coral reef slopes, variations in

coral diversity with increasing depth frequently follow the previously mentioned hypothetical curves. Specific and generic coral diversity increases with depth in the uppermost parts of reef slopes (down to *c.* 10–15 m depth) at Aldabra (Barnes *et al.* 1971), Fanning Island (Maragos 1974), Tuléar (Pichon 1978a), Mascarenes (Faure 1982), Tikehau, Tuamotu (Faure & Laboute 1984), Jamaica (Liddell & Ohlhorst 1988), Thailand and in the China Sea (Titlyanov & Latypov 1991), suggesting that the main diversity control over this depth range is gradual decrease in wave energy (Fig. 9).

The critical depth at which the decrease in light intensity also begins to influence coral diversity varies with region, or even within the same reef, depending on the transparency of water. In addition, this reduction in coral diversity on the lower reef-slope may be influenced by local conditions, such as competition with other sessile groups (gorgonians, sponges, antipatharians, algae), sediment input, morphology of the reef slope and availability of hard substrata (Grassle 1973; Faure 1982; Chevalier & Beauvais 1987; Liddell & Ohlhorst 1988).

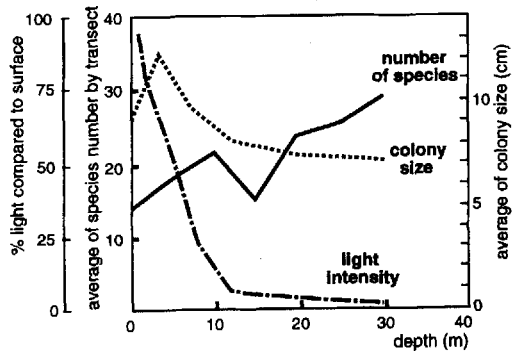


Fig. 10. Relationship between coral species diversity with depth and light, fringing reef of Eilat, Red Sea (from Loya 1972).

In shallow water the main factor limiting coral diversity is water energy which introduces bathymetric and lateral variations with decreasing diversity along an inshore to seaward gradient on reef flats, and also a leeward to windward gradation on the same reef (Done 1983). In particular, on reef fronts where hydrodynamic energy is very high and an algal ridge is developed, conditions are apparently too extreme for corals and their diversity is greatly reduced. As these same conditions appear to favour crustose coralline algae they may therefore also exclude corals from this habitat through competition as evidenced by coralline

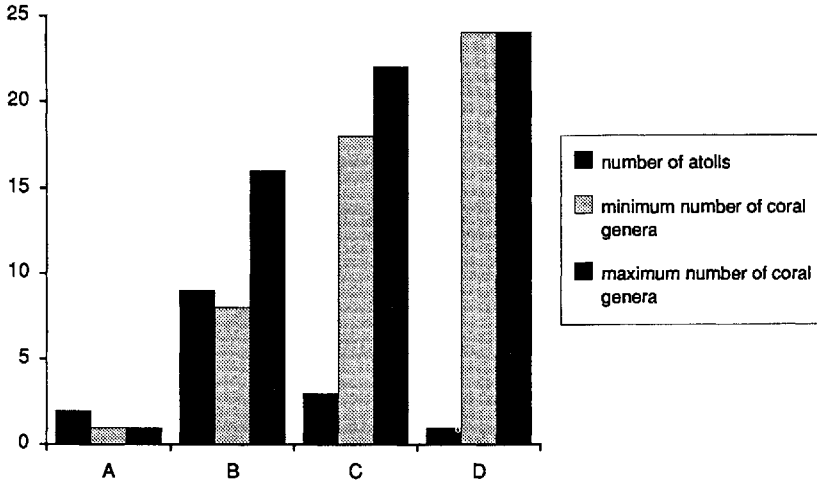


Fig. 11. Relationship between the number of coral genera living in the lagoon and the number of discontinuities (passes and hoas) in the atoll rim, Tuamotu Archipelago, French Polynesia (data from Chevalier & Beauvais 1987). (A) Atolls with periodically open hoas. (B) Atolls with shallow open hoas. (C) Atolls with one or two narrow passes and open hoas. (D) Atolls with one large pass and open hoas.

algae overgrowing corals (see Bosence 1984, 1985).

Local environmental conditions influencing quality of water may also alter the general pattern of coral diversity. Conditions of temperature, salinity and sedimentation may act as limiting factors of coral diversity as on the fringing reef of Eilat (Red Sea). Here, coral diversity is low in the uppermost part of the reef and increases gradually in deeper water down to 30 m (Loya 1972; Fig. 10). Water circulation can also control coral diversity. Thus, in the atolls of Tuamotu Archipelago (French Polynesia), there is a clear positive correlation between the number of coral genera living in the lagoon and the number of discontinuities (passes and channels) in the atoll rim (Fig. 11; Chevalier & Beauvais 1987).

III. Variations of coralline diversity

(IIIa) Introduction There are only a few quantitative or semi-quantitative studies concerning coralline diversity and zonation on reefs. Most quantitative studies have concentrated on algal communities in the shallowest parts of reefs, especially the external reef flat and algal ridge. In addition, the usefulness of this work must now be viewed with caution in the light of the extensive taxonomic revisions of non-geniculate Corallinaceae undertaken by Woelkerling and co-workers (e.g. Woelkerling 1988). Similarly, comparison with fossil taxa must take into account recent taxonomic revisions (Bosence 1990; Braga *et al.* 1993). Many of the genera

used by earlier workers (e.g. Littler 1976; Adey *et al.* 1982; Minnery *et al.* 1985) would now be considered invalid (see Woelkerling 1988). Thus, the measures of abundance and diversity of different genera must be viewed as one worker's assessment of the numbers of genera present and whilst Minnery *et al.* (1985) followed Adey's (1982) generic concepts, and in this sense the two works may be comparable, these genera are different to those currently being used (Woelkerling 1988) as noted by Minnery (1990).

(IIIb) Hawaiian Islands Research by Littler (1973a, b) on Oahu, Hawaii, gives data on occurrence and abundance of corallines with respect to distance from shore and depth. Abundance was measured using a reef-surface photogrammetric technique (Littler 1971), though it is not made clear how overhangs, undersurfaces and other three-dimensional irregularities were recorded. Shallow, fringing-reef sites are presented in Littler (1973a) as distance from shore to the reef front (some 1700 m) with maximum depths down to c. 10 m. Deeper water sites (8–28 m) are given in Littler (1973b). There is no evidence for variation of coralline diversity with depth as both shallow and deeper water sites are dominated by between two and three genera. However, these are not the same genera as the shallow-water taxa are replaced in deeper areas by other taxa (see below). The increased diversity for shallow reef flat sites is accounted for by rare (< 1%) occurrences. The percentage cover by corallines also shows no variation with increasing depth (Fig. 12).

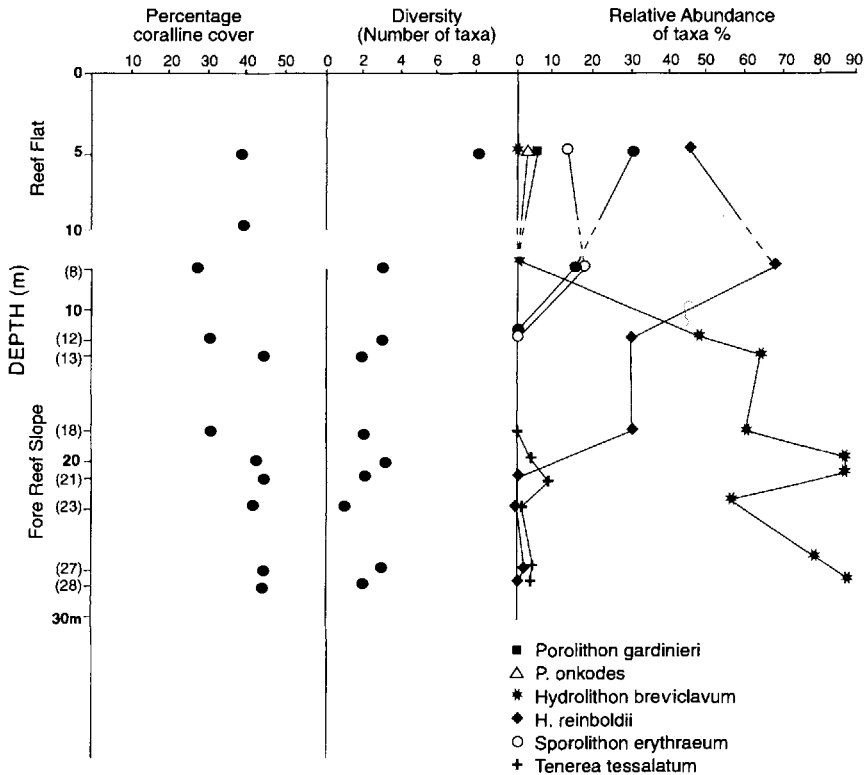


Fig. 12. Variation of coralline algal cover, coralline algal diversity and relative abundance of species with depth (data from Littler 1973a, b). Reef flat sites all averaged within 0–10 m as no depth given in Littler (1973a). Reef slope data combined for sites at Maile (12, 18 and 27 m) with sites at Waikiki (8, 13, 20, 21, 23 and 28 m) from Littler (1973b).

Perhaps the most extensive study of coralline depth distribution on reefs is that of Adey *et al.* (1982). Collections were made by SCUBA and some dredging from fore-reef sites off a number of the Hawaiian Islands. These data are presented as percentage occurrence of different genera on samples from a number of depth ranges (0–3, 3–9, 9–15, 15–21, 21–28, 28–37 and 37–46 m) (Fig. 13). The greatest diversity (nine genera) is found in shallow subtidal sites (3–15 m) with the loss of one genus (*Archaeolithothamnium*, now known as *Sporolithon*) into the intertidal. The diversity gradually decreases with depth as the shallower-water mastophoroids (*Paragoniolithon*, *Porolithon* and *Neogoniolithon*) disappear (Fig. 13). The deepest sites measured at 80 m have six taxa present.

(IIIc) Gulf of Mexico and Caribbean A deeper water study between depths of 20 and 110 m was undertaken by Minnery *et al.* (1985) on the Flower Garden Banks of the Gulf of Mexico. In general, generic diversity decreases with depth

with a maximum of ten between 15 to 36 m (Coral Reef Zone) (Fig. 13). Loss of the shallower-water mastophoroid taxa in the 'Algal-Sponge' Zone (46–88 m) results in a lower diversity (eight genera). This is further reduced in the deeper 'nepheloid' layer (90–110 m) to just two genera.

In a shallower water fringing coral reef site off Curaçao (Netherland Antilles, Caribbean), van den Hoek *et al.* (1975) defined algal zonation and its relationship to that of other reef-builders. Above low-water level coralline diversity is very low with only three species occurring (Fig. 14). The highest diversity is reached between 0.5 and 3.5 m depth which corresponds to the zone of maximum coralline cover. From 3.5 to 20.5 m depth coralline diversity drops rapidly, with just *Hydrolithon boergesenii* being the dominant species in the deepest part of the transect. The detailed analysis of shallow-water and intertidal reef-building coralline algae comes from research in St Croix by Adey & Vassar (1975), and Steneck & Adey (1976). Although quanti-

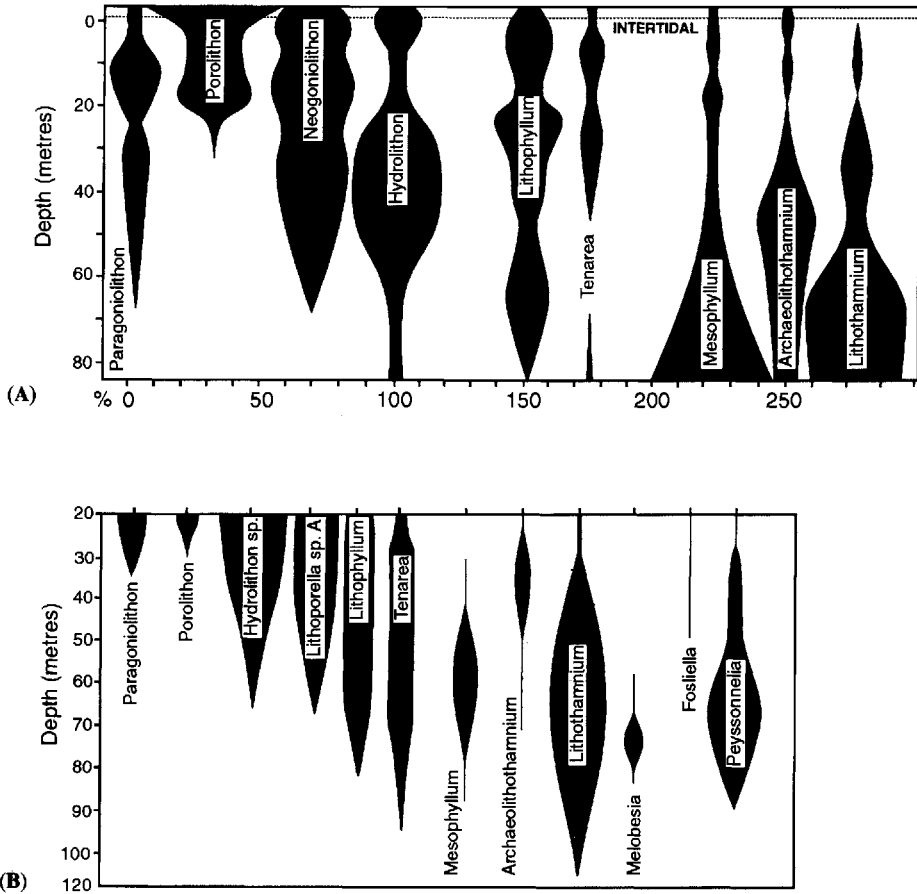


Fig. 13. Variation of coralline algal abundance and diversity with depth. (A) Frequency of occurrence of coralline genera in samples from reef slope transects, Hawaiian Islands (from Adey *et al.* 1982). (B) Qualitative assessment of abundance of coralline genera at different depths on Western Flower Garden Banks, Gulf of Mexico (from Minnery *et al.* 1985).

tative surveys of the surface corallines was not undertaken in St Croix, the occurrence and abundance of corallines was recorded from settlement plate experiments in shallow waters (Fig. 15). No variation in generic diversity was recorded between intertidal and shallow subtidal (< 1.1 m) sites.

(III d) Discussion Any discussion of changes in coralline diversity with water depth is restricted by the small number of geographically widely spaced studies using different techniques and covering different depth ranges. In general there does appear to be a decrease in diversity of coralline algae with depth, this being largely

related to the loss of the shallow-water, and often intertidal, mastophoroid corallines such as *Porolithon* (now known as *Spongites*). However, these shallow-water taxa may be replaced by other, deeper-water taxa, resulting in no overall change in diversity (Littler 1973a, b). Percentage coralline cover may or may not be related to diversity because, for example, Minnery *et al.* (1985) record highest cover (60–90%) in depths with moderate diversity, whereas the shallower sites with only 10–15% coralline cover have the highest diversity. Littler (1973a, b) recorded virtually no change in coralline cover over his < 30 m depth range and no change in diversity of common taxa. However, van den Hoek *et*

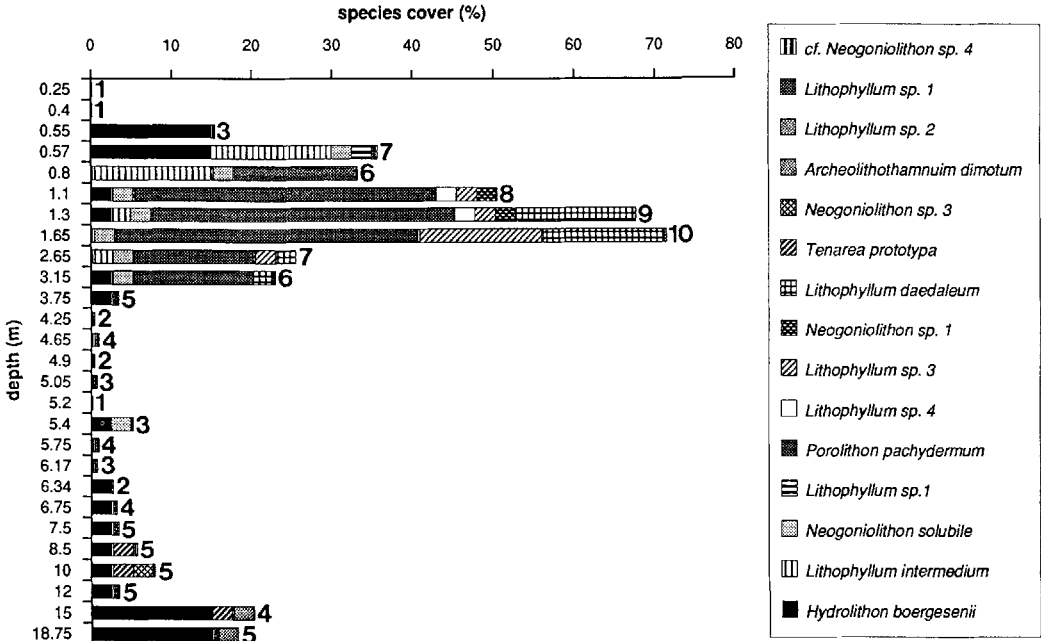


Fig. 14. Variation of coralline algal diversity and zonation with depth, Curaçao, Netherlands Antilles, estimates using the phytosociological method (data from van den Hoek *et al.* 1975).

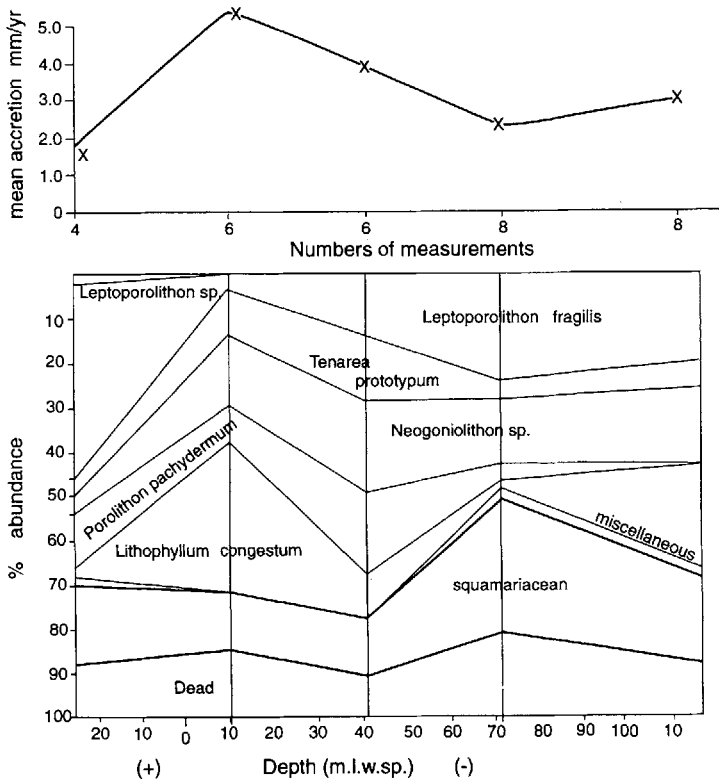


Fig. 15. Percentage abundance and mean accretion rates of coralline algae, St Croix algal ridge (data from Adey & Vassar 1975 and Steneck & Adey 1976). m.l.w.sp., mean low water spring tides.

al. (1975) have shown a positive correlation between increasing coralline cover and diversity. Clearly there is no simple relationship between these two parameters.

Distribution and composition of reef builder assemblages

I. Coral zonation On present-day reefs, coral zonation is an expression of: (1) a gradual morphological modification of individual coral species; i.e. zonation of growth forms and ecomorphs of ubiquitous species; (2) species zonation; and (3) the integrated effect of the latter in terms of gradual modification of communities, i.e. assemblage zonation (see for example Done 1983).

Ia Zonation of growth forms: Stearn (1982) reviewed the relationship of coral morphology (mostly outward shape of colonies) to environmental factors and concluded (on his p. 238): 'No general pattern of shape distribution that is applicable to the great variety of reefs in modern oceans has been found. The shapes of reef animals are not specific guides to environments of modern reefs and should not be expected to be in ancient ones.'

Nevertheless, there is an extensive literature which addresses this subject. Several authors have attempted to establish a general scheme for distribution of coral growth forms with depth or along a lateral gradient (Pichon 1978*a*; James & Ginsburg 1979; Chappell 1980). Thus, independently of taxonomic distribution, a general trend may be characterized by a dominance of branching forms in shallow water down to 10–15 m, whilst further down, domal, massive and columnar colonies are dominant and are gradually replaced with increasing depth by foliaceous shapes. There are, however, large variations on this general scheme, especially in shallow waters (down to *c.* 20 m) where coral growth is strongly controlled by water energy, while on deep slopes it is mainly influenced by light intensity.

Some widely distributed species show a gradual change in morphology in the various reef zones, expressed by changes of size and shape of whole colonies and/or individual corallites (Pichon 1972, Veron & Pichon 1976; Done 1983). The morphological adaptation of individual species to high hydraulic energy results in encrusting or stream-lined ecomorphs of massive species, and in changes in length, size, shape and orientation of branches (Shinn 1966; Graus *et al.* 1977; Done 1983). Decreasing mechanical stress in sheltered areas induces a diversification of coral growth forms whose

distribution is influenced by nutritional requirements of individual species (Porter 1976; Jaubert 1977; Spencer Davies 1977; Porter *et al.* 1980), inter- and intra-specific competition (Lang 1973; Porter 1976; Sheppard 1979), sediment-removing ability (Hubbard & Pocock 1972; Hubbard 1974; Dodge *et al.* 1974; Loya 1976; Bak 1978) and high sedimentation rates (Vaughan & Wells 1943; Morton 1974; Porter 1976).

In some species, particular modifications of colony shape with increasing bathymetry have been related to diminishing light intensity, the most obvious morphological adaptation being a lateral expansion of colonies. The effect of light is more unidirectional in deeper water and flattening of colonies increases the amount of surface area orientated towards the light (Wallace 1978; Chappell 1980; Fricke & Schuhmacher 1983; Porter *et al.* 1980; Titlyanov 1987; Titlyanov & Latypov 1991). One of the most cited examples of this is provided by the Caribbean species *Montastraea annularis* which occurs over a large bathymetric range (<1–80 m) and shows hemispherical forms at shallow depths (1–5 m), peaked or columnar colonies in deeper water (5–25 m) and platy shapes below 25 m (Graus & Macintyre 1976). Recently, Weil & Knowlton (1994) have challenged this view and separate this species into three, each with its own variation with depth.

(Ib) Assemblage zonation Zonation of coral communities has been widely described in present-day reefs, and Done (1982, 1983) has reviewed a wide range of schemes and their controlling factors. Wells (1954, p. 396) defined the term 'zone' as 'an area where local ecologic differences are reflected in the species association and signalized by one or more dominant species'. Thus, in the Atlantic Province, there are five main zones characterized by their respective communities. With increasing water depth, these are: the algal ridge, the *Millepora* zone, the *Acropora palmata* zone, the *Acropora cervicornis* zone and the *Montastraea annularis* zone (Adey & Burke 1977; Geister 1977; Graus & Macintyre 1989). In the Indo-Pacific Province, zonation of coral communities appears much more complex and varied. This is probably related to the much larger number of genera and species compared to the Atlantic Province. The wider geographical area of the Indo-Pacific also encompasses a much wider range of geographical and environmental conditions. It seems therefore very difficult to establish a general zonation of coral species for the whole Indo-Pacific Province. One Indo-Pacific scheme based on higher level taxa distinguishes five first-order assemblages char-

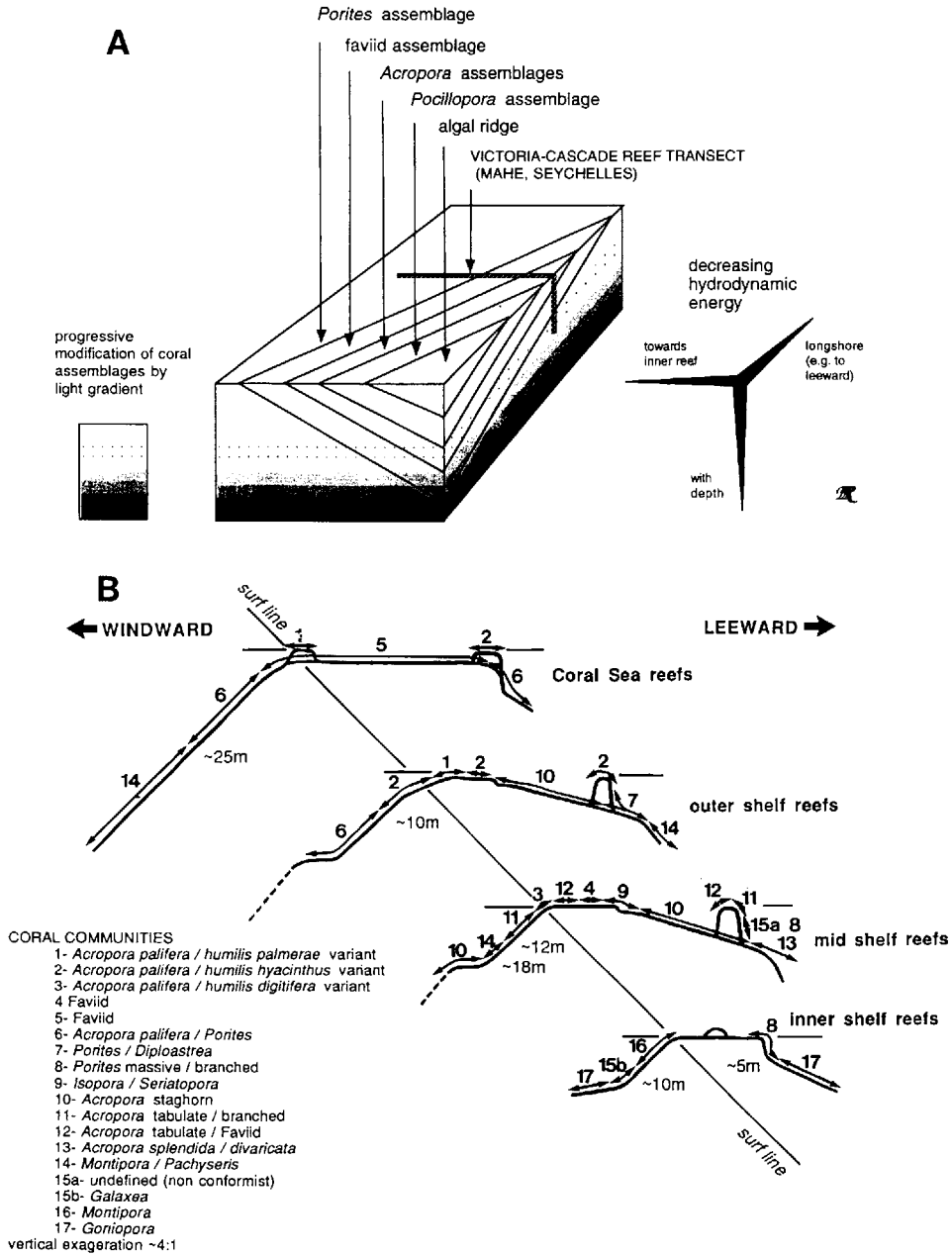


Fig. 16. Coral communities in Indo-Pacific reefs. (A) Schematic relationship of coral assemblages (from Rosen 1975, 1981) showing the reef transect of the Victoria-Cascade area (see Figs 17, 18). (B) Distribution of coral communities in the Great Barrier reefs (from Done 1982).

acterized, respectively, by their dominant genus or families: the algal ridge, *Pocillopora*, *Acropora*, Faviina, *Porites* (Rosen 1975, 1981; and see also Fig. 16). Their distribution (in this order) is considered to be controlled mainly by

hydraulic energy in shallow waters. This sequence therefore can be found (for example) from exposed windward reef margins to protected inner reef habitats, as well as with increasing depth, for more or less equivalent

ambient light conditions. However, as light decreases in deeper water, other taxa become dominant, particularly pectiniids and agariciids (Wells 1954; Barnes *et al.* 1971; Faure 1977; Pichon 1978a; Kühlmann 1983).

At lower taxonomic levels, the number of coral assemblage zones which can be identified on a particular reef is much higher for the Indo-Pacific than for the Atlantic Province. In the Bikini coral reefs of the Marshall Islands, Wells (1954) distinguished eight zones characterized by their coral communities while Done (1982) recognized 17 different coral communities based on their respective dominant species in the Great Barrier Reef, emphasizing, however, the considerable overlap in the composition of these communities (Fig. 16). To some extent, the number of assemblages or communities recognized depends on the method of description or analysis used, e.g. a hierarchy-based approach allows subsets to be recognized (e.g. Sheppard *et al.* 1992).

Zonation of coral communities presents wide lateral variations on the regional scale, in distinct reefs, but also on the scale of one single reef. This is reflected by differences in occurrence and bathymetric range of individual assemblages with respect to the local environmental conditions (Graus & Macintyre 1989; Sheppard *et al.* 1992): hydrodynamics (Rosen 1975; Geister 1977; Done 1982, 1983), turbidity (Titlyanov & Latypov 1991) and availability of suitable substrates (Glynn 1973). The complete zonal sequence may be truncated at one extreme or the other by regional or local conditions or otherwise condensed or attenuated in various ways.

II. Coralline algal zonation

(IIa) Hawaiian Islands Littler's (1973a, b) work was the first modern work to quantify the abundance of different coralline taxa with distance across a fringing reef flat to the algal ridge and then with depth down the fore-reef slope. His data show that whilst cover and diversity are similar over his 30 m depth range there are important taxonomic changes (Fig. 12). Reef flats are dominated by *Porolithon* on the algal ridge, *Sporolithon* and a melobesoid (Littler 1973a) on hard carbonate substrates with soft macrophytic algae, and, *Hydrolithon reinboldii* on mobile sand and rubble. Sites deeper than 10 m have a dominance of *Hydrolithon breviclavum* as both crustose pavements and 'rounded aggregates' (rhodoliths?). Sites deeper than 18 m have up to 8% crusts of *Tenarea*.

Subsequent studies in the Hawaiian islands by Adey *et al.* (1982) were more extensive and covered a greater depth range. However, surface

areas or numbers of plants were not measured because of the complex three-dimensional shapes of crusts and the difficulty of identifying individuals because of overgrowths and fusions. Their data are given as frequency of occurrence on variably sized bottom samples (Fig. 13). A distinct shallow-water (intertidal–20 m) association is dominated by *Porolithon*, *Paragoniolithon* and *Neogoniolithon* (now known as *Spongites*, Woelkerling 1988); intermediate depths (20–50 m) are dominated by *Hydrolithon*, *Neogoniolithon* (now known as *Spongites*) and *Archaeolithothamnium* (now known as *Sporolithon*), and a deeper zone (> 50 m) is dominated by *Mesophyllum* and *Lithothamnium* (now known as *Lithothamnion*). The occurrence of the deeper taxa in cryptic sites in shallower waters (Adey *et al.* 1982) suggests that light is a major factor in the distribution of these coralline genera. These surveys do not confirm Littler's (1973a, b) records of the presence of *Hydrolithon* and *Sporolithon* in shallow reef-crest sites. The other major difference from the earlier study is dominance by melobesoid genera in mid to deep waters.

(IIb) Caribbean and Gulf of Mexico The study by Minnery *et al.* (1985) from the Flower Garden Banks confirms many other observations from both tropical and temperate areas of the world where the cover of corallines dominates over corals in deeper fore-reef or outer ramp environments (Bosence 1983). The shallow occurrence of *Porolithon* is also indicated by these data (Fig. 13B), as is the mid-depth (20–50 m) importance of *Hydrolithon*, and the deeper water (> 50 m) domination by *Lithothamnium* and *Mesophyllum* together with *Peyssonnelia*. A similar pattern was recorded by van den Hoek *et al.* (1975) from fringing reefs in Curaçao (Fig. 14). Three species occur in the intertidal (*Hydrolithon boergesenii*, *Lithophyllum intermedium* and *Neogoniolithon* sp. 1). In the shallow subtidal *Porolithon pachydermum* dominates and, finally, in the deepest part of the transect (20 m) *Hydrolithon boergesenii* is the dominant species (Fig. 14). Adey and his co-workers (see below for details) record slightly different shallow-water associations with *Porolithon* (and *Leptoporpholithon fragilis*) being the main intertidal corallines and *Lithophyllum congestum* being the main coralline of the lower intertidal.

(IIc) Discussion Despite the taxonomic problems associated with coralline algae and the different methods which have been used to assess coralline abundance, a broad pattern of differing intertidal, shallow and deep water associations

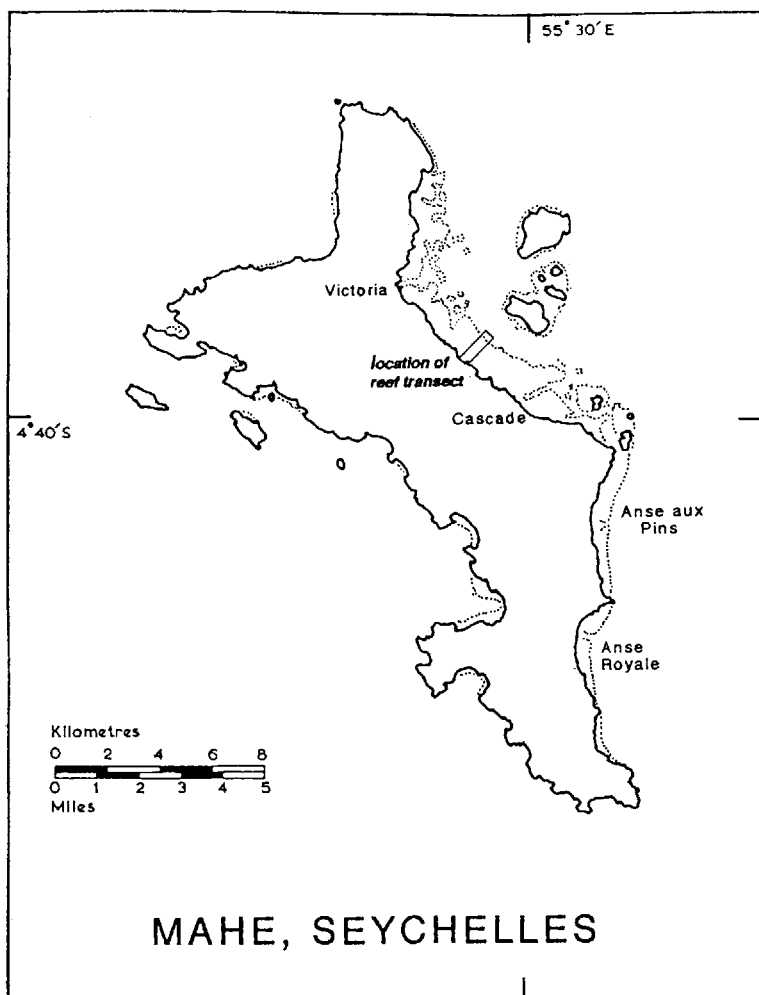


Fig. 17. Place names and location of reef transect on Mahé Island, Seychelles (from Braithwaite 1971).

appears to emerge from this review. Shallow and intertidal reef ridges are built mainly of *Spongites* (previously recorded as *Porolithon*), *Neogoniolithon*, and *Paragoniolithon*. Associated shallow water taxa are species of *Sporolithon* (as *Archaeolithothamnium*), *Lithophyllum* and *Hydrolithon*. Intermediate depths (c. 10–50 m) are often dominated by *Hydrolithon*. The deepest sites from where corallines have been studied in tropical reef slopes are dominated by the melobesioid genera *Mesophyllum*, *Lithothamnion* and by *Sporolithon*. It is therefore convenient to refer to these as the mastophoroid zone of shallow waters and the melobesioid zone of deeper waters following the coral zones described above. The best evidence

that these zones are light (hence depth) related are the observations of Adey *et al.* (1982) and Adey & Vassar (1975) that the genera that occur in abundance on the deep reef-slope seafloor also occur in darkly lit cryptic cavities in shallower reef sites.

Case studies of coral and coralline algal zonation

Coral zonation on the Recent reefs around Mahé, Seychelles (western Indian Ocean)

The coral reefs around Mahé, Seychelles were studied using a semi-quantitative approach

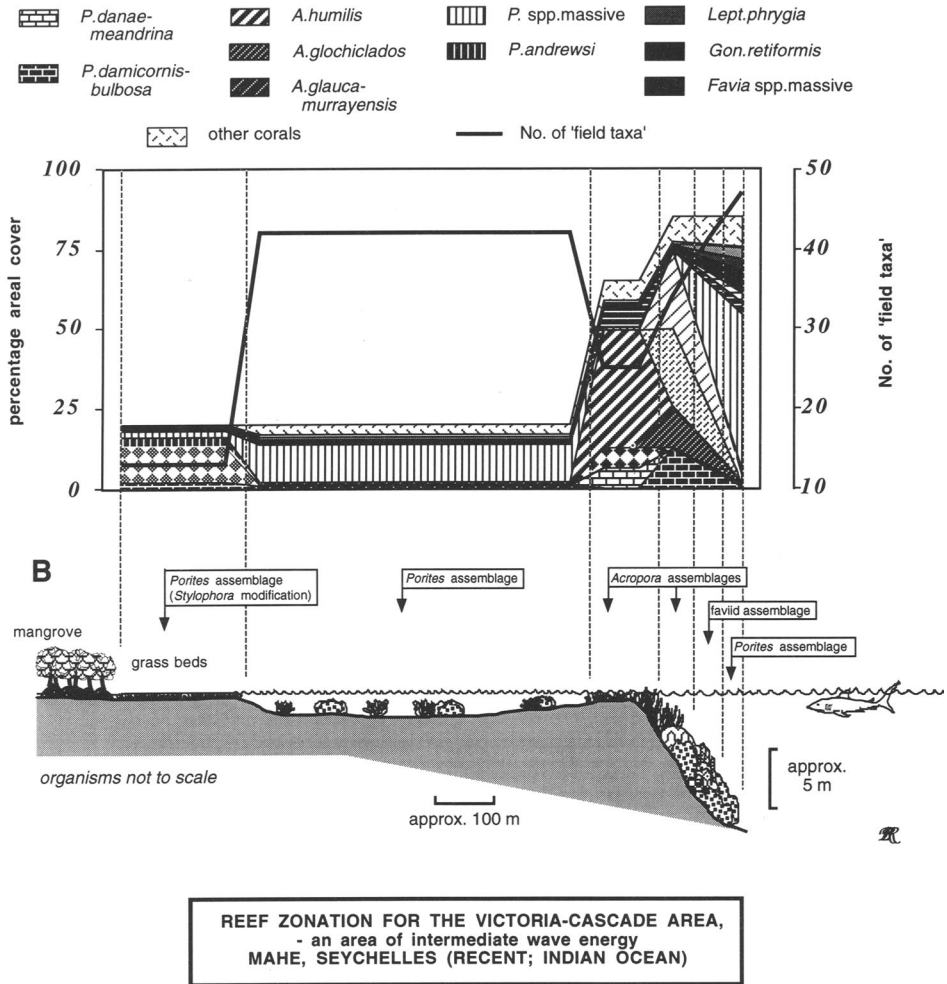


Fig. 18. Coral diversity, coral cover and zonation for reef transect from Victoria-Cascade area, Mahé. (A) Plot of 18 commonest field taxa only, *A.*, *Acropora*; *S.*, *Stylophora*; *P.* (in first column), *Pocillopora*; *P.* (in third column), *Porites*; *Gal.*, *Galaxea*; *Plat.*, *Platygyra*; *Lept.*, *Leptoria*; *Gon.*, *Goniastrea*; (B) Schematic reef profile illustrating generalized coral assemblages.

based on a simple phytosociological method adapted from Oosting (1956). A local scheme of coral zonation was developed (Rosen 1971, 1972) and further modified in general reviews (Rosen 1975, 1981; see above). In origin, it owes much to previous work by Lewis & Taylor (1966), Taylor (1968), and Wells' (1954, 1957) descriptive studies and reviews of habitat distributions of corals in the Marshall Islands

and elsewhere in the Pacific. However, the underlying coral data for Mahé have not previously been published, and details of one particular reef area are presented here for the first time as an example of semi-quantitative studies of general zonation of corals on Recent reefs.

The Seychelles are a scattered group of islands in the near-equatorial part of the western Indian

Ocean (Fig. 17). The islands are very varied in character, the main group consisting of granitic high islands surrounded by fringing reefs. This group includes the capital island, Mahé, on which coral studies were concentrated over two field seasons between 1964 and 1966. A concise review of Seychelles reefs is given by Stoddart (1984) and the reef geology is given in Braithwaite (1971, 1975). In many cases, granite headlands project seawards beyond the reefs, but a more continuous reef system is developed on the eastern (broadly, windward) coast. Here, reefs may extend hundreds of metres from shore and are widest (up to 2 km) in the northeastern area in the broad embayment extending north and south from the capital, Victoria. On the western side and around the southeastern-most shores, reefs are usually only tens of metres across and discontinuous, often amounting to little more than inshore coral thickets. The water depth over the reef platforms rarely exceeds 3 m, and parts of the platforms, like some of the grass beds and some reef-crests, are even emergent at low water. Reef fronts vary from near-vertical to gently sloping features, but there is great variety in their coral cover from steep bioconstructional facies of massive corals to more gently sloping structures some of which appear to be predominantly erosional features cut in older Pleistocene limestones. The slopes of reef fronts mostly reach down to *c.* 8–10 m, beyond which the surrounding floor shelves much more gently to *c.* 20–30 m around Mahé.

Reefs southward of Victoria (Fig. 17) provide the present data for an idealized transect from near shore, across the reef flats and for some way down (*c.* 10 m) the corresponding reef front (Fig. 18). A more complete set of reef flat coral zones is actually present on the reefs further south at Anse aux Pins and Anse Royale (Fig. 17) but data on the variation with depth down the reef front are not available.

I. Methods

(Ia) Taxonomy At the time when the fieldwork for the present study was carried out the corals of the western Indian Ocean had been very little studied. There were no available memoirs which covered all the coral families, and the state of Recent Indo-Pacific coral taxonomy in general was highly confused. Although substantial coral collections were made during the Seychelles fieldwork for taxonomic study, it proved impossible to make consistent one-to-one identifications of all the corals on the reef, relative to the names established from detailed study of the samples. On the other hand, the logistics of fully sampling every study site were both prohibitive

and potentially too damaging to the reefs themselves. Hence, after the first of the two field seasons, a compromise scheme of 121 'field-taxa' was adopted for survey work purposes. These names are retained here (as in Fig. 18) because it is not possible to correlate them retrospectively with modern usage in a consistent way. Note that Sheppard's (1987) taxonomic compilation for the Indian Ocean shows even fewer species (101) for the Seychelles than the above number of field-taxa, but he did not include Rosen's (1972) list of Seychelles coral records. A more realistic number of Seychelles species is likely to be at least 150–200.

(Ib) Field surveys Study sites on Mahé reefs were informally surveyed using subjective estimates of:

1. **Overall coral cover** using a five-point ranked scale of descriptive categories (see Appendix A, Table A.1);
2. **Relative abundance** of individual coral species using a four-point descriptive scale (see Appendix A, Table A.2).

For present purposes, these qualitative categories were converted to arbitrary standardized percentages in order to derive *representational* cover estimates for individual species, the conversion method being given in Appendix A. Although arbitrary, the values obtained do facilitate better comparison of different sites, habitats and areas, and can therefore also be applied to the remaining Mahé data (Rosen 1972).

(Ic) Data synthesis and presentation Cover and Abundance Categories were recorded for all sites visited. Where several sites were visited within the same habitat and the same area, the data were generalized for sets of such sites. A table of these generalized site data for all the habitats studied around Mahé is given in Rosen (1972, table 4 in Part III). For cross-reef transects (as here) the data can be extracted from this source for the appropriate habitats, converted as above, and plotted in the spatial sequence in which they occurred across the reefs of the Victoria-Cascade area (Figs 17 & 18). However, as the total number of field-taxa at any site may be as high as 50 or more, it is difficult to depict cover values for all of them clearly on a single plot. For present purposes therefore, the field-taxa having only the highest two cover values were selected within each habitat. This restriction yielded 18 'field taxa', deemed here to be the most common corals of the Victoria-Cascade Reefs. The cover estimates of these taxa are

followed through to all the other habitats in the transect, even if their actual cover values in those habitats were much lower. All other remaining corals in the area are shown grouped together as 'other corals', and the balance of remaining unspecified cover represents space not occupied by corals. According to study site, this can consist of other organisms or be visually 'barren' sand and rock. This method of data-simplification therefore concentrates on the most ecologically abundant corals, and by implication the main reef-builders.

II. Results Figure 18 shows the cover values of the 18 most common field-taxa present in the Victoria-Cascade area of Mahé. The turbid, very sheltered inshore marine-grass areas are dominated by a narrow branching form of *Stylophora*, '*S. pistillata* (2)'. The other corals here are predominantly poritids. Further out, the marine grass gives way to a sandy area in which numerous small patches and isolated colonies of coral occur. The environment is still very sheltered and relatively turbid. Here, coral diversity is much greater and poritids become important. Approaching the reef crest the water becomes clearer and there is a much higher proportion of hard substrate. Coral cover is much higher in this reef crest area but diversity decreases. The dominant corals are *Acropora* and *Pocillopora*, an assemblage which continues on to the uppermost part of the reef front. The *Acropora* forms are stout branching forms here referred to *A. humilis*. *Stylophora* is also important in this habitat, but its form consists of short stout branches and corresponds to *S. mordax*. Going down the reef front cover continues to rise, firstly with abundant *Acropora*, especially staghorns, table forms and a form (field name, *A. irregularis*) which consists of stout complex branches terminating in numerous, closely set, finely branching 'fingers'. Further down the reef front massive faviids and poritids become dominant.

III. Discussion Ecological zones can be defined and named according to these most abundant corals. The pattern in Fig. 18 also suggests that if the presence of the corals themselves is any indication, conditions on the reef platform and those further down the reef front are not dissimilar. This is particularly true of the occurrence of '*Porites* spp. massive'. As the depths at which these corals occur on reef flats and reef fronts are not the same, this might reflect similar conditions of hydrodynamic energy rather than depth *per se* (alternatively, the actual species within this *Porites* species

complex may turn out to be very different in the two areas). The greater depth of poritid-dominated assemblage on the reef front than on the platform might also demonstrate that the main controlling factor is illumination, since the turbid conditions of the reef flat area might reduce illumination to a level similar to that found in deeper parts of the reef slope. This is also suggested by the presence amongst the less frequent reef slope corals of pectiniids: these are taxa that are often recorded from much greater reef depths in other regions (Wells 1954; Barnes *et al.* 1971; Faure 1977; Pichon 1978a).

Richness of 'field-taxa' is highest in the reef front area, but the mid-reef flats are also rich, though not necessarily at any single site. Richness seems to reflect the greater variety of smaller-scale sub-habitats in both habitats. In addition, the water depth is sufficient to reduce the possibility of corals in these particular habitats being subjected to extremes of emersion, low salinity, insolation, etc., which are hazards of the other habitats in the transect (and also on the shallower reef flats of other areas). The diversity pattern in Fig. 18 may be partly an artefact, however, as there may be many species of *Acropora* and *Porites* obscured within the practical field names like '*Porites* spp. massive' and '*Acropora* sp(p)'.

Similar patterns have been established for numerous reefs elsewhere, and this has led to the derivation of the general scheme (Figs 8A, 16A) discussed above and by Rosen (1971, 1972, 1975, 1981). Figure 16A also shows the relationship of the Victoria-Cascade transect to this scheme. Elsewhere around Mahé (e.g. Anse aux Pins) there is an additional zone characterized by *Pocillopora* and *Millepora* that occurs in higher energy than is usually found in the Victoria-Cascade area. Done (1982) noted that this was not present as a distinct zone in the Great Barrier Reef region, but rather that *Pocillopora* occurred amongst the *Acropora* assemblages in some of the higher energy environments. This observation also holds in the Victoria-Cascade transect in Fig. 16A, but on reef crests elsewhere around Mahé that are exposed more directly to stronger surf, as is also seen around Addu Atoll in the Maldives (B. R. Rosen, personal observation), *Acropora* diminishes seawards on the reef crest leaving these other two corals relatively more abundant. Thus, these reef crests appear to be occupied by two narrow zones very close together, dominant *Pocillopora* lying seaward of dominant *Acropora*. Beyond the *Pocillopora* zone, *Acropora* reappears to seaward on such reefs when the water depth just begins to increase in the upper parts of the reef fronts.

In other regions of the world, where the water energy is greater, corals may give way to a community dominated by crustose coralline algae, examples of which are discussed elsewhere in this paper. Note that the 'algal ridges' reported from Mahé by other authors (e.g. Lewis & Taylor 1966) are not algal ridges in this sense, but are gently raised features constituting the highest parts of the reefs where they occur and dominated by fleshy and branching coralline algae. They are situated shorewards of the *Acropora* and *Pocillopora* zones on some reefs round the island. Although their coralline flora needs to be studied in comparison with those of algal ridges, it appears that conditions are not sufficiently rough around Mahé for true algal ridges to develop. In general, as energy increases (in a spatial gradient sense) a new higher energy zone appears on the reef crest and uppermost reef slope, and the other zones are 'displaced' away from this area, i.e. shorewards, downslope and in a longshore direction. Thus, the same sequence of zones can be traced into calmer water whether this is back across the reef flats, further down reef fronts or in a longshore direction towards more sheltered aspects (Fig. 16A). This means that it is not so much the geomorphological location alone which controls which kind of coral (or algal) assemblage occurs at any one place, but also the hydrodynamic conditions one finds there. This point has commonly been solved by distinguishing the communities on 'windward' reef edges from those on 'sheltered' reef edges (etc.), but this can be misleading as the windward reefs in one region might still be relatively more sheltered than the windward reefs in another region. Thus, the general scheme in Fig. 16A is useful both locally and regionally as a basis for comparing different reefs (Rosen 1975).

The biotic and abiotic influences on zonation schemes like that in Fig. 16A require further study. It is common to find attenuation or condensation of zones. Condensation probably occurs when a critical controlling environmental gradient like water energy is much steeper than usual. In other places, locally unusual conditions seem to modify the expected coral assemblage. Thus, although *Porites* is quite common in the inshore areas of the Victoria-Cascade transect, and the environment there is more or less 'typical' for that genus, there is also abundant *Stylophora* (*S. pistillata* 2) here. This coral's distribution seems to reflect the more variable salinity regime, very high turbidity, soft substrates, or proximity of human habitation, which are present in these areas of the reefs. This is in complete contrast to the reef crest where

Stylophora has the *mordax*-form, *sensu stricto*, typical of higher energy reef crests. These two names in *Stylophora* have been confused, and sometimes considered to be synonyms. Gattuso *et al.* (1991) have recently argued that they should be kept distinct, as their ecology around Mahé also suggests.

Surface communities and internal structure of the St Croix algal ridges

Perhaps the most detailed analysis of present-day reef-building coralline algae and their preservation within the reef framework comes from research in St Croix (Adey & Vassar 1975; Steneck & Adey 1976; Adey 1978; Bosence 1984). Holocene algal ridges are constructed over shallow-water coral reefs fringing the eastern margin of St Croix which are subjected to continuous northeasterly trade winds. Adey (1978) has shown that algal ridge growth in the Caribbean-West Indies area is positively correlated with both wind constancy and strength. *Acropora* frameworks occur in shallow (1–4 m) moderate to high energy sites and these are succeeded upward by coralline frameworks which extend into the inter- and supra-tidal (to a maximum of 1 m above mean sea level Adey & Burke 1976). Even though these reefs and ridges are relatively small-scale structures (Fig. 19) they are of considerable interest to this study as their internal structure indicates the likely mode of preservation of coralline algal zonation within reefs.

I. Surface communities Whilst detailed transects illustrating surface coralline abundance through these reefs have not been published the zonation has been demonstrated by settlement experiments (Adey & Vassar 1975; Steneck & Adey 1976). These give percentage abundance of corallines at depths down to 1.10 m (below m.l.w.sp. tides) from the crest of the algal ridge at Isaacs Reef, St Croix (Fig. 15). The shallow-water coral pavements are overgrown by *Neogoniolithon* and *Leptoporeolithon fragilis* and these taxa dominate over the depth range from 1.1 to 0.4 m below m.l.w.sp. tides. *Lithophyllum congestum* then dominates up to 20–30 cm above m.l.w.sp. tides. Above this *Porolithon pachydermum* is the main ridge-builder. Mean accretion rates ($1\text{--}5\text{ mm a}^{-1}$) on the plates measured over one year are also given (Fig. 15) which reflects the relatively rapid growth rate of the branching coralline *L. congestum* (Steneck & Adey 1976).

Internal structure Extensive drilling by Adey and

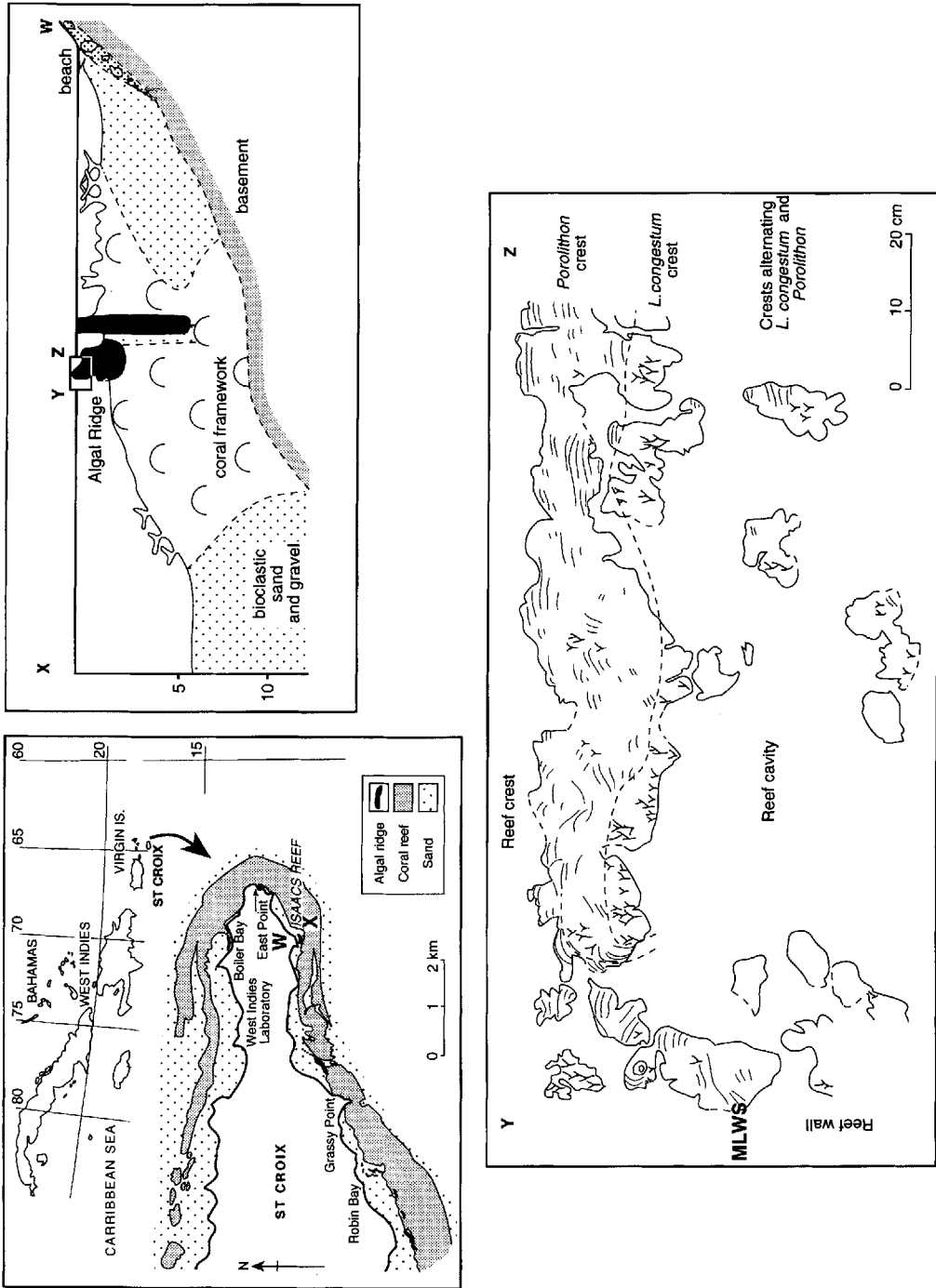


Fig. 19. Location, cross-section (after Adey 1978) and structure of St Croix algal ridge and distribution of coralline algal genera (after Bosence 1984).

his co-workers (1978) and the excavation of slabs from sections across the reefs (Bosence 1984) illustrates their internal structure (Fig. 19). Polished slabs were traced to illustrate occurrence of frameworks, internal sediment and cavities. These areas were then point counted with an overlying grid to obtain their areal abundance (see Bosence 1984). Firstly, the very large amount of bioerosion within this reef should be noted. This has removed much of the original framework leaving borings (3% of reef cross-section), internal sediment (20%) or the very large cavity area (61%) making up most of the reef cross-section. Therefore, the area of preserved framework within this reef is just 16% and the remaining 84% of the reef is made up of cavities, cement or internal sediment. A detailed description of the areas of preserved coralline and secondary frameworks is given in Bosence (1984), and Fig. 19 abstracts the areas dominated by different coralline communities. The primary reef framework makes up 15% (*Lithophyllum* 5% and *Porolithon* 10%) of the reef cross-section. The secondary coralline frameworks comprise just 1% (the remaining 84% is accounted for by sponge borings, internal sediment and cavity). The lowest 30 cm of framework up to present-day m.l.w.s. is very poorly preserved but appears to be a mixture of *Lithophyllum* and *Porolithon*. A central band within the reef is dominated by *Lithophyllum congestum* suggesting intertidal conditions and finally the top of the present-day reef is largely constructed by *Porolithon* reflecting the predominant supratidal conditions of the present-day reef flat. This passes on the reef crest and front to the present-day *Lithophyllum* framework.

II. Discussion The methods used to compare surface and subsurface corallines are clearly quite different. In this example they were developed independently by different workers with different objectives. The settlement plates were measured with a clear plastic grid as planimetric area. The subsurface was measured, again with a clear plastic grid overlay, but at a much larger scale and as a cross-sectional view. It is not possible to measure plan views of the reef slabs as the very irregular original reef surfaces cannot be identified except on a broad view of the entire cross-section. However, it is possible to view the surface frameworks in cross-sectional view but this method has not, to our knowledge, been used. Biologists are clearly interested in surface views and geologists in cross-sectional views. Future work on surface communities could usefully use

vertical sections as this should give an index of occurrence and abundance which is directly comparable with preserved subsurface material. In effect this view is given in the upper and outer reef surface of Isaacs Reef (Fig. 19), but here the difficulty is deciding where the surface ends and the subsurface begins. Qualitatively it is immediately apparent from this cross-sectional view that the percentage of preserved framework decreases from the reef surface to the reef interior.

The cross-sections in Fig. 19 show clearly that the present-day zonation from shallow coral reef to peritidal algal ridge is preserved within the reef with the shallower facies on top of the deeper facies generally indicating a regressive vertical sequence. Similarly, in detail the supratidal *Porolithon* is constructed above the intertidal *Lithophyllum* framework, suggesting that reef growth has outpaced sea-level rise in the recent past. However, the alternation of the two coralline communities in a vertical profile does not illustrate the reef zonation. Rather, it preserves the alternation of two reef zones through time as determined by the local water depth. With our prior knowledge of the Holocene sea-level curve it can be interpreted that the reef crest has more or less kept pace with sea-level rise with some minor fluctuations. There are not enough data within the reef cross-section in Fig. 19 to reconstruct the zonation from first principles, as if investigating a geological section. Reef zonation would only be visible if the entire reef were encased in sediment and the surface communities preserved *in situ*.

Late Miocene reefs from Mallorca

I. Location and previous work During the late Miocene, a reef-rimmed carbonate platform developed in a post-tectonic setting in the Balearic Islands (Spain). On the island of Mallorca carbonate sequences containing reef build-ups form exceptionally well-exposed outcrops on the southern coast, extending to more than 20 km and up to 80 m in thickness (Fig. 20, Pomar 1991). Inland, the reef complex is only known from boreholes. Pomar (1991) has recognized four palaeoenvironments within this platform; a lagoon passing out to a reef and a deeper-water reef slope, and then to an open shelf. The internal structure of the platform shows overall progradation (i.e. regressive sequences) with alternating periods of progradation and aggradation which are considered to be controlled by high frequency sea-level changes (Pomar 1991; Bosence *et al.* 1994). These reefs

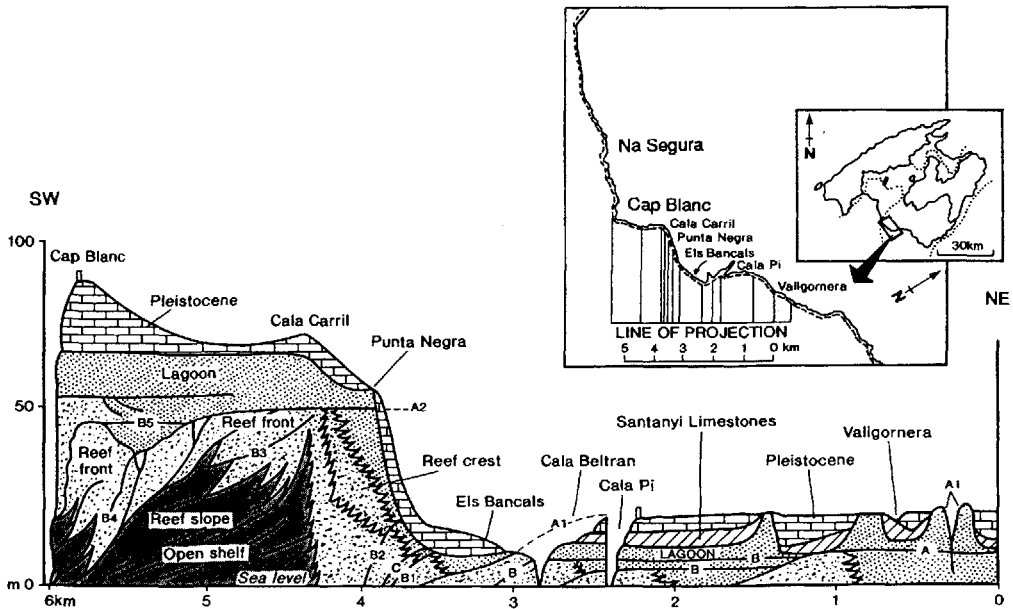


Fig. 20. Location of Cap Blanc and Na Segura reef on the southern coast of Mallorca Island and projected cliff-section (from Pomar 1991; Bosence *et al.* 1994).

correspond to the last stages of coral reef construction in the Mediterranean (Chevalier 1962, 1977; Esteban 1979) and the diversity of the coral fauna is very low. No more than five genera occur, of which only three are common.

II. Application of the line transect to Mallorca reefs Several types of reefs occur on the Mallorca platform. They differ in their size and geometry, their coral diversity and the abundance and diversity of the coralline algae. Two different reefs are presented here as examples. These sections display two-dimensional outcrops on which two different techniques have been used in this study, depending on the orientation of the exposure with respect to the direction of reef accretion (see Methods used in present study).

III. Reef zonation from vertical stratigraphic sections

(IIIa) The Cap Blanc section The Cap Blanc cliffs represent a two-dimensional outcrop oriented slightly oblique to the front of an aggrading reef-rimmed platform margin (Fig. 21). This type-section shows the vertical succession of open-shelf facies and reef-facies consisting of dish-shaped *Porites* change gradually up-section to branching forms which are overlain by massive *Porites* (Fig. 5, p. 249, Pomar 1991). The latter biofacies is truncated at its top by a sharp

erosion surface overlain by reef crest, back-reef and beach facies. This vertical change of reef facies is interpreted as shallowing-upwards and resulting from the southwards progradation of a reef complex (Pomar 1991). This present work has shown that the top of the branching *Porites* facies is marked by a hardground which was bored, eroded and eventually encrusted by coralline algae (cf. Fig. 21 with Pomar 1991, fig. 5). This sedimentary discontinuity indicates a decrease of sedimentation rate followed by a period of erosion and therefore separates two distinct shallowing-upwards reef units in this section.

(IIIb) Vertical succession of reef communities A A vertical section through the reef front is shown in Fig. 22 with data recorded as previously described (see Methods used in present study, Fig. 1). This section illustrates the excellent outcrop of the reef as 16 out of 20 sample lines have 100% exposure. Only two sampling lines (located, respectively, at 4 and 7 m along the section) intercepted poorly preserved outcrop. This information on quality of outcrop is required when comparing different sampling lines and sections. The framework density increases upwards over the entire section but also independently in each one of the two reef units. Only two coral genera are present at Cap Blanc, the dominant *Porites*, and rare colonies of

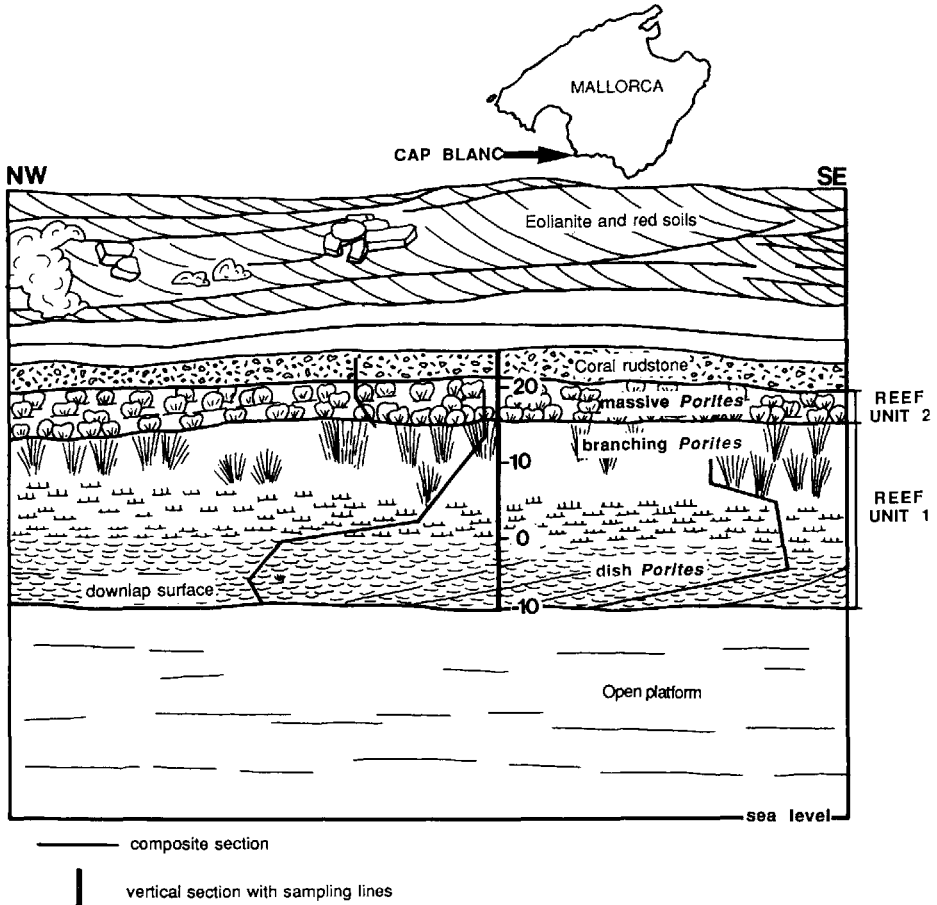


Fig. 21. Sketch of Cap Blanc cliff, Mallorca, showing facies, reef units and occurrence of major coral growth forms (after Pomar *et al.* 1983), and location of vertical sections of this study (see Fig. 22).

Siderastrea which occur only locally at the top of the upper reef unit.

Four coralline algal genera and one peyssonnelid have been recognized on this section. The other reef-builders are represented by encrusting serpulids and bryozoans occurring in small amounts in the upper reef. Associated fauna are molluscs, echinoids and rare miliolids.

The lower reef unit has a framework density reaching 40% at the top of this unit and is characterized by a gradual upward change in colony growth form. Dish- and cup-shaped *Porites* colonies form the reef framework in the lower parts of the section. Upwards they change gradually to short branching forms and then to large elongate-branching colonies which are well developed in the upper part of the reef. Crustose

coralline algae in growth position are scarce and located in the upper part of this reef but they do not exceed 1% of the facies. The relative abundance of coralline algal genera has been established from a composite of three overlapping vertical sections on the same outcrop (Fig. 23). The measured sections extend to lower levels in the reef-front facies to include coralline crusts on isolated corals, which may or may not be preserved *in situ* on this slope. The occurrence of coralline algae is shown on the composite section in Fig. 23 as kite diagrams of percentage abundance. *Spongites* can be seen to be the dominant encrusting and frame-building coralline alga which occurs as both crusts and small (up to 1 cm thick) branching frameworks on corals. *Lithoporella* is found as thin crusts. *Lithothamnion* is uncommon and appears to be

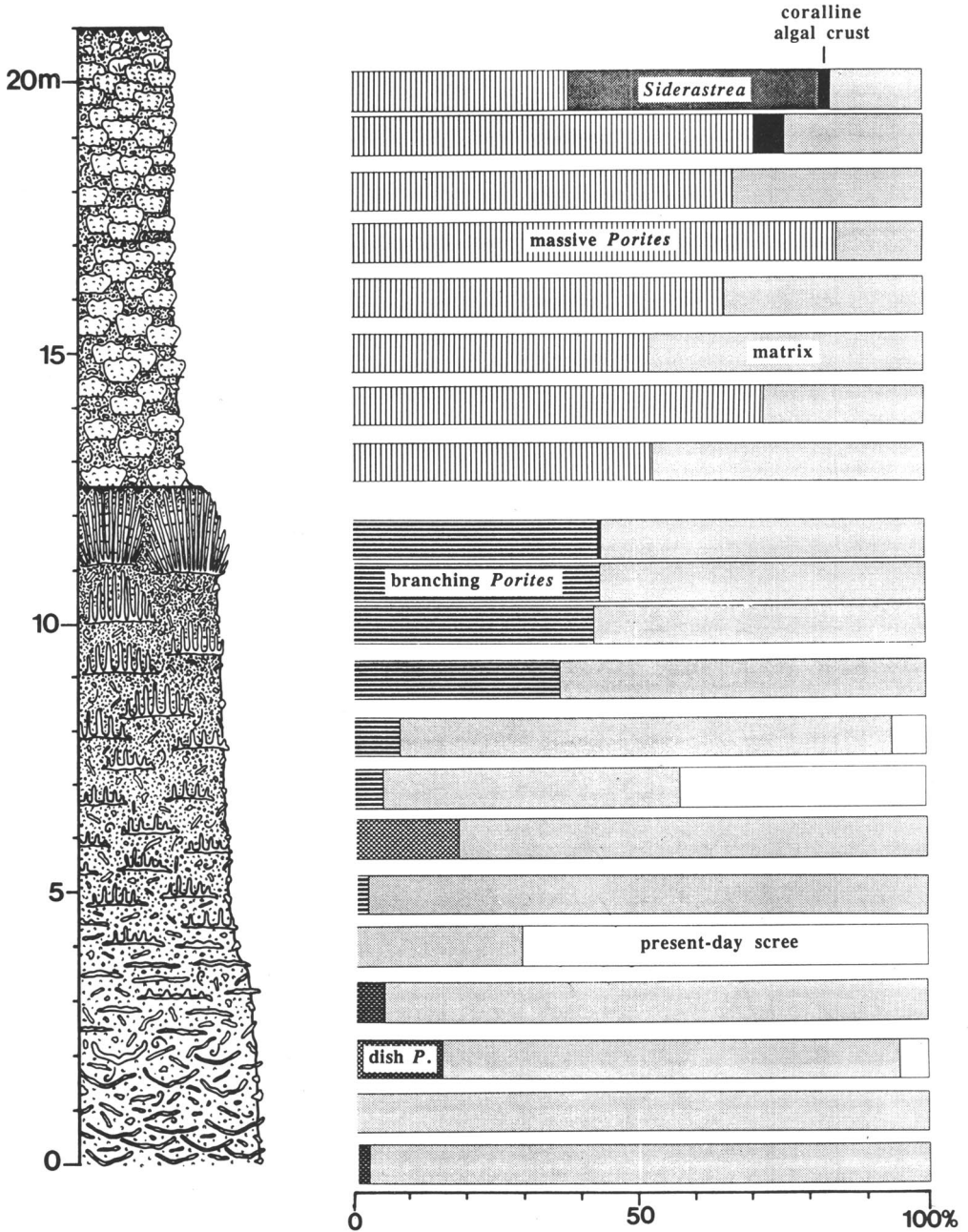


Fig. 22. Two-dimensional vertical section through Cap Blanc *Porites* reefs, Mallorca, showing the percentages of the different reef components measured along horizontal 1 m sampling lines (cf. Fig. 1).

confined to the lower part of the section. *Lithophyllum* and a peysonnelid alga are recorded only from the central part of the section which lies within the lamellar and cup

Porites zone. Matrix is a biodetrital muddy packstone with coral and coralline algal fragments and debris of molluscs and echinoids. Micritic crusts (no more than 1 mm thick)

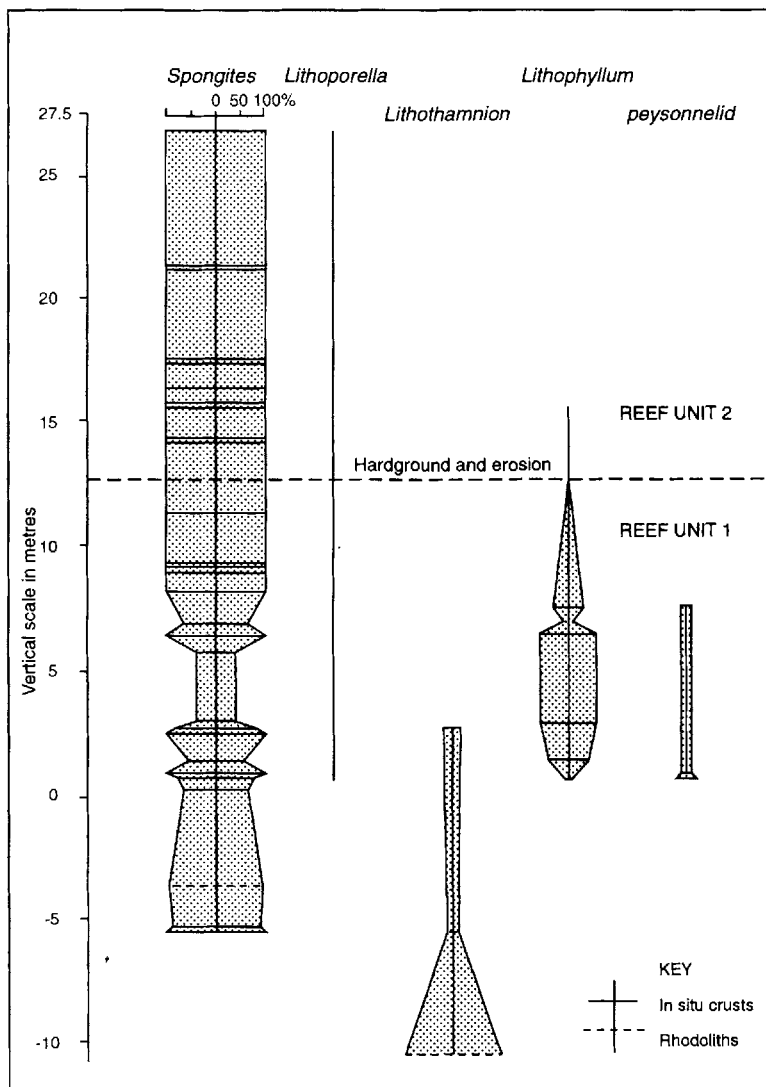


Fig. 23. Composite vertical section from three measured sections on Cap Blanc reefs (Fig. 21), Mallorca, showing the relative abundance of crustose coralline algal genera (stippled areas: extrapolate abundance between data points).

develop on branching *Porites* or on the coralline algae encrusting the corals.

The upper reef unit is mainly built by massive *Porites* with a framework constituting 52–85%. Secondary frameworks are constructed by coralline algae and serpulids and rare bryozoans. Coralline algae are most abundant at the top of the upper reef unit where they reach 5%. They are dominated by *Spongites* associated with thin crusts of *Lithoporella*. Serpulids occur mainly in the lower part but they form less than 1% of the framework. This framework has been intensively

bored by *Lithophaga* (see Perry in press). Sediment is a biotrital packstone.

(IIIc) Discussion These data suggest an up-section successive replacement of corals and corallines, possibly reflecting an original depth related distribution, from a lower *Lithothamnion* zone on the fore-reef open shelf upwards to dish-shaped corals and *Lithophyllum*, *Spongites* and a peysonnelid. This is gradually replaced by a reef-slope environment with branching *Porites* and *Spongites*. In the upper part of this reef the

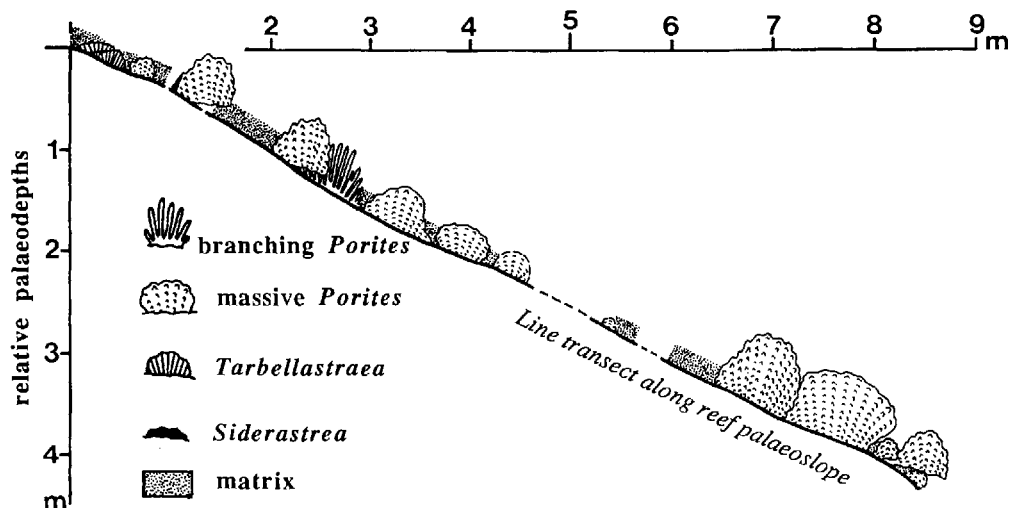


Fig. 24. Two-dimensional profile along a reef palaeoslope in Na Segura, Mallorca, showing the distribution of coral colonies and matrix (size of coral colonies true to scale).

coralgal framework is often coated by thin micritic crusts probably indicating a degradation of the environmental conditions favourable to reef accretion. The slowing down of reef growth and the decrease of sedimentation rate are followed by early lithification and submarine erosion. The upper reef prograded over this surface and is represented at Cap Blanc by the shallowest part of the reef front which is dominated by massive *Porites* and *Spongites*. This dense framework is truncated by an erosion surface overlain by coral-molluscan rudstones.

Because of the vertical growth of the reef during sea-level rises vertical heights in the Cap Blanc cliff-section cannot be equated with palaeodepths as previously reported, and the palaeodepths of these communities cannot be quantified. Water depths probably changed with time during the reef development according to differences between rates of reef growth and rates of sea-level rise (Davies & Montaggioni 1985; Neumann & Macintyre 1985). However, the relative depths of these assemblages can be established as described above.

IV. Reef zonation along a palaeo-reef slope

(IVa) Na Segura section This consists of a number of two-dimensional palaeo-reef slopes outcropping normal or oblique to a reef front showing overall progradation. These reefs are located c. 5 km northwest of Cap Blanc (Fig. 20) and correspond to about the same stratigraphical level.

(IVb) Quantitative distribution of reef-builders

The reef framework is mainly built by corals represented by *Porites*, *Tarbellastraea*, *Siderastrea* and very rare mussels, whilst coralline algae are very scarce in the upper part of these reefs. The coral framework does not occur below 12–13 m of relative palaeodepth and is replaced below 20 m by bioclastic sands with rhodoliths and bryozoans. Matrix is a packstone with fragments of corals, coralline algae, molluscs, bryozoans, echinoids, forams and serpulids. Framework density is highly variable in the individual sampling lines and it averages 50% or more in the shallowest line transects. The profile shown in Fig. 24 is an example measured from the shallower part of the reef body where the coral framework density is commonly higher than 50%. Percentages of present-day scree and unidentified material show a relatively good preservation of the outcrop except between 2.5 and 3 m relative palaeodepth (Fig. 25). At the profile scale, *Tarbellastraea* and *Siderastrea* occur in the shallower parts. However, *Siderastrea* is very rare (<5%) and therefore it is difficult to generalize about its pattern of distribution (Fig. 25). By contrast, *Tarbellastraea* is quite common and can locally reach 60%. Massive *Porites* are largely dominant throughout the profile. Branching forms are more localized and their abundance can reach 15–20% in shallower areas (Fig. 25).

Several transects were measured on reef palaeoslopes of Na Segura. The profiles oriented more normal to the reef front show steep slopes up to 35–40°. Similar distribution and relative abundance of reef-builders were ob-

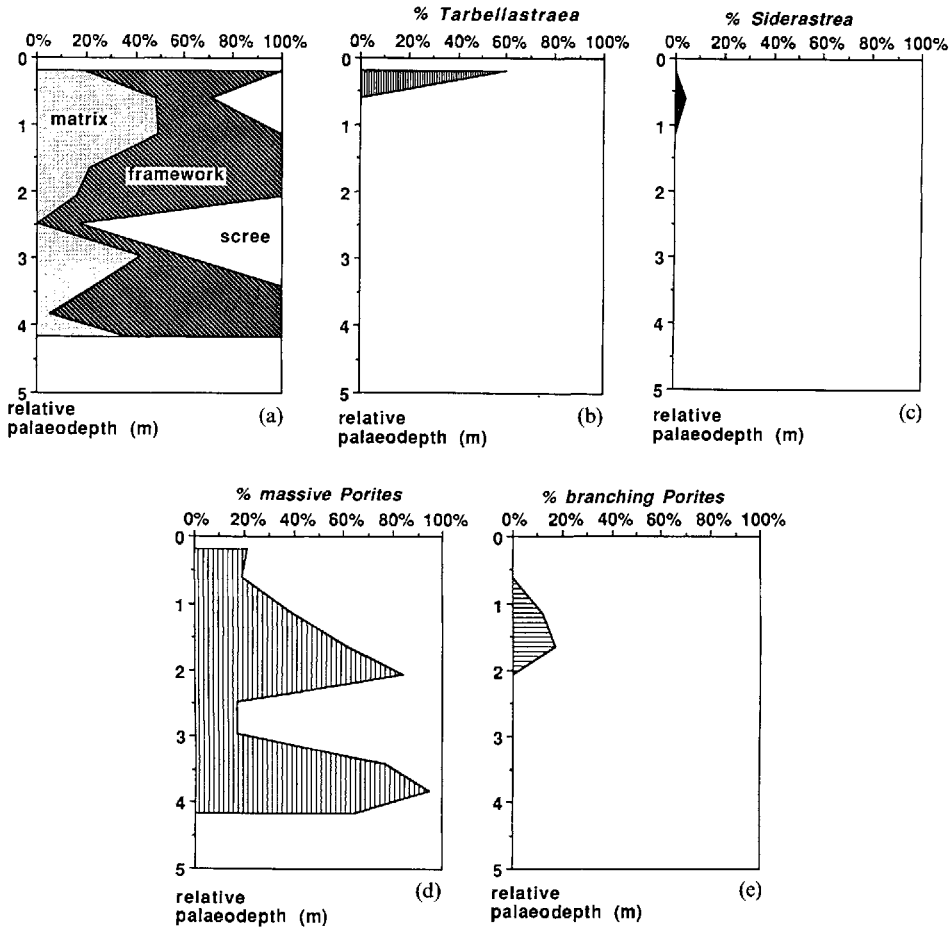


Fig. 25. Relative percentages of the different reef components measured along the Na Segura reef palaeoslope, Mallorca, shown on Fig. 25. (a) Framework, matrix, present-day scree and poorly preserved material. (b) *Tarbellastraea*. (c) *Siderastrea*. (d) Massive *Porites*. (e) Branching *Porites*.

tained from these line transects. In detail, differences result from the occurrence of rare and uncommon corals like *Siderastrea*, mussels and very rare branching *Tarbellastraea* and, to a lesser degree, branching *Porites*. In addition, the very gentle apparent slopes (i.e. cliffs oblique to the reef front) record both lateral- and depth-related variations of reef-builder assemblages and they often show a patchy distribution of massive *Tarbellastraea*. In the transects reaching the lower part of the reef slope, the deepest coral framework occurs down to 13–15 m of relative palaeodepth and consists of large-sized massive colonies of *Porites* which downslope are replaced by bioclastic sand. Below 20 m of relative palaeodepth the fore-reef slope is

characterized by rhodoliths associated with encrusting bryozoans.

(IVc) Discussion The Na Segura reefs differ from those on Cap Blanc in that they have steeper slopes, higher diversity of corals, fewer coralline algae within the reef framework, an absence of gradual modification in coral growth forms and presence of rhodolith facies on the lower slopes. Because of the low diversity of the coral fauna, and the scarcity of coralline algae in the Na Segura reefs, there is no clear zonation present in the shallow section described. Similarly, zonation is difficult to define quantitatively due to the occurrence of one dominant genus with a wide distribution and the presence of rare forms.

Distribution of the latter has to be confirmed from other profiles. However, the coral distribution obtained from the various profiles shows a broadly similar pattern. The distribution of dominant massive *Porites* does not appear depth-related except for the largest colonies which occur in deeper water (c. 10 m of relative palaeodepth). *Tarbellastraea* tends to grow in the shallow parts of the reef slope but may show a patchy distribution in some transects. Less common corals such as branching *Porites* and *Siderastrea*, when present, show a narrow depth range, with the first genus occurring at a few metres palaeodepth and the second being restricted to the shallowest part. This occurrence of *Siderastrea* is compatible with the data obtained from the Cap Blanc section. The mussids occur in small isolated colonies whose occurrence is too rare to allow comment on their relationship with depth.

Comparison of reefs

The field techniques applied on the reefs of St Croix, Mahé (Seychelles) and Mallorca are markedly different and therefore the values of the various parameters obtained on each reef cannot be compared directly. However, because the principle of these techniques is the same, the resulting general trends in framework density, diversity and zonation pattern may be compared.

I. Comparison of vertical sections: St Croix and Cap Blanc reefs Assuming that the linear percentages obtained from the offset sampling lines are proportional to the areal relative abundance of reef-builders, values of framework density from the St Croix and Cap Blanc reefs may be compared. The Miocene reefs of Cap Blanc show average framework densities per metre of 16.9–33.7% in the lower unit and between 48.4 and 69.2% in the upper one. The data for the internal structure of the St Croix algal ridge indicated lower proportions of preserved framework (areal percentage of 16%) due to intensive bioerosion. A vertical replacement of reef-building assemblages was clearly shown in both Holocene and Miocene reefs. In St Croix, where the sea level is independently documented, this succession can be directly related to the fine-scale zonation of the present-day algal ridge. In Cap Blanc, the environmental variations had to be deduced from independent geometrical and sedimentological criteria.

The method proposed in this paper, applied on vertical sections, has proved useful for characterizing reef communities and thereby

changes during reef growth, and hence also for inferring variations of environmental conditions through time at a given site on the reef. From the above two examples, it appears that this approach can be used on very different scales: detailed study of short-term changes in the reef crest of St Croix or as evidence of larger and longer palaeoecological variations in the reef succession of Cap Blanc.

II. Comparison of transects: Seychelles and Na Segura reefs The overall coral cover estimated from a phytosociological method in the Victoria–Cascade reefs reaches its maximum value on the external parts of the reef (i.e. > 75% on the front and upper slope). On the palaeoslopes of the Na Segura reefs, the maximum average of coral framework reaches 60%, and the highest values were obtained from the shallowest parts of the transects. Whilst these slight differences in cover values between the study areas may simply reflect the rather arbitrary numerical categories used in the Seychelles study (see Appendix A), the overall patterns of spatial change in the two study regions can still be usefully compared. Extension of coral framework downslope is also similar in both reefs. Coral colonies occur down to 13–15 m in the Miocene reefs of Na Segura whilst their maximum depth is 8–10 m on Mahé reef slopes, this being the general depth at which the slopes level out to the surrounding seafloor (Braithwaite 1971). However, the most obvious contrast is in coral diversity. While in the Seychelles regional coral species richness is probably at least 150–200, and 121 ‘field-taxa’ were defined for ecological field work, only five coral genera are present in Na Segura reefs. For the framework builders in particular, there are about ten important ‘field-taxa’ in the Seychelles profile of Fig. 18, compared with two genera at Na Segura (Fig. 24).

III. Influence of diversity on reef zonation

Characterization of reef zonation is closely dependent on the diversity of the reef-builders present. In highly diverse reefs, like those of the Seychelles, zonation is recognizable in the distribution of the common and dominant corals alone. In the low diversity reefs of Na Segura there is no clear zonation because of the overall dominance of one genus throughout and the presence of three rare genera, but a general distribution pattern of reef-builders can be defined from several line transects. In monogeneric reefs, like the Cap Blanc *Porites* reefs, coral zonation is defined in terms of morphology reflecting the apparently high potential for skeletal plasticity in this coral.

Conclusions

The line intercept transect applied to fossil reefs requires detailed study of well preserved outcrops with reef-builders in growth position. Accurate depth-related zonation may only be established from continuously outcropping reef palaeoslopes.

This new method has several important advantages over previous qualitative approaches:

1. It considers only reef-builders preserved in growth position.
2. Direct measurements of relative palaeodepths can be made in the field, so making subjective palaeobathymetric interpretations unnecessary. This approach removes the need to extrapolate water depths from Recent environments and organisms.
3. By quantifying framework density in terms of the amount of rigid biologic framework present, reef facies can be readily characterized as a spectrum ranging from scattered reef-builders to dense framework. This therefore removes the imprecision arising from the strict reef definitions and related controversy about 'ecological reefs' vs 'stratigraphic reefs'.
4. Quantitative assessment of the parameters which characterize reef zonation, such as framework density, diversity and organism abundance, can be obtained for individual reefs. Moreover, by using the same technique for reefs of different ages, including living reefs, objective comparison of reefs throughout the geological record may be made for the first time without encountering problems arising from 'transferred ecology' (Lawrence 1971).

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Appendix A: Methods used for Seychelles data, to convert field cover and abundance rankings into standardized percentages

(Brian R. Rosen)

Overall coral cover

The original field categories are given in Table A.1 together with their paraphrased original

descriptions (Rosen 1972). The descriptions clearly indicate that the categories do not represent a linear sequence of actual cover values, and Table A.1 therefore explains how the original categories were converted to the cover values used in the present paper. The resulting values are necessarily arbitrary, but serve to convey the original observations.

Abundance of individual corals (i.e. proportion of substrate cover occupied by individual corals)

In the simplest instance one could derive a value for the abundance (substrate cover) of individual corals by taking the Overall Coral Cover (per cent) at a given site and dividing it by the number of species present there. This method, however, would take no account of different relative abundances of corals, so Abundance Categories can be used to weight their share of Overall Coral Cover. The four original abundance classes are shown in Table A.2. Abundance of individual corals is even harder to judge subjectively than overall cover, and only four categories seemed consistently practical in the field. The same four abundance categories were used at all study sites, but they cannot be translated directly into cover values for individual species when different study sites are being compared. This is because both Overall Coral Cover (see above) and species richness, vary between sites. Thus, for the Relative Abundance categories of individual corals to be converted to actual percentage cover values for individual corals, these percentages have to be standardized for both Overall Coral Cover and the richness of 'field taxa' at different sites. Clearly, the coral cover of an individual species ranked in Abundance Category 3, along with ten other species, at a site whose Overall Coral Cover is 50%, probably occupies more actual substrate than a species of the same abundance rank at a site whose Overall Coral Cover is also 50%, but where 30 other species have the same abundance ranking. The assumption here, therefore, is that species within the same Abundance Category share an equal amount of cover. The overall calculation has three steps, as follows.

1. **Conversion of Relative Abundance Categories to a cover value for the sum of all the species within each Abundance Category**
From the descriptions of the Relative Abundance Categories (Table A.2), it is clear that a linear scale would be unrepresentative, e.g. the Dominant category

Table A.1. *Original field categories of overall coral cover and their conversion to percentage cover values*

Cover class and category	Original description	Basis for conversion to percentage cover	Overall coral cover (%)
1. Almost absent; very sparse	Corals completely inconspicuous over quite large areas, i.e. at a given study site, fewer than c. five colonies found altogether.	The area of a single study site might be up to c. 1000 m ² , and the few corals seem might only occupy c. 1 m ² of this in all. Therefore, a working mid-point cover value for Class 1 is:	0.1%
2. Sparse	Corals not prominent; rarely more than a few small colonies in sight at any one place. Total area not occupied by corals (i.e. visually 'barren' substrate and/or substrate occupied by other organisms) greatly exceeds that occupied by corals	Let the amount of substrate clearly visible in detail from a single point be c. 100 m ² , of which corals probably occupy c. 0.5 m ² . This gives a working mid-point figure for Class 2 = c. 0.5%. However, the maximum cover for Class 2 is c. 4% (see below). The mid-point of these two estimates is 2.25%, so a working mid-point cover value for Class 2 is:	2%
3. Scattered	Corals common, but occupy less substrate area than visually 'barren' areas and/or areas occupied by other organisms.	'Ground truth' (quadrat work) on the reef margin at Anse aux Pins indicates that Cover Class 3 ranged from 4 to 35%, suggesting a mid-point of 19.5% for this class. Hence, working mid-point cover value for Class 3 is:	20%
4. Close	Corals prominent, occupying about the same amount of substrate as other organisms and/or visually 'barren' areas.	This implies a minimum cover value of 50%, and as cover range of Class 5 is c. 80–90%, Class 4 cover range is therefore 50–80%. Hence, working mid-point cover value for Class 4 is:	65%
5. Dense; continuous	Corals dominate all other organisms present, and are largely in contact with each other.	The simplest approximation for continuous coral cover is a close-packing arrangement. This gives a cover value of 79% for square-packing and 91% for hexagonal packing. This suggests that the mid-point cover value for Class 5 is:	85%

implies that dominant corals occupy as much area, or more, than all the other corals present put together. The following method was therefore used to derive an arbitrary conversion of Relative Abundance to Areal Proportions. Disregarding substrate area not occupied by corals, consider a standardized area of 100 m² made up entirely of the coral species present at a given site. Each coral in this standardized area occupies the same proportion of substrate in relation to the other corals present, as it does within the actual study site. The resulting proportions (percentages) of overall coral cover occupied by each Abundance Class (Table A.2)

can then be used as working constants for different sites. They represent percentages relative to the total amount of substrate occupied by coral not percentages relative to the total space available. The latter are obtained in the next step.

- 2. Conversion of areal ratios for each Abundance Category to cover values for same**
 The amount of substrate occupied by all the corals within a given Abundance Value relative to the total area occupied by all the corals (Table A.2) can now be converted to the proportional area they occupy of the total available substrate by combining their relative abundance value with the

Table A.2. Categories of individual 'Field-taxon' abundance and conversion to areal ratios

Abundance class and category	Original description of category	Basis for conversion to percentage cover (in relation to area occupied by all the corals at a site, standardized to 100 m ² - see text)	Total cover for all corals in this category (%)
1. Rare	Taxon seen or collected from a single colony or small patch only.	Let a single colony or small patch by c. 200 mm across, this category can be said to occupy 0.03 m ² , a percentage of: For the remaining area (= 100 - 0.03 = 99.97 m ²) all the corals in each abundance class can be grouped together such that the total area occupied by the corals in each successive category is double that of the previous category, i.e. 1:2:4)	0.03%
2. Infrequent	Taxon occurs, and may be conspicuous in a few places general background species.	Standardized proportion of total coral cover = 1/7 of 99.97 m ² =	14.28%
3. Abundant	Taxon common, but definitely secondary in importance to (4).	Standardized proportion of total coral cover = 2/7 of 99.97 m ² =	28.56%
4. Very abundant	Taxon common or visually predominant over other corals (i.e. dominant species).	Standardized proportion of total coral cover = 4/7 of 99.97 m ² =	57.13%
			Total 100%

Overall Cover Values for all corals combined (Table A.1), i.e. at the same site. This actual value is the quotient of both together, e.g. an Abundance Value of 14.28% (Abundance Class 2) at a site whose Overall Coral Cover is 65% (Cover Class 4) represents a cover of 14.28% of 65% = 9.28%. This gives a standardized cover value (percentage) for the combined set of corals within a particular Relative Abundance category, for any site, relative to the total space available.

3. **Cover values for individual corals** The number of corals recorded for any given Relative Abundance category varies from site to site. The percentage area they occupy can be obtained by dividing the above cover percentage for that Abundance Category [(2) above] by the number of species recorded in that Abundance Category, e.g. if in the above example [see step (2)], 13 species were recorded in Abundance Class 2, the proportion of

substrate area each occupies is (9.28/13)% = 0.71%.

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Palaeoenvironmental interpretation using bryozoans: a review

ABIGAIL M. SMITH

Department of Marine Science, University of Otago, PO Box 56, Dunedin, New Zealand

Abstract: Bryozoans are colonial marine organisms, found in the fossil record since the early Ordovician. They have many possible applications in palaeoenvironmental interpretation. Their presence or absence, diversity and abundance, zooid morphology, colonial plasticity, colonial growth form, and reef-like structures all provide information about habitat. Temperature, salinity, water energy, water depth, substrate character, sedimentation rate, and even tectonic stability, may be indicated by bryozoan faunas. Examples are given to show palaeoecological applications of bryozoans, from shelf and deep-sea sediment studies to interpretation of Tertiary limestones and Palaeozoic environments. Caution is needed, particularly in interpreting very ancient faunas, due to the confounding factors of sampling bias, interdependent controls, taxonomic evolution and taphonomic selectivity. Bryozoans are nevertheless a tool of considerable value in palaeoenvironmental interpretation, particularly if corroborated with other lines of evidence.

Bryozoans are modular colonial animals, comprising many small individuals (zooids). In most marine bryozoans, the zooid's body wall is calcified, so that the colony that remains after the decay of soft parts is a preservable skeleton. Bryozoan skeletons may form large carbonate sediment deposits, and have a long history as fossils; the phylum is over 450 Ma old.

Bryozoan species are differentiated primarily by their skeletal features, including spines, surface structures, and size and shape of pores. Species identification in some taxa can be difficult, particularly of damaged specimens. The form of the colony, including the arrangement of zooids, can be helpful under such circumstances. Although a complex nomenclature of colonial growth form has arisen in bryozoology (summarized by Schopf 1969), a simpler growth-form classification for bryozoans has been developed for use by non-specialists (Nelson *et al.* 1988*a*). A slightly modified version of this latter scheme will be used here (Fig. 1).

Modern bryozoans are suspension feeders and occupy a wide variety of environments. Some species can tolerate low salinities, but most are found in salinities ranging from 32 to 37‰ (Ryland 1970). They are generally found in waters with temperatures from 10 to 30°C, but Antarctic bryozoans may tolerate water temperatures as low as -15°C (Domack 1988). Many species are intertidal; still more live subtidally. They are most abundant on the continental shelf, although bryozoans have been found down to 6000 m water depth.

Although of usually minor significance in tropical reef environments, bryozoans are major components of temperate shelf carbonate















Life habit	Zooid arrangement	Abbrev.	Schematic diagram
ENCRUSTING	uniserial	ENus	
	unilaminar	ENul	
	multilaminar	ENml	
ERECT	articulated	EFar	
	delicate branching	EFde	
FLEXIBLE	foliose	EFfo	
	rooted	EFrt	
ERECT	delicate branching	ERde	
	robust branching	ERro	
	foliose	ERfo	
	RIGID	fenestrate	ERfe
massive		ERma	
radiate		ERra	
FREE-LIVING	motile	FLmo	
	rooted	FLrt	

Fig. 1. A simplified scheme for classifying bryozoan colonial growth forms (based on Nelson *et al.* 1988*a*; Smith 1992).

sediments. They are dominant producers of carbonate on the Australian (e.g. Wass *et al.* 1970) and New Zealand (e.g. Nelson *et al.* 1988*b*) shelves. Northern Pacific sediments also

contain bryozoan carbonate (e.g. Smith 1970; Nelson & Bornhold 1984). In the north Atlantic both the North American (e.g. Slatt 1977) and the European (e.g. Dobson *et al.* 1971; Bouysse *et al.* 1979; Scoffin *et al.* 1980) shelves include bryozoan-rich carbonates. Even in the Antarctic (Domack 1988) bryozoans are sub-dominant producers of carbonate.

Bryozoans are an ancient group, having produced calcified skeletons from the early Ordovician. Five of the six known Palaeozoic orders became extinct at the beginning or end of the Triassic, but one order, the Cyclostomata, has persisted from the Ordovician to the present, dominating many faunas in the Mesozoic. The other important modern marine group (Cheilostomata – comprising the anascans and ascophorans) arose in the late Jurassic and became dominant in the late Cretaceous and Cenozoic (see, for example, McKinney & Jackson 1989, fig. 1.14).

Interpretation of fossil bryozoans has been largely based on studies of modern species, with the acknowledged danger of applying uniformitarianism to a system in which evolution has occurred. The ecology, morphology and associations of living bryozoans, nevertheless, are the only systems comparable to fossil bryozoans available for study. Cheilostomes are best used in studying Cenozoic faunas, cyclostomes are more useful in the Mesozoic, and, unfortunately, no extant group is closely related to Palaeozoic bryozoans, though comparisons with cyclostomes are generally made.

Aspects of bryozoans that have been studied with respect to palaeoenvironmental interpretation include: the presence or absence of taxa and species, ecological parameters, zooid size and shape, colonial shape, and formation of reef-like structures. The methods using colonial growth form have proved to be particularly popular, as geologists without specialist knowledge of bryozoans have been able to use relative growth form abundance to make palaeoenvironmental interpretations.

Methods of using bryozoans in palaeoenvironmental interpretation

Presence, abundance and diversity

Perhaps the simplest aspect of bryozoans to determine is their presence or absence. The presence of bryozoans does not indicate a particular climatic or latitudinal range (as would, for example, the presence of hermatypic corals). Dominance of a fauna by bryozoans,

however, along with the presence of other temperate organisms, would indicate a non-tropical setting (e.g. Marshall & Davies 1978). Abundance and species diversity provide more information, as both are generally lower under stressful environmental conditions (Harmelin 1988).

Thermal tolerances of many bryozoan species have been shown to be wide; they may survive in water temperatures from -15 to 40°C . In a six-year study of bryozoan species at Long Beach and Los Angeles, California, Soule *et al.* (1979) used multivariate and discriminant analysis to correlate environmental factors with bryozoan occurrences. Temperature emerged as the single most important factor correlated with bryozoan species distribution, followed by phytoplankton abundance. Ranges of thermal tolerance varied among species. This study is unique in its long time frame and its specific and precise determination of modern ecological ranges.

Some bryozoan species are euryhaline, but many prefer normal marine salinity (Ryland 1970). Low species diversity is reported from estuarine conditions (Tasch 1973; Butler & Cuffey 1991) and may indicate that low salinity (*c.* 20‰) is environmentally stressful to marine bryozoans. Extensive monospecific bryozoan build-ups of *Membranipora aciculata* occur in South Australia's Coorong Lagoon, a shallow, atidal, evaporitic lagoon with wide annual ranges of temperature and salinity (Bone & Wass 1990; Bone 1991). The extreme conditions and intense variability may account for the very low species diversity.

Some intertidal bryozoans have reasonably specific intertidal ranges (Rao & Ganapati 1986); but many shelf bryozoans are nearly eurybathic. Some Ordovician bryozoans of the order Trepostomata have been broadly correlated with water depth (Brown & Daly 1987). Overall, bryozoan abundance peaks on the continental shelf (at *c.* 40–90 m according to Cuffey & Turner 1987) and falls off with increasing water depth (Gordon 1987; Harmelin 1988; McKinney & Jackson 1989). Deepening over time can reduce bryozoan numbers (Reguant *et al.* 1991). The moderate water energy of the shelf may enhance bryozoan growth by providing a continuous food supply and removing small sediment particles may also result in high species diversity (Ziko & Hamza 1987). Low energy faunas may, however, be quite diverse (e.g. Kelly & Horowitz 1987).

Like other sessile suspension feeders, bryozoans are quite vulnerable to sedimentation and turbidity. Areas of moderate to high sedimentation often have few bryozoans (Lagaaij &

Gautier 1965), due both to the direct limitation on feeding and the indirect swamping of potential substrate (Harmelin 1988). High diversity in bryozoans appears to require low rates of sedimentation (Kelly & Horowitz 1987). Other disturbances, such as predation, bioturbation and substrate movement, can reduce bryozoan abundance (McKinney & Jackson 1989).

Availability of suitable substrate or shelter may be another limiting factor. Bryozoans will colonize particulate and flexible substrates, but diversity is greatest on hard substrates. Even a small single shell can support tens of species (Harmelin 1988). Among particulate substrates, diversity of bryozoans is higher on gravel than on sand (Cuffey & Turner 1987). Particulate substrates may become highly abrasive under high energy conditions such as storms. Periodic storms may therefore remove small delicate species from particulate substrate (Scholz & Cusi 1991). Diversity and abundance may be increased in certain sheltered environments such as caves and algal holdfasts (Harmelin 1988).

A diverse and thriving bryozoan community, then, is characteristic of the temperate shelf 'normal marine environment' (Schmid 1991), though bryozoans occur in many other settings. A total absence of bryozoans where they might otherwise be expected could indicate smothering by suspended sediment, very low salinity, lack of or instability of substrates, regular disturbances, or a very deep or very shallow environment.

Intraspecific colonial plasticity

Sessile organisms are necessarily limited in their possible responses to environment. In order to find a favourable environment, attached species must either select their environment when in a motile larval stage or grow towards a more suitable environment (Buss 1979). Colonial organisms are best able to use this second tactic, as their modular nature means that mortality of part of the colony need not affect the overall growth (Buss 1979). Colonies may add zooids in a preferred direction, perhaps in response to substrate (e.g. the direction of growth of an algal frond), food availability, or other stimuli, resulting in a distinctive colonial form. Of course, variability in growth form is a reflection of both genotype and environment. Some species indicate environmental conditions in their colonial form more than others.

In different biotopes bryozoan colonies of the same species may have different morphological characters. Careful biometry has shown that

branching characteristics, colony robustness and distribution of zooids among individuals of various cyclostomes varies depending on environmental factors (Harmelin 1973, 1975; Schopf *et al.* 1980). Colonies of '*Idmonea atlantica*' from caves, for example, appear more slender, elongated and poorly branched than those from open rock faces, a fact which may be related to light and hydrodynamic regime (Harmelin 1973). *Heteropora pacifica*, in contrast, shows a continuum of robustness related to water depth but not, apparently, to currents or suspended sediment (Schopf *et al.* 1980). Both modern and ancient fenestrate forms have similar morphological gradients, probably related to hydrodynamic regime (McKinney & Gault 1980; Cuffey & McKinney 1982; Harmelin 1988).

In some environmentally sensitive species the overall colonial growth form may vary. Experimental culture of *Conopeum tenuissimum* showed that the colonial form is often a unilaminar sheet if the settling location is favourable, but uniserial runners occur if the colony is 'hunting' for a better location (McKinney & Jackson 1989). Thus, in such 'plastic' species, which make up 24% of 1430 Atlantic species surveyed, growth form varies intraspecifically depending on external forces such as physical factors, food competition and predation (McKinney & Jackson 1989). The two most common intraspecific growth form variations are encrusting unilaminar to uniserial (e.g. Winston 1976) and encrusting to erect rigid (e.g. Cook 1986). In an extreme case, *Cateschara denticulata* is unilaminar in the littoral zone, erect foliose in deep active water and delicate branching in deep sheltered water (Stach 1937).

Colonial plasticity within a single genus has been used to interpret the facies found in a Carboniferous build-up (Wyse-Jackson *et al.* 1991). *Leioclema* spp., from the extinct order of trepostomes, were generally erect rigid delicate branching in basal facies, encrusting unilaminar or erect foliose in the bulk facies and encrusting multilaminar in the capping facies. Thus, the basal facies was interpreted to be deep water, low energy; the bulk and capping facies were shown to be shallower, high energy environments.

Zooid morphology

Aspects of the morphology of individual bryozoan units (zooids) may indicate environment. Size of zooids and of colonies have been shown to vary bathymetrically, both decreasing with depth (Flor 1973; Schopf *et al.* 1980). Micro-

evolutionary changes in zooid morphology in the Lower Permian trepostome *Tabulipora carbonaria* also show gradation with depth (Pachut & Cuffey 1991). Temperature, both in culture and in natural populations, may also affect size; zooids are larger in cooler water, whether temperature variation may be seasonal or geographic (Okamura & Bishop 1988). In some species, formation of specialized zooids is temperature-controlled (Morris 1976); in others these zooids appear in response to competition, predation or substrate irregularities (Silén 1977). This appears to contradict an earlier view that temperature controls rate of calcification and growth rather than overall form (Schopf 1969).

Analysis of morphological variability of zooids within and among colonies may be linked to environmental stability. The frequent stress-inducing disturbances of an unstable environment leave their mark on bryozoan zooids (Key 1987). Unstable environments tend to produce more variation within colonies than among different colonies. This may be due to micro-environmental changes or episodic events, such as storms stunting or damaging parts of a living colony. Stable environments appear to be dominated by variability among rather than within colonies, perhaps due to genetic and developmental regulation (e.g. Wass 1991). Thus, the relative importance of zooidal variability within and among colonies may indicate the stability of the environment (Key 1987).

Dominant colonial form

In addition to affecting intraspecific variation, environment may determine overall morphologic composition of a bryozoan population. Some colonial growth forms may be suited to a particular environment, and therefore will dominate a fauna from that environment. Stach (1936a, 1937) first pointed out the association of living bryozoan growth forms with such environmental parameters as depth, hydraulic energy and substrate. Since most growth forms are found in most habitats, overall relative abundance of colonial growth forms is the measure used (e.g. Stach 1936b). Lagaaij & Gautier (1965) modified this approach, including sedimentation rate as an important control on bryozoan distribution in their application of growth-form analysis to Rhône Delta sediments. Schopf (1969) and Kelly & Horowitz (1987) have summarized and evaluated this growth form approach (Table 1). The study of growth form associations in indurated limestones can be made easier by thin sections (e.g. Nelson *et al.*

1988a). Thin sections may show bryozoan fossils that are often inconspicuous in outcrop, as zooids may be filled with cement or mud. Species identification may be very difficult in such limestones, but growth forms have characteristic shapes and arrangements of zooids that can be discriminated in thin section.

Growth forms have been correlated with water depth (e.g. Harmelin 1988), water energy (e.g. Harmelin 1977), substrate (e.g. McKinney & Jackson 1989) and sedimentation rate (e.g. Lagaaij & Gautier 1965). The technique is most easily applied to Cenozoic settings (e.g. Askern 1968; Cheetham 1971; Balson 1981; Reguant *et al.* 1991; Ziko 1991), but has certainly been used with both Mesozoic (e.g. Brood 1972; Pitt & Taylor 1990) and Palaeozoic (e.g. Bigey 1987; Anstey & Rabbio 1990; Pachut & Cuffey 1991) faunas.

Growth form abundance has been widely used to interpret palaeobathymetry (for example, James & Bone 1991; Schmid 1991). Water depth has indirect effects on bryozoan distribution, through primary depth-related controls such as temperature, light, salinity, sedimentation rate and hydrology (Harmelin 1988). Most growth forms occur at a wide range of depths so will not be particularly accurate bathymetric indicators. There are, however, some broad trends which seem to be generally applicable.

Encrusting forms dominate over erect ones in shallow water, perhaps due to the degree of physical and biological disturbance (McKinney & Jackson 1989). In a large sample of Atlantic faunas, McKinney & Jackson (1989) found 65% encrusters in shallow water, reduced to only 30% at depths *c.* 30 m. In deeper shelf waters, erect rigid and flexible forms become more abundant, up to 50%.

Stach (1936a) indicated that a fauna dominated by erect flexible forms implies an intertidal/subtidal environment as flexible forms could survive considerable wave action. This was confirmed in several small-scale studies (e.g. Stach 1936b; Annoscia & Fierro 1973). Harmelin (1988) found, however, that erect flexible forms in the Mediterranean are widely distributed to 100 m, and less important than encrusting forms in the intertidal. In modern New Zealand sediments, articulated erect flexible forms are dominant at inner- to mid-shelf depths (Smith 1992). In addition, when articulated colonies die individuals may produce disproportionately many fragments, and thus will be over-counted. In the light of this disparity, dominance by erect flexible forms is probably not a good indicator of very shallow water.

Table 1. Published environmental associations of bryozoan growth forms (based on Stach, 1936a., 1937; Lagaaij & Gautier, 1965; Schopf, 1969; Ryland, 1970; Harmelin, 1975, 1988; Kelley & Horowitz, 1987; Nelson, et al., 1988a; McKinney & Jackson, 1989). Abbreviations for growth forms defined in Fig. 1.

Controls on growth form			Substrate			
Water depth	Hydraulic regime	Sedimentation rate	Short-term, fairly stable, flexible	Moderate- term, unstable, particulate	Moderate- term, fairly stable, hard	Long-term, stable, hard
Intertidal 0–5 m	Strong wave action, turbulent	Moderate to high	EFde ENul EFar	EFar EFfo ENml	ENul	ENul
Subtidal, 5–10 m	Strong wave action, turbulent	Moderate to high	EFar ENul EFde	ERfe ENul	ENul	ENul
	Weak wave action, sheltered	Moderate to high	ENml	ENml	ENul	ENul
Inner shelf, 10–50 m	Moderate strength, tidal currents, storm waves	Low to moderate	EFar ENul EFde	ERfo FLmo FLrt	ENul	ENul
Mid to outer, shelf 50–200 m	Low to moderate strength, tidal currents, geostrophic currents	Low		ERfo FLmo FLrt	ERde	ERde
Slope rise, abyss, > 200 m	Low strength, geostrophic currents	Low		ERfo FLmo FLrt	ERde EFde	ERde EFde
	High energy currents	Low		FLmo	ERfo ERro	ERfe ERro

Erect rigid forms are most common at depth and the erect rigid delicate branching variety has often been cited as indicating deep quiet water, primarily due to the apparent fragility of these forms. Shallow calm microenvironments, such as caves (Kobluk *et al.* 1988) and kelp holdfasts (Smith 1992), however, offer appropriate niches for erect rigid delicate forms, which presumably could therefore be preserved in a shallow environment.

Bryozoans are often part of the deep-sea sedimentary record (e.g. Gordon 1987), and can reflect changes in environment over time. Analysis of DSDP core 282 west of Tasmania showed two different bryozoan faunas associated with two sedimentary facies (Wass & Yoo 1975). A Lower Miocene fauna of 23 species, mainly branching erect forms, reflected a shallow, calm environment. Above it there is a Late Pleistocene fauna of 79 species, mainly erect flexible delicate branching and articulated forms, indicating a deeper shelf environment subject to more agitation (Wass & Yoo 1975). The use of bryozoans in analysis of deep-sea sediments is still rare but has considerable potential as the modular nature of bryozoans means that very small fragments can still be identified (Cook 1981).

Whereas bathymetric associations of bryozoans have been reasonably well considered using large data sets and corroborating evidence (especially by Harmelin 1988 and McKinney & Jackson 1989), hydrodynamic effects are less clearly demonstrated. Water movement has important effects on marine organisms, and there is no shortage of supposition and inference about morphological adaptations among bryozoans to hydrodynamic conditions. Wave action, tidal currents and deep water currents may cause abrasion and damage, but they may also provide a constant food supply and may remove settling sediments (Ryland 1970). Perhaps it is this combination of beneficial and detrimental effects that has caused so much confusion about bryozoan hydrodynamic associations.

Low energy environments are alleged to favour erect rigid forms which are supposedly too fragile to survive much water motion (Stach 1936a). It has indeed been shown that rigid erect colonies are more vulnerable to damage by currents than encrusting and flexible species (Cheetham & Thomsen 1981), and that erect colonies dominate at depths (600–1000 m) where water motion may be slight (McKinney & Jackson 1989). Harmelin (1975), however, noted

that low energy environments ought to favour an encrusting lifestyle because nutrients and food can settle onto a flat colony. If the erect lifestyle is, as is commonly thought, an adaptation to 'catch' food from a moving water column, then quiet waters would not require the investment of erect growth. Harmelin's (1988) data show clearly that encrusting forms dominate in the intertidal and at depth in the Mediterranean, perhaps with little regard to hydrodynamics. In the Miocene of Malta, however, encrusting form is associated with shallow turbulent water (Pedley 1976). The effects of hydrodynamics and bathymetry cannot be separated using these data and no experimental data appear to address these contradictory theories.

Erect rigid fenestrate growth forms are strongly calcified and reinforced by cross-bars. Because of their similar form to a major Palaeozoic order, the Fenestrata, they have potential to be useful in palaeoenvironmental reconstruction. Stach (1936a) inferred from the robust shape that they were strong enough to withstand intense hydrodynamic forces and should therefore be dominant in areas of active waves and currents. This was substantiated to some extent in Rhône Delta sediments (Lagaaij & Gautier 1965). In later studies fenestrate forms appeared in moderate to low energy environments (Schopf 1969; Pedley 1976). In fact, hydrodynamic morphological gradients have been found in modern fenestrate forms (Cuffey & McKinney 1982; Harmelin 1988) as well as in Palaeozoic fenestrates (McKinney & Gault 1980). These gradients show that the fenestrate growth form occurs in a variety of hydrodynamic settings. Indeed, several modern species of fenestrate form are limited to quiet cryptic environments (e.g. Cuffey & McKinney 1982). Very recent work indicates that most modern and Palaeozoic fenestrate forms prefer quiet sheltered conditions and require an unusual lyre-shaped form in order to colonize higher-energy environments (McKinney *et al.* 1993).

It is tempting to invent 'just so' stories about the adaptation of growth form to hydrodynamic conditions. In the case of whether encrusting or erect forms are dominant in a low-energy regime, contradictory inferences and a lack of data make the ratio of encrusting to erect forms useless. In the case of fenestrate forms, guesses based on shape have had to be considerably modified after the consideration of real data. There is considerable potential in the association of growth form with hydrodynamics, but it has not yet been realized. Experimental data that

tease out the effect of hydrodynamics from the effects of water depth and substrate will be required to confirm or deny the inferences of Stach and others.

Substrate is another important factor in determining relative abundance of different growth forms. Bryozoans can provide indirect evidence of changes in available substrate, as in the biofacies of the Miocene of Florida where bryozoan growth forms indicate substrate availability (Scolaro 1968), and even earlier in the Carboniferous of Mississippi, USA (Snyder 1987). Some bryozoans may provide more direct evidence as to the nature of their environment as they retain impressions or fragments of their own substrate.

Many encrusting bryozoans live on flexible, rather short-lived substrates such as algal fronds. These may retain useful impressions of the substrate on the basal surface (Voigt 1981), or indicate type of substrate by holes or indentations in the colony (Pedley 1976). The availability of algal substrates is of course related to water depth, being limited to the photic zone.

Hard substrates, moderately long-lived and fairly stable, such as shells, bottles or cobbles, attract other bryozoans. Intertidal and upper subtidal encrusters live preferentially on the undersides of such substrates. Larvae may actively choose undersides, or there may be reduced survival of young colonies on upper sides (Ward & Thorpe 1991). Very long-lived, stable, hard substrates such as rock walls, reefs, boulders and pilings are also important. On these long-lived substrates, competition becomes important, and bryozoans may lose space to other organisms such as sponges, ascidians or algae (McKinney & Jackson 1989). Most erect rigid growth forms require hard substrate (Harmelin 1988).

Particulate substrates pose special problems. Organisms living among unstable sand grains need to be able to regain the surface after burial (either by growth or by moving), to clean their surfaces of debris, to stay in a stable position or to survive disturbance. The bryozoan solutions to these problems include rooted colonies, motile colonies and interstitial colonies (McKinney & Jackson 1989). In some cases, the grain size of a particulate substrate may be another controlling factor.

The free-living growth form is particularly characteristic of sandy bottoms. Although free-living species tolerate wide ranges of temperature, salinity and depths (Lagaaij 1963), they may be good indicators of sandy substrate. Many settle on a grain of sediment which is

subsequently incorporated into the colony; these individuals provide insight into the types of sediment available where they lived.

Although depth has been shown to correspond with gross distribution of colonial growth forms in some New Zealand carbonate shelf sediments (e.g. Nelson & Hancock 1984) substrate type appears to be most important in determining growth form distribution. In New Zealand sediments, as elsewhere, rooted and free-living forms are found on soft bottoms, whereas encrusting forms are more common on hard bottoms (Gordon 1967, 1987). In general, New Zealand bryozoans, particularly erect delicate branching forms, are most abundant on coarse-textured gravelly sediments (Probert *et al.* 1979; Whitten 1979).

A greater variety of forms is noted in some New Zealand shelf gravels than is predicted in published associations, perhaps due to occasional large shells (Smith 1992). It would probably be of help if future workers defined grain sizes within loose sediments more carefully, as different grain sizes clearly support different bryozoan faunas. Bryozoans are notably absent in samples with greater than 90% mud.

The majority of bryozoan habitats are found in areas of low sedimentation; in fact, when sedimentation rates are greater than 100 cm ka⁻¹, bryozoans are generally absent (Lagaaij & Gautier 1965). The main exceptions are the free-living forms which are able to tolerate moderate rates of sedimentation (Di Geronimo *et al.* 1991), due either to a certain degree of motility or to moving surface setae that can keep the feeding surface clear (Lagaaij 1963). Variation in sedimentation rate may be important in both growth and distribution of bryozoans (e.g. Hu & Spjeldnaes 1991). Erect forms, both flexible and rigid, may well tolerate more sedimentation than encrusters (Pedley 1976).

Relative abundance of bryozoan growth forms is an understandably popular tool for palaeoenvironmental reconstruction. There is an appealing logic to the idea that overall colony form is more indicative of environment than particular species. There are, however, serious problems with the approach. There are many diverse faunas composed of many different growth forms. This may call into question the idea of growth forms occurring or dominating in specific environmental niches. There is a subjective aspect to the process: just how dominant is dominant?

An over-reliance on adaptationist inference has meant, in some cases, that early ideas have had to be modified in the light of data. Modern

data are most clearly applicable to Cenozoic faunas. The older bryozoan orders that thrived in Palaeozoic seas are mainly extinct and may have lived under different conditions (Kelly & Horowitz 1987). Applications of modern growth form associations to these older faunas obviously have serious limitations. The technique, with all its drawbacks, may be useful for application to palaeontology, particularly if considered in the light of other corroborating evidence.

Zoarial diversity

A measure of growth form variability introduced by Moyano (1979) called by him 'zoarial diversity' treats colonial forms as if they were species, and species as if they were individuals. High zoarial diversity indicates favourable conditions for development of many bryozoan forms. In Antarctic bays such favourable conditions include hard substrate and stable, predictable environmental conditions. Periodically disturbed areas and soft substrates lead to low zoarial diversity (Moyano 1979). This measure is not generally used, and it is unclear whether Moyano's (1979) observations would be borne out by investigations in other areas.

Bryozoan structures

Bryozoan colonies may grow together to form bryozoan structures, including reefs, bioherms and masses (e.g. see Cuffey 1974). Aspects of these structures have been shown to indicate their environment of formation.

Moissette & Pouyet (1991) describe bryozoan 'masses' mainly of encrusting growth forms that nucleate on pebbles or algae. Under stable conditions (low energy) they grow into hemispherical shapes; under a more vigorous hydrodynamic regime they form subspherical nodules. As growth of these masses is very slow (up to thousands of years) they may indicate conditions over a long period of time.

Larger bryozoan nodules also indicate water energy. Mediterranean pebble-sized 'globstones' formed of many bryozoan species indicate low water energy, whereas much larger 'cruststones' (up to 8 cm in diameter) are made of fewer species and indicate active currents providing high concentrations of nutrients (Reguant and Zamarreño 1987). These cruststones are similar to nodules described in coastal Virginia (Dade & Cuffey 1984).

Encrusting bryozoans may, under certain conditions, help to form frameworks or reefs. Bryozoan reefs are rare, but occur with enough

frequency to require an expanded classification of reefs (e.g. branchstone and lettuce stone, after Cuffey 1985). In general, bryozoan reefs are associated with tropical conditions. The onset of bryozoans as reef-builders may indicate an environmental change that is detrimental to more common reef-builders such as corals (Cuffey 1974). Conversely, the cessation of bryozoan reef-building may suggest an episode of rapid sedimentation (Cuffey *et al.* 1991).

Potential problems in bryozoan palaeoenvironmental analysis

Patchiness and sample size

There are few real data about modern marine bryozoans and their ecological requirements, and many of the studies that do exist are too narrowly focused. Cryptic habitats and micro-environmental refuges are critical for bryozoans, resulting in a patchy distribution (Harmelin 1988). This means that sampling programmes have to be sufficiently thorough to recognize and characterize microenvironments. In addition, studies of small localized populations may not be representative of larger trends in the rest of the world. Some rather sweeping statements about bryozoan associations with environment have been made on the basis of small samples from narrow geographical areas at a single point in time. Seasonal or annual variability has been often left out of most studies of modern associations. A notable exception is the six-year study of bryozoan ecology by Soule *et al.* (1979).

Linkages

If disturbance decreases with depth, and erect rigid forms become more common, is it the depth or the level of disturbance that has caused the increase in abundance? Many marine environmental factors are inextricably linked and evaluation of one in isolation is both impossible and irrelevant. It will require carefully planned and controlled laboratory experiments to evaluate the relative importance of different environmental factors in determining bryozoan distribution.

Uniformitarianism vs evolution

Palaeoenvironmental analysis can depend rather heavily on the classical uniformitarian underpinning of geoscience. In taxonomic uniformitarianism observed ecological requirements of

modern organisms are extrapolated to fossil faunas. The assumption of temporal stasis in ecological requirements used by this approach is most tenable in interpreting very young fossils. With increasing age the assumption becomes more tenuous, particularly in the Palaeozoic. Bottjer & Jablonski (1988) demonstrate that, for several macroinvertebrate groups (including cheilostome bryozoans), environmental associations have varied, often in a systematic way over time. Evolution of environmental requirements within taxa thus undermines the basis of palaeoecology through taxonomic comparison.

Bottjer & Jablonski (1988) suggest that overall taxonomic structure (e.g. percentages of various subtaxa) may provide a better index of environment. Along the same lines, Gordon (1987) found a fairly consistent percentage of growth forms among modern bryozoan species irrespective of environment. He found encrusting species tended to form 60–75% of a fauna and erect rigid species 0–20%, and suggested that if this were borne out in further studies it might help in 'correcting' a fossil fauna from a similar climatic and geographic region. There is, however, no evidence to show that this ratio has remained consistent over time. In fact, it has been suggested that different growth forms have dominated at different times (McKinney & Jackson 1989), making corrections based on a modern ratio impossible.

Both the possibility of a 'normal' ratio of growth form types, and of temporal change in that relationship, call into question some of the assumptions of the technique of applying dominant growth forms to palaeoenvironment.

Taphonomy

In the complex process of becoming a fossil a skeleton is subject to preservational selection processes. At any stage in the fossilization sequence it may be destroyed or rendered unidentifiable. The destructive processes that disqualify most organisms from preservation may be considered taphonomic filters, removing material and only allowing a subset through to preservation (Fig. 2). If the selection is non-random, as it appears to be for bryozoans (Smith & Nelson 1994), then the fossil fauna is not a true representation and living fauna and ecological analysis breaks down. Even in a short time skeletal sediments may not reflect living faunas (e.g. Bosence 1979; Kidwell & Behrens-meyer 1988).

A limitation common to palaeoenvironmental studies is that early seafloor processes, transport and mixing with relict sediments may have

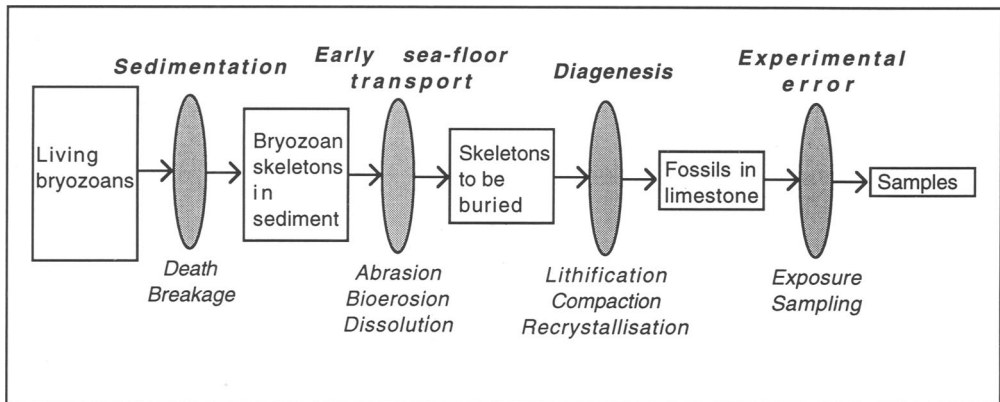


Fig. 2. The effect of taphonomic filters on the preservation of bryozoans in the fossil record.

distorted the environmental 'signature' of the forms present. Bryozoans from adjacent environments could easily be mixed before final deposition, confusing any environmental signal. There is often lithologic or diagenetic evidence available of transport and mixing such that situations involving transport can be identified. Clearly, fossil bryozoans that are in life position are the best candidates for palaeoenvironmental interpretation (as noted by Reguant *et al.* 1991).

The advantage of multiple lines of inquiry

In Tertiary deposits, modern analogues can be applied without much difficulty. There are many useful and interesting studies on Tertiary bryozoans, in which several different lines of evidence support the conclusions. Ziko (1991), for example, used a combination of bryozoan presence/absence, species present and dominant growth form to interpret a succession from shallow shelf lagoon to winnowed platform to reef build-up in the Marmorica Formation in Matruh, Egypt. In southern Australia, bryozoan diversity and growth forms were used to determine the water depth of an Oligo-Miocene platform (James & Bone 1991). Schmid (1991) recently used bryozoan diversity and ecological association of similar living taxa to deduce palaeodepth, temperature and salinity of a Miocene deposit near Vienna, Austria. Pedley's (1976) study of the Miocene of Malta used lithology, brachiopods and bryozoans in determining palaeoenvironment.

Palaeoenvironmental interpretation of bryozoans in the distant past offers several chal-

lenges. Species, families and even whole orders of Palaeozoic bryozoans are extinct, making modern analogues difficult to apply. Often the best tactic is for bryozoan data to be considered in the light of other factors, including chemical, geological, physical and other biological evidence. The advantages of confirming palaeoenvironmental reconstructions by pursuing several independent lines of inquiry are self-evident.

Conclusions

Bryozoans have proved to have many possible environmental applications. Their presence or absence, diversity and abundance, zooid morphology, colonial plasticity, colonial growth form and reef-like structures all provide information about habitat. Among the environmental parameters indicated by bryozoan faunas are: temperature, salinity, water energy, water depth, substrate character, sedimentation rate. Numerous examples show the usefulness of bryozoans, from shelf and deep-sea sediment studies to interpretation of Tertiary and even Palaeozoic faunas. Although caution is needed, particularly in interpreting very ancient faunas, bryozoans are a tool of considerable value in palaeoenvironmental interpretation.

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Microfossil indicators of ocean water masses, circulation and climate

JOHN W. MURRAY

Department of Geology, University of Southampton, Highfield, Southampton SO17 1BJ, UK

Abstract: Circulation within oceans is closely linked to climate through feedback mechanisms and both are controlled by insolation and the rotation of the Earth. Because the distribution of organisms is related to the water masses in modern oceans their distribution in the fossil record can be used as a proxy of past water masses. For surface waters the main proxies are calcareous nannofossils, diatoms, radiolaria and planktonic foraminifera. Transfer functions have been derived to determine sea surface temperatures from planktonic microfossils from the Pleistocene and Pliocene. Upwelling regions have distinctive characteristics, notably a great abundance of diatoms and a high dominance of *Globigerina bulloides* d'Orbigny. For bottom waters the principal proxies are benthic foraminifera and, to a minor extent, ostracods. Some assemblages of epifaunal benthic foraminifera seem to be correlated with specific bottom-water masses, but this is not so for infaunal assemblages. The development of thermohaline circulation caused benthic taxa to adjust their depth distribution patterns; some species became extinct and were replaced by others. Changes in distribution patterns in the Neogene have been interpreted as indicating changes in bottom-water mass structure and distribution. For instance, *Nuttallides umboniferus* (Cushman) has been used by several authors to map the past distribution of Antarctic Bottom Water. Sometimes processes operating at the ocean surface produce effects on the ocean floor which override benthic processes. Examples of this include seasonal input of phytodetritus which leads to blooms of *Epistominella exigua* (Brady), and deposition of laminated diatom mats which inhibit bioturbators.

In this review the order of treatment of topics is as follows: surface water masses, upwelling, bottom-water masses, surface–bottom water interactions. For each comparison is made between modern microfossil distribution patterns and those in the fossil record in order to try to reconstruct past oceanic conditions.

The atmosphere and the oceans form linked systems which are constantly moving. Both have their own three-dimensional patterns of circulation but their plane of interaction is the two-dimensional surface of the sea where they affect one another through feedback loops. Energy from the Sun and the rotation of the Earth (Coriolis force) provide the driving mechanisms. The Coriolis force causes currents to be deflected to the right in the northern hemisphere and to the left in the southern hemisphere.

Wind drag on the sea surface moves the surface water but the combined effects of friction (Ekman motion) and the Coriolis force leads to a mean transport direction of surface waters at right angles to the wind direction. Insolation causes variations in water temperature and salinity which in turn affect its density. Because dense water sinks, modern oceans have a thermohaline stratification with relatively warmer and less saline surface waters and cooler and more saline bottom waters. Two principal deep waters form in high latitudes, particularly in the

Weddell Sea off Antarctica, where the coldest and densest deep water is formed (Antarctic Bottom Water, AABW) and in the North Atlantic (North Atlantic Deep Water, NADW). The circulation of deep waters is influenced by the Coriolis force. It is beyond the scope of this review to consider oceanic circulation in detail; a clear account is given by Brown *et al.* (1989) and in standard oceanography textbooks.

Palaeoceanography is the study of the oceanography of past oceans. Because it is clearly impossible to have a direct record of former oceanic conditions it is necessary to use indirect evidence (proxies). These include both the sedimentary and the microfossil records, and it is the latter which is considered here.

Following the Lyell dictum that 'the present is the key to the past' the modern ocean is used as a model for interpreting past ocean history. Therefore, it should be considered to what extent the modern ocean is representative. To quote Berger (1981, p. 1458): 'The present ocean is rather unusual. When seen against the background of Phanerozoic seas, it is unusually well oxygenated. Shelf seas are unusually restricted. Environmental contrasts are large, and provinciality is greatly enhanced. Within the spectrum of Cenozoic oceans, the present one is unusually cold, its poleward edges being constantly frozen. Deep circulation is largely thermally driven and

fertility is unusually high. Relative to the last half million years, the present ocean is unusually warm, and sea level is unusually high'.

These differences have to be borne in mind when reconstructing ancient oceans. In reality, the physical, chemical and biological processes which are seen operating in modern oceans are obviously applicable to the past, but they differ in intensity through time. However, the biota has undergone evolution through time and this has had a profound effect on the geochemistry of the oceans and also affected the atmosphere. Prior to the Late Triassic there were no calcareous nannofossils and planktonic foraminifera appeared in the mid Jurassic. Neither group became significant contributors to sediment formation until the Late Cretaceous and since then large quantities of biogenic calcium carbonate have accumulated in the ocean basins. It follows that the geochemistry of oceans has changed markedly between the Late Triassic and the Late Cretaceous. Furthermore, the calcareous plankton plays an important role in the carbon cycle (Brasier this volume).

In this brief review no attempt is made to synthesize the vast quantity of literature either on changing microfossil distributions through time or on palaeoceanography in its broadest sense. Instead, various aspects of the ocean-climate system have been chosen to illustrate how the microfossil evidence can contribute to the interpretation of its past record of variation. Various planktonic groups are proxies of surface water events: diatoms, radiolaria, calcareous nannofossils, planktonic foraminifera, dinoflagellates. Proxies for the bottom waters are mainly benthic foraminifera and, to a lesser extent, ostracods.

Surface water masses

It has long been known in a general way that the distribution of planktonic organisms is closely linked to the temperature, salinity and circulation pattern of the surface waters of the oceans. However, Haedrich & Judkins (1979) have pointed out that oceanic circulation can cause organisms to be transported into areas where, although they are able to survive, they are unable to reproduce; this phenomenon is called **expatriation**. Some expatriate distributions are continuously maintained by major currents transporting individuals into the expatriate area (for example western boundary currents such as the Gulf Stream; Haedrich & Judkins 1979) but others may be ephemeral where currents meander or send out eddies.

Expatriate individuals of a species are gen-

erally healthy-looking adults. Expatriate distributions include those of warm-water species carried into cooler areas and oceanic species transported over continental shelves. Many, perhaps all, distribution maps of planktonic taxa include undifferentiated expatriate areas and this is potentially misleading in understanding the ecological controls on the distribution of the reproductively viable population of each species.

Methods

Planktonic foraminifera Ecologists collect plankton either with plankton nets or by Scuba diving (see Hemleben *et al.* 1989 for details). Plankton nets vary in mesh size; 10–35 μm mesh sizes are used to collect juvenile tests but 75 or 202 μm mesh sizes are used to collect young and mature specimens. Because plankton is patchy in its distribution it is difficult to determine reliable concentrations of tests per unit volume of water. Scuba divers operate at depths of 3–5 m below the surface, capturing individuals in jars; this method is not suitable for quantitative studies.

The flux of tests to the seafloor can be determined by means of sediment traps. These are devices which are left on the seafloor for a period of time and then retrieved. Tests settling through the water column, either individually or as marine snow, are gathered in the trap. Since both the area of the trap aperture and the duration of the collecting period are known, it is possible to calculate annual fluxes of tests to the seafloor (Hemleben *et al.* 1989).

Sediment samples are generally collected by corer (for modern to late Pleistocene sediments) or by drilling, as on the various phases of the ocean drilling programmes.

If meaningful comparisons are to be made between modern assemblages and those from the fossil record it is essential that similar size fractions are used. This has not always been the case. As noted above, plankton nets as fine as 10 μm are sometimes used, whereas sediments are usually washed through 149 μm meshes.

Berger (1971) was the first person to address the problem of the similarity between the assemblages living in the water and those preserved in the sediment. Much of the plankton production is lost to predation and is therefore not available to be sedimented. The loss of the tiniest juveniles before they settle to the sea floor creates an immediately obvious difference between plankton and sediment samples. This loss is almost certainly due to dissolution (Hemleben *et al.* 1989), even in areas apparently saturated with respect to calcium

carbonate. Sediments deposited above the lysocline may suffer limited dissolution, but those deposited at or below the lysocline will have suffered significant amounts of loss. Berger (1971) demonstrated that each species has its own response rate to dissolution; some dissolve faster than others. As a consequence, under conditions of extreme dissolution, only the most resistant tests will be left. This affects the number of species preserved as well as their relative abundances.

A further complicating factor is bioturbation. Infaunal organisms cause mixing of deep-sea sediments down to a depth of some tens of centimetres. Since the sedimentation rate is commonly only 2–3 cm ka⁻¹ there is potential mixing of assemblages of quite different ages. This might not matter if conditions were uniform over very long periods but during times of faunal change a blurring of the record takes place.

To overcome some of these problems, it has become common for the distribution of modern planktonic foraminifera to be determined not from plankton studies but from their occurrence in the surface layer of sediment but only in areas subject to negligible dissolution (e.g. CLIMAP 1981). This is on the principle that the modern sediment assemblages, and those from the fossil record, have undergone comparable post-mortem modifications.

The distribution of modern planktonic foraminiferal assemblages in surface sediments has been summarized for the world ocean by Bé (1977), CLIMAP (1981) and Murray (1991a).

Sea-surface temperature

Early studies of planktonic foraminifera from ocean cores were used to determine relative temperature changes. Thus, Phleger *et al.* (1953) divided the fauna from Atlantic deep-sea cores into low, mid and high latitude groups and plotted downhole curves showing 'warmer-than-present' and 'cooler-than-present' intervals. Ericson & Wollin (1956) used a similar approach and divided the fauna into 'warm' and 'cold' groups. Apart from providing an indication of climatic variability, these 'temperature' curves can be used to correlate one core with another. However, more objective methods of temperature determination are needed; these include the oxygen stable isotope record and the use of transfer functions.

Past water temperatures can be determined from the oxygen stable isotope record preserved in microfossil hard parts. There is a large

literature on this topic and it is discussed in detail by Corfield (this volume). However, palaeotemperature calculations depend on several assumptions, one of which is an estimation of the isotopic composition of the contemporary ambient water to allow for the ice effect. Thus, temperature determinations are not entirely objective. For this reason it is important to have an independent method of determining temperature and the most commonly used method is the transfer function discussed below. Another reason is that in high resolution studies it is sometimes evident that the changes in the species composition of the fauna was not entirely synchronous with the changes in the oxygen stable isotope record (Thomas & Vincent 1988).

The transfer function This is a powerful technique. First, multivariate statistical analysis of modern 'microfossil' census data (usually from core tops) was carried out to group the samples into a small number of factor assemblages. Then multiple regression was undertaken to develop equations relating those abundances to physical and chemical parameters. The technique was introduced by Imbrie & Kipp (1971) and successfully applied in the CLIMAP reconstructions of the last glacial maximum (McIntyre *et al.* 1976; CLIMAP 1981) and last interglacial (CLIMAP 1984). In the CLIMAP study, temperature determinations were accurate to $\pm 1-1.5^{\circ}\text{C}$. Ruddiman & McIntyre (1984) have pointed out that it is not possible to estimate SST values lower than *c.* 0 $^{\circ}\text{C}$ in February and *c.* 6 $^{\circ}\text{C}$ in August using planktonic foraminifera [because such temperatures in modern oceans are associated with 95–100% abundance of *Neogloboquadrina pachyderma* (Ehrenberg)]. Therefore, SST estimates of 0 $^{\circ}\text{C}$ for February and 6 $^{\circ}\text{C}$ for August must be regarded as maximum values. Molino *et al.* (1982) evaluated the comparative reliability of transfer functions based on planktonic foraminifera, calcareous nannofossils and radiolaria. They concluded that the geographic distribution of all three groups is very similar and statistically the oceanic provinces are the same. Temperature is the primary control for all three groups at high latitudes but other ecological controls, perhaps including nutrient supply and depth of the thermocline, may be more important at low latitudes. They established that the three transfer functions were comparable; the standard error for warm season planktonic foraminifera was 1.2 and for cold season coccoliths, 2 $^{\circ}\text{C}$.

The use of transfer functions on assemblages which include extinct taxa requires certain

assumptions (such as the ecological equivalence of a modern and a fossil species) but, as long as part of the fauna (or flora) is extant, the transfer function can be tested against a modern data set (Dowsett & Poore 1990).

Edwards (1992) has argued that the use of the transfer function on dinocyst data is inappropriate for various reasons. Instead, she developed the *Impagidinium* Index [$100 \times (\text{number of } I. \text{ aculeatum (Wall) + } I. \text{ striatum (Wall)}) / \text{total } I. \text{ impagidinium}]$. This seems to give fairly reliable winter SST estimates; for example, for Hole 552A 3.95–3.98 Ma 10–13°C compared with 11°C based on planktonic foraminiferal transfer function (Dowsett & Poore 1990).

Use of transfer functions to estimate Pliocene–Pleistocene sea surface temperatures In the CLIMAP reconstruction of the last glacial maximum (LGM), the distributions of coccolithophorids, diatoms, planktonic foraminifera and radiolaria were used to produce maps of sea surface temperature (SST) for February, August and seasonality (warmest minus coldest) (CLIMAP 1981). These distribution and temperature patterns can be compared with the modern ones to infer climatic differences.

It is beyond the scope of this review to discuss all the CLIMAP conclusions but a few important results will be highlighted. Whereas there was little difference in microfossil distribution in the tropical/subtropical equatorial regions between the LGM and now, there were major differences in mid to high latitudes. In both northern and southern hemispheres the polar assemblages expanded toward the equator leading to narrow subpolar and transitional assemblage zones abutting the subtropical/tropical zone. For instance, in the LGM North Atlantic only the polar assemblage was found north of 43°N. In the tropical regions increased upwelling is indicated by the expansion of characteristic upwelling assemblages along the west coasts of S America and Africa.

These distribution changes were matched by significant SST differences, particularly in high latitudes where the temperatures were lowered. However, in large areas of low latitudes of the Pacific, S Atlantic and Indian oceans there was either no temperature change or conditions were warmer at the LGM.

In terms of surface water, ocean circulation, the LGM was characterized by more intensified currents and more upwelling. These led to more rapid turnover of intermediate and surface waters, a southward shift of the Gulf Stream to c. 40°N and a steepening of thermal gradients along frontal systems.

Low latitudes The surface, mixed waters of the equatorial regions form the major heat reservoir of the oceans. The Trade Winds (Hadley circulation) are convection cells (Hadley cells) in which heat is transported polewards. In the modern Atlantic, the tropical surface water mixed layer is divided into a western region, with minimal variations in SST and maximum heat storage, and an eastern region with the opposite characteristics. Because of the asymmetry of continent and ocean geography the effects on the ocean and wind circulation patterns is to cause transfer of southern hemisphere heat into the northern hemisphere in the western part of the ocean. McIntyre *et al.* (1989) investigated three cores from this equatorial area to document the history of the surface waters during the last 250 ka and to test the effects of orbital forcing as a cause of change.

SST were estimated from planktonic foraminifera using transfer functions defined by Molino *et al.* (1982). Four foraminiferal assemblages control the estimated SST: tropical, transitional, divergence and subpolar. The tropical assemblage lives in the warmest surface layer; transitional and subpolar assemblages live at cooler temperatures within or below the thermocline; divergence assemblage is adapted to the nutrient conditions associated with the thermocline. The thermocline itself is subject to annual variation in depth and slope due to seasonal wind forcing of surface waters. This in turn causes changes in the relative importance of the four assemblages.

Over the past 250 ka the western tropical Atlantic shows minimal variation of its surface waters, except during periods of maximum glaciation. However, in the eastern part, the equatorial SST signals showed variation of a 23 ka precession cycle. They were in advance of northern hemisphere SST but in phase with, or slightly lagged, southern hemisphere SST. From this it was concluded by Molino *et al.* (1982) that southern hemisphere climate was a more important influence on the eastern tropical region than that of the northern hemisphere. The causes were considered to be variations in trade wind velocity and advection of heat from southern latitudes.

High latitudes Hole 552A on the southwest margin of Rockall Plateau (latitude 56°N) provided the first almost complete high resolution record through the latest Neogene and Quaternary of the North Atlantic. Hooper & Funnell (1986) selected 40 samples, representing maxima of glacial and interglacial events, for the time

period 2.5–0 Ma. They related the planktonic foraminifera $> 150 \mu\text{m}$ to surface water temperature using a transfer function. Extinct *Neogloboquadrina atlantica* (Berggren) was substituted for extant sinistral *N. pachyderma* and *Globorotalia puncticulata* (Deshayes) for *G. inflata* (d'Orbigny) for the Pliocene data. They determined that the Pleistocene interglacial temperatures were $c. 16^\circ\text{C}$ in the summer and 9°C in the winter, whilst glacial temperatures were 9°C in summer and 0°C in winter. In the late Pliocene glacial events, the temperatures were 8°C in summer and 2°C in winter.

warmer intervals were considered to be warmer than those of any of the Pleistocene interglacial periods. Winter and summer SST variations are similar in pattern and the difference between them is a measure of seasonality. At present, seasonality in this area is $5\text{--}6^\circ\text{C}$. During the Pliocene warm intervals it was $c. 10^\circ\text{C}$ whereas, during the cool intervals it was $c. 4^\circ\text{C}$.

Other techniques for estimating sea surface temperature It is not possible to use transfer functions for pre-Pliocene planktonic assemblages because few of the taxa are extant. A morphological approach was used by Bandy (1960, 1964); he noted that tropical keeled planktonic foraminifera had their limit of distribution at the 17°C surface water isotherm and that this is situated between latitudes $20\text{--}40^\circ\text{N}$ and S , according to local circulation conditions. He argued that this morphological feature could be used to plot the past boundaries of the tropical zone. However, modern keeled planktonic foraminifera do not live in the surface waters but deeper in the water column (Bé 1977), and Corfield & Cartledge (1991) used stable isotopic evidence to infer that morphologically similar forms have changed their depth preference through geological time.

Biogeographic distribution patterns are commonly used to infer temperature conditions and circulation patterns. It has been shown from studies of surface water phytoplankton, and from surface sediment samples, that the coccolithophorids, diatoms and dinocysts are sensitive indicators of these environmental conditions (see Baumann & Mathiessen 1992 and references therein). They therefore serve as useful proxies for past surface water mass distributions.

The Norwegian–Greenland Sea lies between the cold Arctic Ocean and the relatively warm North Atlantic. Thus, it is an area having marked contrasts in its surface water conditions. Along the Norwegian coast is the relatively warm northward-flowing Norwegian Current. On the western side of the sea is the south-flowing East Greenland Current of cold, less saline waters which are seasonally ice-covered. The warm Atlantic and cool polar waters meet at the Arctic Front (Fig. 2). Baumann & Mathiessen (1992) studied the history of the past 15 ka in cores from beneath the area of influence of the present Norwegian Current. They compared the results from the coccoliths and dinocysts with the summer SST determined from a diatom transfer function (Koc Kapuz & Schrader 1990). There was a major environmental change $c. 10 \text{ ka}$ marked by

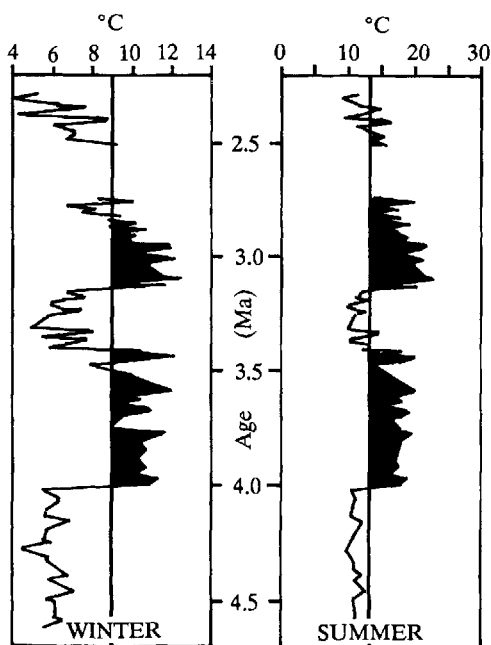


Fig. 1. Estimates of winter and summer sea surface temperature for Hole 552A. The vertical lines give the mean annual sea surface temperature at this site today. Warm intervals have been blocked in black. (After Dowsett & Poore 1990.)

Dowsett & Poore (1990) determined SST using planktonic foraminifera for the time interval 2.3–4.6 Ma. Pliocene species, now extinct, were considered to have ecological requirements similar to their ancestors. *Neogloboquadrina* was divided into warm and cool categories. A new transfer function, GS18, was devised to take these changes into account. The Pliocene SST record (Fig. 1) shows intervals when conditions were warmer (blocked in black) or cooler than the present day average SST. The

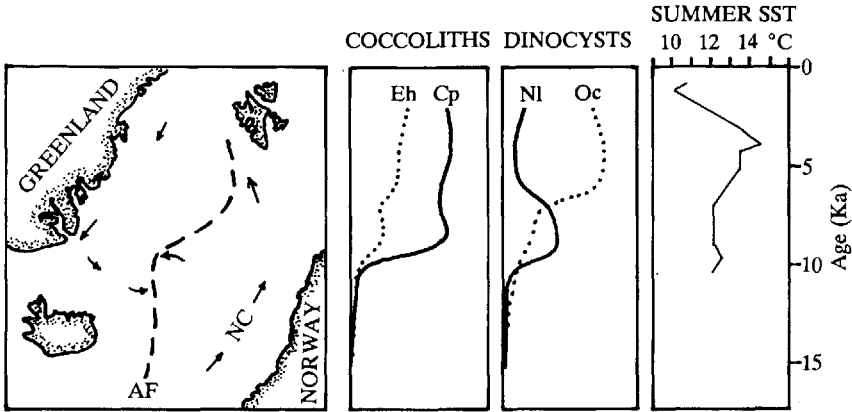


Fig. 2. The position of the modern Arctic Front (AF) in the Norwegian–Greenland Sea. For the area of the Norwegian Current (NC), the graphs show (from left to right) changes in the absolute abundances of the main coccolith and dinoflagellate cysts in relation to sea surface temperature (estimated from the diatoms). Eh, *Emiliania huxleyi*; Cp, *Coccolithus pelagicus*; Nl, *Nematosphaeropsis labyrinthus*; Oc = *Operculodinium centrocarpum*. (After Baumann & Mathiessen 1992.)

the initiation of the high absolute abundance both of coccoliths and dinocysts. They interpret this as evidence that the inflow of warmer Atlantic Water became permanently established at this time. The cold water coccolith species *Coccolithus pelagicus* was dominant suggesting conditions similar to those of the modern Arctic.

Another palaeoclimatic event took place in the Norwegian–Greenland Sea between 7500 and 6000 years BP. There was an increase in the abundance of *Emiliania huxleyi* (Lohmann) and of *Calcidiscus leptoporus* (Murray and Blackman), *Gephyrocapsa muelleri* Bréhéret and *Syracosphaera pulchra* Lohmann. The increase in dinocysts was more marked. These changes are considered to mark the Holocene climatic optimum which is evident throughout the North Atlantic region and represents a reorganization of the water circulation following the melting of the ice sheets.

A good example of the use of fossil biogeographic patterns of planktonic foraminifera in reconstructing surface waters is that of Wright & Thunnell (1988) on the Neogene of the Indian Ocean. They studied 5 time slices through the Miocene and Pliocene using data from DSDP sites back tracked to their original geographic positions. During this period the seaway between Antarctic and Australia/S America was widening and allowing a more vigorous development of the circum-Antarctic current (Figs 3 & 4). Also, the gateway between

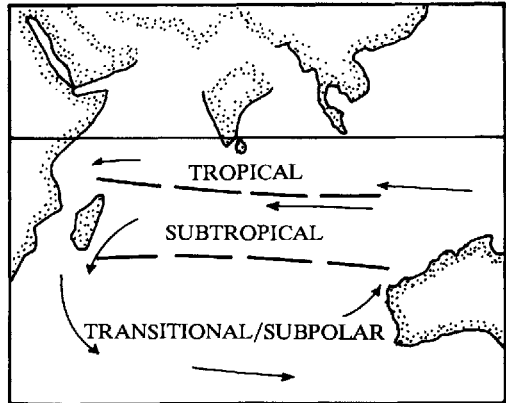


Fig. 3. Early Miocene planktonic foraminiferal biogeographic provinces and inferred surface water circulation. (After Wright & Thunnell 1988.)

Australia and the Philippines was getting narrower, thus reducing the exchange of waters between the Pacific and Indian Oceans. In the early Miocene three biogeographic divisions were recognized (Fig. 3), and these had gradational boundaries because of the low latitudinal thermal gradient of the surface waters. During the middle Miocene, the thermal gradient increased and by the late Miocene there was increased provinciality of the planktonic foraminifera (Fig. 4).

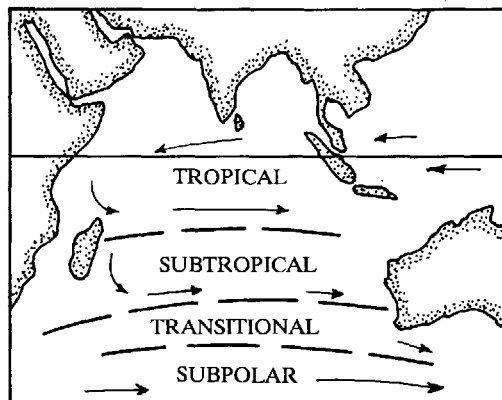


Fig. 4. Late Miocene planktonic foraminiferal biogeographic provinces and inferred surface water circulation. (After Wright & Thunell 1988.)

Apart from using biogeographic patterns, additional information can be gained from general attributes of the faunas, such as the trend of increasing diversity from high to low latitudes. For planktonic foraminifera, Bé (1977) recorded this in terms of total number of species: five in polar regions to 18–20 in transitional to tropical regions. The number of species encountered in a sample is partly dependent on sample size, so it is better to use a statistical measure of species diversity. Ottens & Nederbragt (1992) used the information function $H' = -\sum p_i \ln p_i$, where p_i is the proportion of each species, i.e. per cent divided by 100; they also used equitability ($E' = e^{H'}/s$, where s is the number of species in a sample). Equitability is on a scale of 1 (when all the species are equally abundant) to zero, (with progressive domination of the assemblage by a single species).

The results from modern plankton tows show that samples from blooms are dominated by a single species. The information function and equitability values are low, and indeed this is true of variable environments in general, for example, eddies and upwelling areas. Frontal zones, where there are sharp changes in temperature and/or salinity, have high information function and equitability values because the mixing enhances the abundances of those species occurring in both water masses. Of course, the plankton record preserved in the sediments is time-averaged and may not reflect short-term events such as blooms unless they persistently occur in the same place. Ottens & Nederbragt (1992) applied these techniques to the interpre-

tation of heterohelicid planktonic foraminifera from the Late Cretaceous of El Kef, Tunisia and concluded that conditions became more variable in the Maastrichtian at a time when rates of extinction were increasing.

Upwelling

Upwelling is the term popularly used to describe the vertical movement of subsurface water to the surface layer of the ocean. Wind stress on the sea surface causes horizontal movement of the top 10–100 m of water in a vertically integrated transport direction at 90° to the wind direction (Ekman transport). In the northern hemisphere movement is to the right and in the southern hemisphere to the left (due to the Coriolis force). Upwelling takes place where divergence develops. This occurs along the eastern margins of oceans at mid to low latitude, where the mean wind direction is towards the equator for a season or longer. Ekman transport is away from the ocean margin causing coastal upwelling. Also, in the open ocean, the westward trade winds cause Ekman transport away from the equator and hence there is equatorial upwelling.

Upwelled water is normally relatively enriched in nutrients and cooler than the displaced surface water. Areas of upwelling are therefore regions of high primary productivity with a high input of planktonic skeletal material and organic matter to the underlying seafloor. The bottom sediments are sometimes organic-rich because the bottom waters become depleted in oxygen; this adversely affects the benthos. Among the siliceous plankton, diatoms are dominant in upwelling waters. Radiolaria are present in upwelled areas but only in modest abundance (Thiede & Jünger 1992). The ratio of diatoms to radiolaria can be used to define the areas of maximum upwelling (high diatoms, low radiolaria: Diester-Haass 1983; Thiede & Jünger 1992).

Diatoms

Off NW Africa, coastal upwelling occurs throughout the year off Cape Blanc. The diatoms *Chaetoceras* and *Thalassiosira* are indicators of strong and persistent upwelling. Abrantes (1991) found that over the past 120 ka increases in diatom accumulation rates are synchronous with those of radiolarians and silicoflagellates. Since these forms have different susceptibilities to dissolution, this led her to infer that the changes were a true reflection of productivity variation. In this region productivity was higher than now in glacial stages 6 and 2. Jansen & Van

Iperen (1991) demonstrated that oceanic and coastal upwelling are not always synchronous off Zaire. From an analysis of the diatoms floras they concluded that over the past 220 ka coastal upwelling was greater during glacial stages 6, 4 and 2, and weaker than now during stages 5 and 3. Oceanic upwelling was strong during stages 6 and 2, and also in the 5d–5c transition stage. They considered that *Chaetoceras* resting spores not only record the variability of coastal upwelling but also variability in continental precipitation and erosion.

Dinoflagellate cysts

Although not all dinoflagellates form cysts which are preserved in the geological record those that do can be used to infer variations in the rates of upwelling. Lewis *et al.* (1990) demonstrated that, off Peru, the modern assemblages are dominated by peridinacean (P) species in areas of strong upwelling, whereas gonyaulacacean (G) cysts dominate in areas of weak upwelling. They interpreted Quaternary variations in the P:G ratio as evidence of variation in intensity of upwelling.

Planktonic foraminifera

Since most upwelling areas are in mid to low latitudes, the planktonic fauna is tropical or subtropical. There are no indigenous upwelling planktonic foraminifera but the subpolar species *Globigerina bulloides* is characteristic of upwelling areas throughout the world (Hemleben *et al.* 1989).

Globigerina bulloides often forms >40% of the plankton tow assemblage (>125–150 μm) off NW Africa and Peru (Thiede & Jünger 1992). Other species well adapted to upwelled waters include *Globigerinoides ruber* (d'Orbigny), *G. sacculifer* (Brady), *Neogloboquadrina dutertrei* (d'Orbigny) and *Globigerinita glutinata* (Egger). Off California, sediment trap studies have shown that in the early stages of upwelling the dominant species >125 μm is *Globigerina quinqueloba* Natland, a form associated with high phytoplankton levels, and the later stages are dominated by *Globigerina bulloides*, a form associated with high zooplankton levels. From the stable isotope composition of the tests it was shown that these taxa migrate upwards during upwelling. Immediately after upwelling has ceased, *Neogloboquadrina dutertrei*, a form associated with the thermocline, increases in abundance (Thunnell & Sauter 1992).

The planktonic foraminiferal assemblages (>150 μm) of the surface sediments off Oman

show gradients away from the shore (Anderson *et al.* 1992). *G. bulloides* decreases from >35% nearshore to <20% offshore. *G. glutinata* increases from 25% nearshore to 32% 250 km from shore to 28% 500 km offshore. Together, these two species dominate the eutrophic upwelling region from the shore to 500 km offshore. Beyond this, tropical species such as *Globigerinoides ruber* dominate the oligotrophic warm waters of the Indian Ocean.

Further information is provided from the stable isotope record (Steens *et al.* 1992). *Globigerina bulloides* is a surface water species whereas *Neogloboquadrina dutertrei* lives in the thermocline, so the difference in their $\delta^{18}\text{O}$ values should be large. When upwelling takes place the thermocline is destroyed and both species then grow at essentially the same temperature. At peak upwelling the difference in their isotopic values should be zero. In the case of the stable isotopes of carbon, *N. dutertrei* shows the most negative $\delta^{13}\text{C}$ values in the initial phase of upwelling whereas *G. bulloides* is most enriched during the last stages of upwelling. Therefore, the difference between the $\delta^{13}\text{C}$ values of these two species is less under upwelling conditions than is normally the case. Steens *et al.* (1992) applied these relationships to the late Quaternary succession of Site 728 off Oman. They inferred that during the last 374 ka there was strong upwelling in the interglacial phases but there is an overall trend towards a decrease in upwelling to the present day. The record older than 374 ka was less easy to interpret and further developments in understanding are required.

Benthic foraminifera

Off Oman upwelling is caused by seasonal monsoonal conditions and beneath this there is an oxygen minimum zone (OMZ) which intersects the continental slope. Hermelin (1992) defined an assemblage 'A' which spans the bathymetric interval of the OMZ and which he regards more as an indicator of monsoonal upwelling than of low oxygen conditions: *Bolivina ordinaria* Phleger and Parker, *B. pygmaea* Brady, *B. seminuda* Cushman, *Bulimina* sp., *Chilostomella ovoidea* Reuss, *Ehrenbergina trigona* Goës, *Hyalinea balthica* (Schröter), *Lenticulina iota* (Cushman), *Textularia bermudezi* Cushman and Todd, *Tritaxia* sp., *Uvigerina peregrina* Cushman and *Virgulinitella pertusa* (Reuss). These species make up 75–90% of the benthic assemblage >125 μm at depths ≤ 1000 m and decrease with increasing depth (Fig. 5). Hermelin (1992) used variations in the abundance of assemblage 'A' in sediments of late

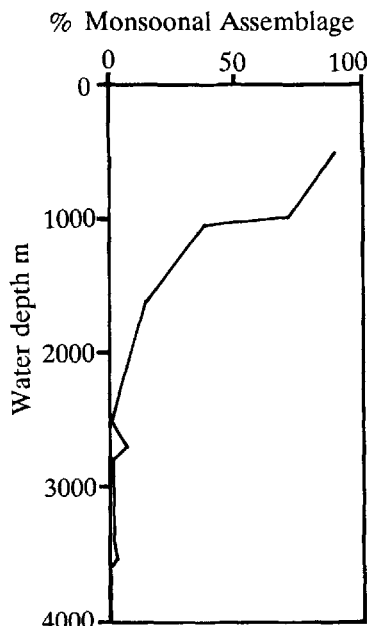


Fig. 5. Relative abundance of the monsoonal upwelling indicator assemblage (A) in recent sediments from the NW Arabian Sea. (After Hermelin 1992.)

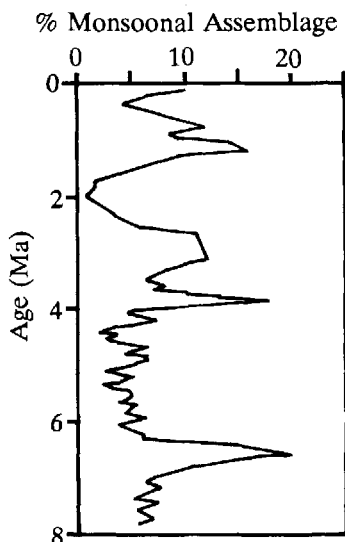


Fig. 6. Relative abundance (three-point moving average) of the monsoonal upwelling indicator assemblage (A) at Site 728 (water depth 142m) on the Oman margin. (After Hermelin 1992.)

Miocene to Pleistocene age from the same area as an index of variability in monsoonal upwelling (Fig. 6). For instance, on the Owen Ridge,

the lower boundary of the OMZ became deeper between 6.5 and 3.0 Ma, with a maximum at 5.0–4.5 Ma, as shown by the increase in assemblage 'A' in Holes 721B, 722B and 731A.

Pteropods

Off Peru and NW Africa three species of *Limacina* and one species of *Cresieis* are typical of upwelled water masses (Thiede & Jünger 1992).

Conclusions regarding surface water masses and upwelling It can be said that the estimation of SST, using multivariate analysis of census data on planktonic microfossils and transfer functions relating assemblages to temperatures, yields valuable oceanographic data independent of that derived from oxygen stable isotopes. Such data are essential for reconstructing the patterns and intensity of surface water circulation. Upwelling is characterized by an abundance of diatoms, a dominance of *Globigerina bulloides* and certain dinoflagellate cyst, pteropod and benthic foraminiferal associations.

Bottom water masses

The continental shelves are bathed in bottom waters which are linked with the local climate. Shallow, vertically mixed waters show seasonal temperature changes. Areas beneath seasonal thermoclines experience a smaller annual temperature range and their upper temperatures are lower than those experienced above the thermocline. On the continental slope and in the deep ocean the water is universally cold. This is because modern oceans have thermohaline stratification. The oceanic bottom waters form in two main areas: off Antarctica, to give AABW, and in the Norwegian–Greenland Sea, to give NADW. In both areas the water is cooled at the surface, becomes denser and therefore sinks. It then flows along the ocean floor away from source, following topographic features such as continental margins (e.g. Western Boundary Undercurrent off eastern North America) and mid-ocean ridges (which influence the northward passage of AABW away from source in the Weddell Sea). The Coriolis force causes deflection to the right in the northern hemisphere and to the left in the southern hemisphere. As it moves away from source each water mass slowly changes through mixing with adjacent water masses. For instance, in the deepest parts of the North Atlantic, AABW makes up 10–15% of the bottom water in the western basin and only 5% in the eastern

basin (Heezen & Hollister 1971). Nevertheless, palaeoceanographers use water mass names even for those areas where the water has been considerably altered by mixing. Thus, the term AABW is still used for the bottom water over the Madeira abyssal plain even though the AABW component is only 5%. Oceanographers are more circumspect in their usage of water mass names (Brown *et al.* 1989).

It is generally believed that the thermohaline circulation is largely driven through the production of NADW (Raymo *et al.* 1990; Gordon *et al.* 1992). All other deep water masses are essentially modified from either NADW or AABW through mixing. NADW introduces oxygen into the deep ocean and modulates local climate through the release of evaporative heat. It may also be important in controlling interglacial-glacial changes in atmospheric CO₂. Because of its great significance for the ocean-climate system, Raymo *et al.* (1990) reconstructed the history of NADW production since the late Pliocene using $\delta^{13}\text{C}$. Newly formed NADW has a $\delta^{13}\text{C}$ value of 1.0–1.5‰, but as it travels away from source and ages the values decrease to 0.3‰ in Southern Ocean Water and to negative values in the Pacific. From their study of two N Atlantic and one Pacific core, they concluded that there was a significant decrease in NADW during glacial periods after 1.5 Ma, especially between 1.13–1.05, 0.83–0.70 and 0.46–0.43 Ma.

The Cenozoic history of oceanic bottom-water circulation is closely linked with climatic change and the development of continental ice sheets. Most of the understanding of this has come about through the compilation of detailed stable isotope records and the interpretation of their significance. Two studies laid the foundations for this. In 1975 Shackleton & Kennett published stable oxygen isotope curves for the subantarctic Pacific. Both the planktonic and the benthic curves showed a progressive trend from negative values in the late Palaeocene (warm) to strongly positive values in the Pleistocene (cold). This showed that both surface and bottom waters were cooling through time. In addition, the records showed steps (rapid changes towards more positive values) and even reversals. These can be interpreted as showing phase changes from water to ice or vice versa. The second study was that of Savin (1977) who published curves for the tropical North Pacific. Here, the benthic foraminiferal trend was similar to that of the subantarctic but the planktonic curve showed very little change between the early Palaeocene and the present. This could be interpreted to show that the

surface waters underwent very little temperature change but that the bottom waters had become cooler through time.

Deep-sea faunas

It is appropriate to start the discussion by considering some of the problems. Because of the vast extent of oceans, relatively little is known of their modern deep-sea faunas. Among the organisms with preservable hard parts the benthic foraminifera are by far the most abundant with ostracods being the only other significant group. After nearly three decades of drilling a stage has now been reached where probably more is known of the fossil record of deep-sea benthic foraminifera than is known of their modern distribution patterns and ecology. This undoubtedly limits our ability to interpret the fossil record. If further advances are to be made in understanding palaeoecology/palaeoceanography using benthic foraminifera this problem will have to be addressed by funding basic research both on deep-sea foraminiferal ecology and standardization of taxonomy.

There is also a need to follow a sound methodology, i.e. to interpret fossil forms with reference to data on their modern representatives. Perhaps because of the limited data on modern forms, authors sometimes have no alternative but to put forward speculative suggestions on the palaeoecological significance of particular fossil taxa or associations. This is the normal scientific practice of putting forward a hypothesis which can be tested. However, in some cases these unproven hypotheses are treated as established facts and used to interpret other fossil assemblages; this is poor scientific practice and should be avoided.

Ideally, ecological studies should be carried out on living material (or samples which are preserved and stained to distinguish living from dead). In practice, this is difficult for deep-sea material. In most oceanic sediments, benthic foraminiferal tests are outnumbered at least 99 to one by planktonic foraminiferal tests. The benthic tests can only be separated out by picking and this is slow and laborious. Furthermore, it is known that the standing crop of living individuals is low, because of the limited food supply (Murray 1991*b*), and the rate of sediment accumulation is commonly only a few centimetres per thousand years. This means that it is extremely time-consuming to isolate the small number of stained (living) tests from the dead ones. However, in many cases only dried sediment is available for study and therefore there is no opportunity to differentiate living and

dead. Consequently, nearly all studies of the distribution of modern deep-sea benthic foraminifera are based on total assemblages (living plus dead).

There has been a lack of consistency in the use of sieve size. In shallow water studies a 63 μm sieve is normally used. To speed observations on deep-sea samples the size fraction examined is sometimes >125 , >149 or $>250 \mu\text{m}$. However, it is clear that much information is lost if the $>63 \mu\text{m}$ fraction is not examined (Schröder *et al.* 1987; Sen Gupta *et al.* 1987). Some of the key taxa, such as *Epistominella exigua*, are inadequately sampled on sieves with $>125 \mu\text{m}$ aperture. This is important because comparisons of results obtained using different sieve sizes can be misleading.

Benthic foraminifera occupy both epifaunal and infaunal habitats. Epifaunal niches include the sediment surface, attachment to substrates raised above the sediment surface (such as sponges and hydroids) and within clumps or mats of phytodetritus which has descended from the ocean surface (such as *Epistominella exigua* as described by Gooday 1988). Infaunal examples live down to a depth of at least 15 cm and different taxa live at different depths below the surface (Corliss 1985).

It is of consequence both to faunal and stable isotope studies that an infaunal foraminiferan living at a depth of 15 cm could be within sediment that is 5000 years old (if the sedimentation rate is 3 cm ka^{-1}). Thus epifaunal and infaunal assemblages in the same sample may not be exactly contemporary.

Different morphotypes occur in different settings. For instance, in the Norwegian Sea (Mackensen *et al.* 1985), epifaunal planoconvex forms are typical of depths of 200–500 and 1600–2700 m, biconvex forms of 1500–4000 m, and milioline ones of 3000–4000 m. The infauna has tapered, cylindrical and rounded planispiral tests at depths of <1000 m and flattened ovoid forms from 800–1500 m. Epifaunal individuals were found to dominate in regions where the organic carbon flux was $<3\text{--}6 \text{ g m}^{-2} \text{ a}^{-1}$ (Corliss & Chen 1988). In a further study of tests $>150 \mu\text{m}$ from the NW Atlantic, Corliss (1991) noted that only epifaunal taxa have wall pores restricted to one surface; infaunal taxa have pores on all surfaces. The pore-water chemistry influences the stable isotopic composition of infaunal tests; the $\delta^{13}\text{C}$ values are lower than those of epifaunal taxa (McCorkle *et al.* 1990).

Deep-sea benthic foraminiferal assemblages are diverse with 50 or more species commonly present in an assemblage of 250 individuals (Murray 1991b). This may be partly real, with

many species co-existing, but as many records are of total assemblages it may reflect time-averaging of successive slightly different faunas over a period of several hundreds or possibly a thousand years. Normally there is not high dominance by any one species and many taxa are represented by one or just a few tests. Most data sets are interpreted through multivariate statistics such as principal component or varimax factor analysis to obtain objective species groupings (Weston & Murray 1984). The number of taxonomic units is usually reduced to <40 by excluding very rare species and grouping related forms together.

Compared with the plankton, the deep-sea foraminiferal faunas are much more stable. Some modern species range back to the Palaeogene and by the mid Miocene the fauna was essentially modern. The low numbers of living individuals, limited seasonality of the environment (apart from seasonal pulses of phytodetritus), may favour asexual reproduction and this could be a major factor in their slow rate of evolution (Murray 1991b). Three periods of Cenozoic faunal turnover are known: Palaeocene–Eocene boundary (Kennett & Stott 1991; Pak & Miller 1992; Miller *et al.* 1992), middle Eocene–early Oligocene (Miller 1982; Thomas 1992), and early to middle Miocene (Schnitker 1986). In each case a significant proportion of the fauna has continued without alteration and the changes have been attributed to restructuring of the bottom-water masses through events such as cooling.

The distribution of recent benthic foraminifera from the North Atlantic was first described by Phleger *et al.* (1953). Both Streeter (1973) and Schnitker (1974) reinterpreted their data using Q-mode factor analysis. Schnitker also studied additional samples. Both Streeter and Schnitker suggested a correlation between foraminiferal distributions and bottom-water masses and this has been the case with many other studies.

In a review of modern deep-sea benthic foraminifera, Murray (1991b) pointed out that only a small number of associations (named after the dominant species) have been recognized. Three, characterized by epifaunal taxa, are widely distributed throughout the oceans:

1. *Epistominella exigua* (Brady) association, in North East Atlantic Deep Water, Pacific Deep Water and Southern Ocean Water. As it is now known that *E. exigua* shows a strong correlation with phytodetritus, the correlation with water masses may be suspect (see below).
2. *Fontbotia wuellerstorfi* (Schwager) associa-

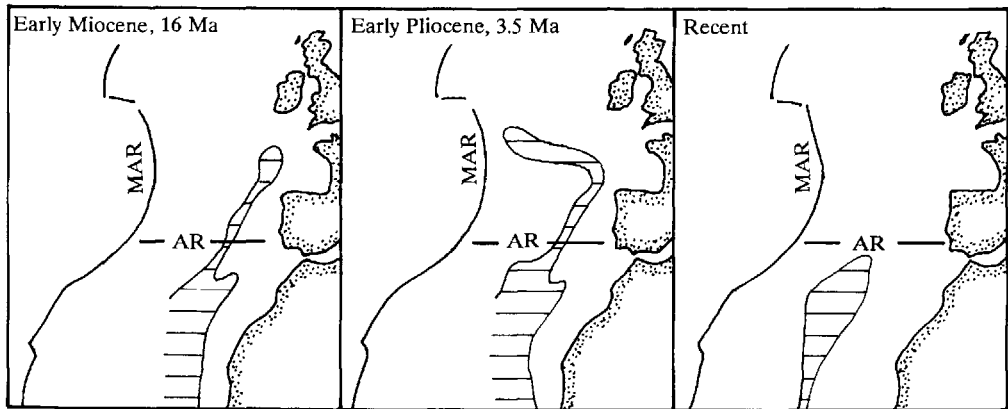


Fig. 7. Distribution of Antarctic Bottom Water (shaded), as defined by the occurrence of assemblages containing *Nuttallides umboniferus*, from the Miocene to Recent in the NE Atlantic. AR, Azores Ridge; MAR, Mid Atlantic Ridge. (After Murray 1988.)

tion (also known as *Planulina*, *Cibicidoides* or *Cibicides*) in NADW in both the Atlantic and Indian oceans.

3. *Nuttallides umboniferus* (Cushman) association (also known as *Osangularia* or *Epistominella*) in AABW in all the major oceans.

Three associations characterized by infaunal taxa are widely distributed in areas having higher contents of organic carbon: *Globocassidulina subglobosa* (Brady), *Melonis barleeanum* (Williamson) and *Uvigerina peregrina* Cushman associations. The latter is dominant where the flux of organic carbon exceeds $2\text{--}3\text{ g m}^{-2}\text{ a}^{-1}$ (Altenbach 1988). These associations show no obvious correlation with bottom-water masses.

The information on the bottom water at the sediment-water interface is very sparse. In almost all studies, data on the bottom waters have been derived from oceanographic data banks, often from observations far removed from the sediment sample both in time and space. Thus, there is no doubt that the suggested relationships between benthic foraminifera and their environment are over-simplistic. For example, the association of *Nuttallides umboniferus* with AABW was first established by Streeter (1973) and Schnitker (1974), based on the apparent overlap of their distributions. Subsequently, Bremer & Lohmann (1982) argued that *N. umboniferus* is related more to the carbonate undersaturation of the water rather than specifically to AABW. Even though AABW is diluted to form only *c.* 5% of the

bottom water in the NE Atlantic south of the Azores Ridge, there is nevertheless a *N. umboniferus* association in this area (Fig. 7) and Weston & Murray (1984) took this to represent AABW.

Past water mass distribution If the correlation between water masses and foraminiferal assemblages is real, then changes in the depth distribution and geographic extent of water masses can be documented in the fossil record from changes in the benthic foraminiferal distribution patterns in time and space. As with studies of surface water masses, there are two different approaches: determination of changes through time in individual borehole successions (Murray *et al.* 1986) and reconstructing the areal extent of water masses at specific time slices (Woodruff 1985).

Development of thermohaline circulation It has already been noted above that the isotopic record shows a progressive cooling of the deep waters of the oceans during the Cenozoic. Miller *et al.* (1991) have pointed out that up to 1980 it was assumed that the world was essentially ice-free prior to the middle Miocene. Deep-sea drilling during the 1980s yielded Oligocene sediment successions which show the existence of glacial ice-rafterd sediments off Antarctica. The Oligocene oxygen stable isotope record of *Cibicidoides* spp. shows peak values of $\delta^{18}\text{O} > 1.6$ (Fig. 8). Miller *et al.* (1991) argued that there was an Oligocene ice-cap on Antarctica and that there may even have been some ice

during the Eocene.

The $\delta^{18}\text{O}$ curve for bulk sediment calcium carbonate from the Atlantic shows a positive increase of *c.* 1‰ at the Eocene–Oligocene boundary. Shackleton (1986) interpreted this as representing a temperature decrease of *c.* 4°C over a period of 10^5 years and considered it to be a global climatic change. The thermohaline structure of ocean circulation became established with this event. The cold water introduced into the ocean basins has been termed the psychrosphere (Benson 1990).

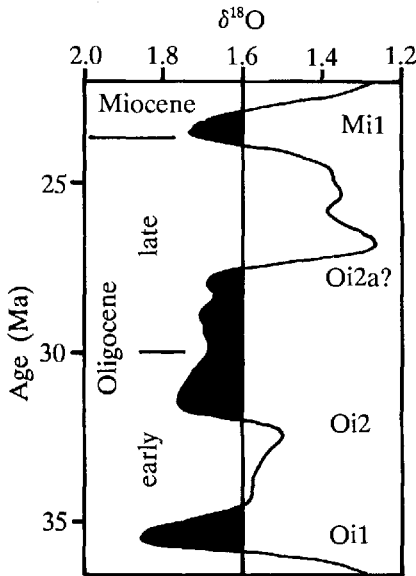


Fig. 8. The oxygen stable isotope record, based on *Cibicidoides* spp., for the Oligocene–early Miocene showing the stable isotope zones. (After Miller *et al.* 1991.)

The influence of this cold water on the benthic fauna should have been profound. The ostracods show a progressive faunal change which started in the late middle Eocene and continued into the early Oligocene with the establishment of a so-called psychrospheric fauna (Benson 1990). The species composition became essentially modern with ornate, reticulate forms such as *Bradleya*, *Posidonamicus* and *Agrenocythere*. Some of these forms are thought to have started in shallower polar waters and migrated with the cold water into the deep sea. However, Lipps & Hickman (1982) have argued that, since the mid Cretaceous, species diversification of the deep-sea foraminiferal fauna has taken place in the deep sea and not through immigration from shallow water.

Neogene events Changes in the benthic foraminiferal faunas > 150 μm from 25 DSDP sites in the Pacific Ocean have been described by Woodruff (1985, 1992). The 110 species were grouped into five factor assemblages using principal component analysis. The results were expressed both as distribution maps for specific times and as depth/latitude plots in which the boreholes were plotted at their Miocene backtracked water depths.

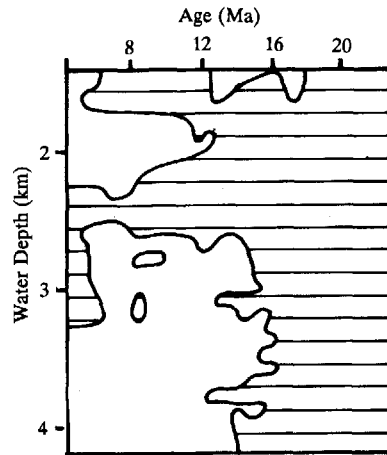


Fig. 9. Changes in the depth distribution of *Cibicidoides kullenbergi* (> 2% shaded, < 2% blank) in the Miocene of the Pacific Ocean. (After Woodruff 1985.)

In the early Miocene (22–16 Ma) the foraminifera show a fairly uniform distribution with respect to depth, and this can be interpreted as evidence of a warmer and less stratified ocean than at present. For example, *Cibicidoides kullenbergi* (Parker) is distributed from 1 to 4 km at this time (Fig. 9), but from the mid Miocene (14 Ma) it was essentially confined to depths < 2.5–3.5 km. This suggests that a change in the deep waters, beyond the range of tolerance of this species, occurred at this time. The associated change to more positive values of $\delta^{18}\text{O}$ suggests that the deep waters cooled. Therefore, *C. kullenbergi* is thought to have migrated to shallower depths to remain within the warmer, intermediate water mass. The newly cooled deep bottom water became colonized by *C. cenop* Woodruff at depths > 2.5 km.

The development of increased water stratification in the mid Miocene is indicated by a period of faunal turnover and a change in the benthic assemblages. Woodruff (1985) recognized an

area of particularly cool bottom water (modern temperature $<1.1^{\circ}\text{C}$) which she termed the Pacific bottom water corridor. Her assemblage 5 correlates with this area throughout the Miocene but, significantly, the area of its occurrence expanded in the mid Miocene to occupy the whole Pacific Basin (Fig. 10). This correlates with the increased build-up of ice on Antarctica.

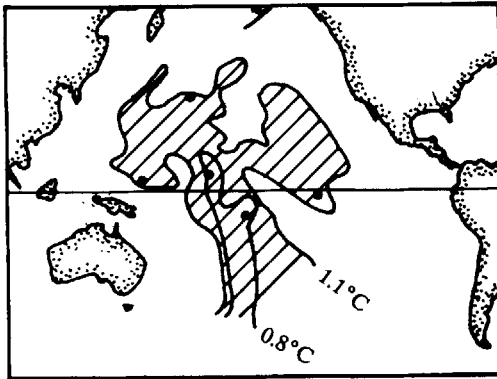


Fig. 10. The distribution of Miocene benthic foraminiferal assemblages indicating cold water at DSDP sites (•); the distribution of the modern cold waters is shaded and bounded by the 1.1°C isotherm. (After Woodruff 1985.)

The distribution of factor 1 assemblage composed of *Melonis*, *Uvigerina* (taxa known to prefer infaunal microhabitats rich in organic matter), suggests an increase in equatorial surface water productivity. This increase commenced in the east Pacific (where it is still present today) and progressively later in the west (Fig. 11). The strengthening of the latitudinal thermal gradient and associated more vigorous atmosphere-ocean circulation is thought to have led to equatorial upwelling.

The early Miocene assemblages of the Pacific, Indian and Atlantic Oceans were essentially the same, but from the mid Miocene those of the Pacific became progressively different from those of the other oceans. The reasons for this remain unknown (Woodruff 1992).

In the late Miocene of the Pacific, *Nuttallides umboniferus* (recorded as *Epistominella* by Woodruff 1985, 1992) changed its upper depth limit from c. 3.5 to 2.5 km by 6 Ma. This may have been due to an increase in the quantity of AABW which filled the basin to a higher level or to a shoaling of the calcite compensation depth.

The history of bottom-water masses in the NE Atlantic since the middle Miocene has been investigated by Murray *et al.* (1986), Schnitker (1986) and Murray (1988) using benthic foraminifera $>125\ \mu\text{m}$. Stratification of the water masses is clearly shown by the differences in the faunas between the shallower and deeper sites. It was found that AABW represented by the *Nuttallides umboniferus* assemblage has been present south of the Azores Ridge at depths $>3300\ \text{m}$ from the mid Miocene to early Pliocene. To the north of the ridge it has been variably present up to the late Pliocene, but since then it has been absent (Fig. 7). NEADW (or input of phytodetritus) was sporadically present north of the Azores Ridge throughout the mid to late Miocene but during the Pliocene and Pleistocene it became very significant both north and south of the ridge. These changes can be linked with palaeoceanographic and climatic events. A rapid build-up of ice took place on Antarctica in the early-middle Miocene (Shackleton & Kennett 1975) and the Labrador Current was initiated in the early Pliocene, leading to the formation of NEADW (Berggren & Schnitker 1983).

The foraminiferal changes associated with the onset of northern hemisphere glaciation have been investigated by Loubere & Banois (1987) at Site 548 (depth 1253 m) on Goban Spur off Ireland. At present this area is bathed in Mediterranean Water (temperature $7\text{--}8^{\circ}\text{C}$) and the benthic assemblage comprises abundant *Uvigerina peregrina*, *Sigmoilopsis schlumbergeri* (Silvestri), *Cibicides pseudoungerianus* (Cushman), *Melonis barleeanum* and *Bulimina mexicana* Cushman. In the late Pliocene record the onset of glaciation is marked by a change from an assemblage dominated by *Globocassidulina subglobosa* to one with abundant *Uvigerina*, *Bulimina* and *Melonis*. However, there is considerable variation in the assemblages through the glacial interval and these cannot be directly related to individual environmental parameters. Loubere & Banois (1987) used canonical analysis to confirm an inverse relationship between *G. subglobosa* and *M. barleeanum*, and to show that, as the *G. subglobosa* assemblage was replaced by the *M. barleeanum* assemblage, the diversity of the planktonic assemblage increased. Nevertheless, the authors were unable to explain the variations in abundance observed in many of the taxa. They speculated that the principal cause of the changes may have been the supply of food which was related to a change from less productive central gyre to more productive subpolar waters.

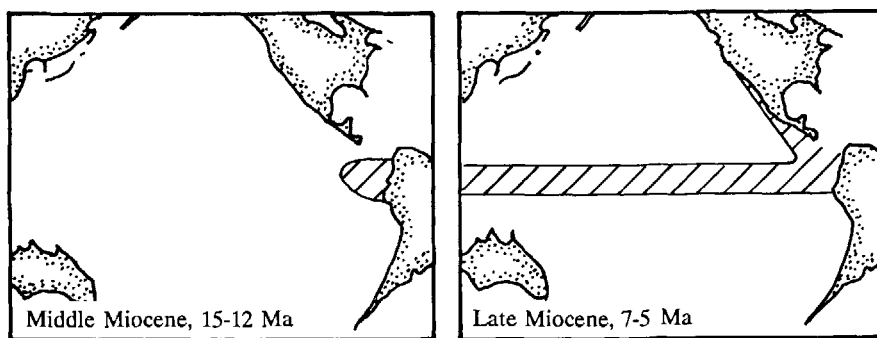


Fig. 11. Changes in the distribution during the Miocene of an assemblage characterizing sediments rich in organic matter. (After Woodruff 1985.)

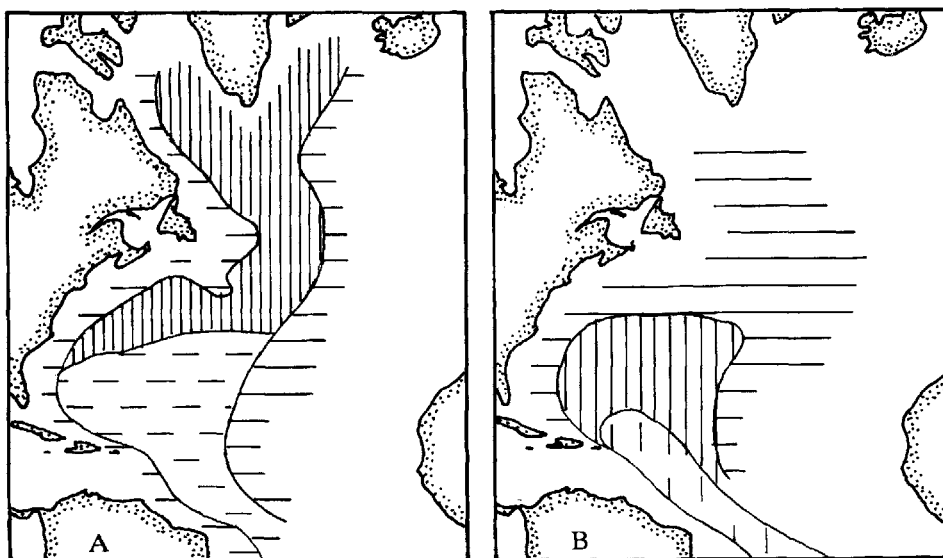


Fig. 12. Distribution of benthic foraminiferal assemblages in the NW Atlantic. (A). Modern. (B). Last glacial maximum (LGM). Key to shading: Horizontal line, *Hoeglundina*; vertical line, *Epistominella exigua* for Recent and plus *Hoeglundina* for the LGM; horizontal dashed, *Nuttallides umboniferus*; vertical dashed, mixed *E. exigua* and *N. umboniferus*. (After Schnitker 1974.)

Quaternary Schnitker (1974) compared the $> 125 \mu\text{m}$ assemblages of the NW Atlantic for 17 and 120 ka with those seen at present. He divided the modern assemblages into three main groups. One, dominated by *Epistominella exigua*, was said to be associated with Arctic Water (subsequently identified as Norwegian Sea Overflow Water; Schnitker 1980), another by *Nuttallides umboniferus* (as *Osangularia*) with AABW and the mid-ocean ridge has an assemblage characterized by *Hoeglundina*, *Uvigerina* and *Gyroidina* said to be indicative of

NADW (Fig. 12A). The assemblage distribution pattern for 17 ka was quite different (Fig. 12B). The *Hoeglundina* assemblage had expanded its distribution to most of the western area north of 40°N . South of this was a mixed *Hoeglundina*-*Epistominella exigua* assemblage and this gave way to a mixed *E. exigua*-*Nuttallides umboniferus* assemblage. From this, Schnitker concluded that the bottom-water circulation was very different from now. Norwegian Sea Overflow Water was no longer present, glacial AABW must have differed in character from

the modern AABW, and the northern area was occupied by a water mass similar to but not identical with NADW. As discussed above, it is now believed that the production of NADW during glacial phases was much reduced (Raymo *et al.* 1990). The reconstruction of distributions for 120 ka (interglacial) was essentially the same as now, indicating a similar hydrographic regime.

Low oxygen conditions From the works of Phleger & Soutar (1973), Douglas (1981) and Bernhard (1986) it is known that some foraminifera survive under very low oxygen conditions. Bernhard recognized fossil examples of low oxygen faunas by studying organic-rich sediments inferred to have accumulated under low oxygen or anoxic conditions. She showed by this means that the morphotypes of modern and Mesozoic anoxic assemblages differ. Kaiho (1991) has used the limited modern data on proven low oxygen morphotypes to infer the oxygen preferences of Cenozoic foraminifera. This is rather speculative and must in part be wrong. For instance, his anaerobic category includes unornamented *Bulimina* and flattened *Bolivina*, yet many such morphotypes are known to live in well-oxygenated modern environments (see, Murray 1991b). He devised a dissolved oxygen index (OI): $A/[A/(A+N) \times 100]$ where the number of aerobic and anaerobic specimens are *A* and *N*, respectively. This index was applied to the Cenozoic deep-sea record and it revealed periods of low-oxygen bottom waters in the early Eocene and late Oligocene–early Miocene. He considers the Palaeocene/early Eocene faunal turnover to be related to the start of the low oxygen event and the middle Miocene turnover to equate with high oxygen. In principle, this approach has worthwhile potential but this can only be fully developed when the oxygen requirements of individual taxa are better understood.

Surface–bottom water interactions

In one sense, all benthic activity is related to processes at the ocean surface because ultimately it is primary production by phytoplankton which supplies the food. In most parts of the ocean only a small proportion of surface production reaches the ocean floor to be consumed by the benthos. However, in areas of enhanced surface productivity the input of organic material to the deep seafloor is sufficiently great to have a marked influence on the benthic foraminifera. In other words, the surface

water processes override those of the deep sea. Four examples will be discussed: East Pacific Rise productivity gradient, *Epistominella exigua* and phytodetritus, diatom mats forming laminated sediments, and the high abundance of bolivinids.

East Pacific Rise productivity gradient Loubere (1991) sampled a transect of stations from 2641 to 3211 m water depth within the same bottom water mass on the East Pacific Rise to investigate the effects of changes of surface water productivity and the flux of organic matter to the ocean floor. The benthic foraminifera ($> 62 \mu\text{m}$) from the top 2 cm of the sediment showed a strong relationship with surface productivity. Species associated with the high productivity area included *Uvigerina* sp. (of *aubेरiana* type), *Melonis barleeanum* (both infaunal) and *Cibicidoides wuellerstorfi* (epifaunal). Beneath the area of low productivity the assemblage was dominated by *Nuttallides umboniferus*. Thus, surface water productivity overrode the influence of bottom water type.

Epistominella exigua and phytodetritus Open ocean areas, well away from the influence of coastal upwelling, experience seasonal blooms of plankton which provide seasonal pulses of food to the deep sea. The degraded plankton descends through the water column as marine snow or phytodetritus. When it reaches the ocean floor, it is rapidly colonized by opportunistic species, notably *Epistominella exigua* and *Alabaminella weddellensis* (Earland), which reproduce and increase their numbers in a period of a few months (Gooday 1988; Gooday & Lambshead 1989; Gooday & Turley 1990). This process is widespread in the NE Atlantic but is thought to occur more generally. Previous correlations of the abundance of *E. exigua* with bottom-water masses may therefore be incorrect. The principal control on the abundance of this species is almost certainly the input of phytodetritus. It may, therefore, be possible to recognize periods (of some tens of years duration) of enhanced phytodetritus production from the fossil proxy record of this taxon (Smart 1992; Smart *et al.* 1994).

Laminated diatom mats Widespread Neogene laminated diatom ooze in the eastern equatorial Pacific was deposited at a rate exceeding 100 cm ka^{-1} (Kemp & Baldauf 1993). The lamination is not due to bottom anoxia but to the rate and nature of diatom disposition as a mat. The principal diatom, *Thalassiothrix*, is elongate and slender (4 mm by $5 \mu\text{m}$). It is believed that the

interlocking frustules within the mat form a substrate which is impenetrable by macro-infaunal bioturbators because it is too strong and environmentally inhospitable; hence the preservation of the lamination. Preliminary studies of the benthic foraminiferal assemblages within the laminated diatom mats, and in adjacent bioturbated calcareous oozes, show that foraminifera are present throughout and none of the taxa present is indicative of low oxygen conditions. However, epifaunal morphotypes are much more abundant in the laminated sections than in the calcareous oozes (King *et al.* in press).

Boliviniid-rich assemblages The early Miocene (nannoplankton biozone NN4) of the NE Atlantic sites 608 and 610 is characterized by a high abundance of small boliviniids in the $>63 \mu\text{m}$ fraction. These have thin test walls and show no signs of abrasion so they are thought to be *in situ* rather than transported (Thomas 1986b). Subsequently, assemblages of this type have been recorded at numerous sites in both the North and South Atlantic Ocean and many of these are synchronous (Smart 1992; Smart & Murray 1994). Both Thomas (1986a,b) and Smart & Murray (1994) have discussed reasons for believing that they might represent a period of sluggish circulation and reduced oxygen conditions in the bottom waters, although the sediments do not have an elevated organic carbon content or any carbon stable isotope event in support of this interpretation. Thus, the explanation is still an enigma.

Conclusions

At present there is little detailed information on the ecology of deep-sea benthic foraminifera and this limits the interpretation of the fossil deep-sea record. Nevertheless, in a general sense, epifaunal associations show a correlation with bottom-water masses and therefore serve as proxies of past water masses. Infaunal taxa respond to the organic carbon content of the substrate and this, in turn, is related to surface water productivity. Certain epifaunal taxa also respond to food inputs, for example, *Epistominella exigua* responding to seasonal inputs of phytodetritus in open ocean areas. Two features known only from the fossil record are the development of widespread laminated diatom mats in the Pacific Ocean which influenced the contemporary benthic fauna, and assemblages rich in small boliviniids which perhaps represent periods of sluggish bottom-water circulation.

Summary of conclusions

Surface water masses: the estimation of SST, using multivariate analysis of census data on planktonic microfossils, and transfer functions relating assemblages to temperatures, yields valuable oceanographic data independent of that derived from oxygen stable isotopes. Such data are essential for reconstructing the patterns and intensity of surface water circulation in the Pliocene-Pleistocene. For the pre-Pliocene transfer functions cannot be used because the planktonic species were different. Instead, biogeographic patterns and stable isotope studies provide the basis for estimating past temperatures.

Upwelling is characterized by an abundance of diatoms, a dominance of *Globigerina bulloides* and certain dinoflagellate cyst, pteropod and benthic foraminiferal associations.

Bottom-water masses: at present there is little detailed information on the ecology of deep-sea benthic foraminifera and this limits the interpretation of the fossil deep-sea record. Nevertheless, in a general sense, epifaunal associations show a correlation with bottom-water masses and therefore serve as proxies of past water masses. Infaunal taxa respond to the organic carbon content of the substrate and this, in turn, is related to surface water productivity. Certain epifaunal taxa also respond to food inputs, for example, *Epistominella exigua* responding to seasonal inputs of phytodetritus in open ocean areas. Two features known only from the fossil record are the development of widespread laminated diatom mats in the Pacific Ocean which influenced the contemporary benthic fauna, and assemblages rich in small boliviniids which perhaps represent periods of sluggish bottom-water circulation.

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Marine Palaeoenvironmental Analysis from Fossils

edited by

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and

P. A. Allison (University of Reading, UK)

This volume critically reviews the use of fossils for the analysis of palaeoenvironments. The papers are multi-disciplinary, drawing on a host of geochemical, palaeoecological and palaeontological methods from traditional taxonomic uniformitarianism to more recently developed geochemical isotopic analyses.

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