4.19 Fossils as Environmental Indicators

4.19.1 Climate from Plants

R. A. SPICER

Vegetational physiognomy

Vegetation, unlike marine organisms, is directly exposed to the atmosphere. The physiognomy (structure and composition) of environmentally equilibrated (climax) vegetation is in large part controlled by, and therefore reflects, climate (Wolfe 1979). Interpretations of climate based on vegetational physiognomy, foliar physiognomy, or wood anatomy are more reliable for pre-Neogene studies than taxon-dependent climate signals (those used in Nearest Living Relative — NLR — methods). Fundamental vegetational types can be recognized in modern vegetation and, provided water is not limiting, correlate with temperature regimes (Fig. 1). These vegetational types can be recognized with some confidence back to late Cretaceous (Cenomanian) times.

Features of leaves useful in determining palaeoclimate

Angiosperm vegetative organs exhibit considerable morphological diversity and flexibility with respect to climate. The following features are those of angiosperms except where indicated:

Leaf margins. In modern vegetation the ratio of non-entire (toothed) to entire (smooth) margined leaves correlates strongly with mean annual temperature (MAT) (Wolfe 1979; Fig. 2). Generally, in the Northern Hemisphere a change of 3% in this ratio corresponds to a change in MAT of 1°C. In the Southern hemisphere, with a higher proportion of evergreen taxa, a 4% change corresponds to 1°C. Because major tooth types had evolved by the Cenomanian, and because Cenomanian leaf margin ratios correlate with palaeolatitude, this technique seems applicable from the early Late Cretaceous to the present. A minimum of 20 leaf species are required at any one locality to make this technique reliable, and taphonomic factors have to be taken into consideration.

Leaf size. This is related strongly to temperature, humidity/water availability, and light levels. Large leaves occur in humid understories, and size decreases with decreasing temperature or precipitation. Size classes are used to characterize vegetational types and to construct leaf size indices (which are used to characterize overall leaf size parameters for a given vegetational type). In fossil assemblages leaf size suffers strong taphonomic bias.

Drip tips. Highly attenuated leaf apices occur most frequently in evergreen leaves in humid environments, and are particularly common in the understorey of multistratal rain forests. Drip tips may

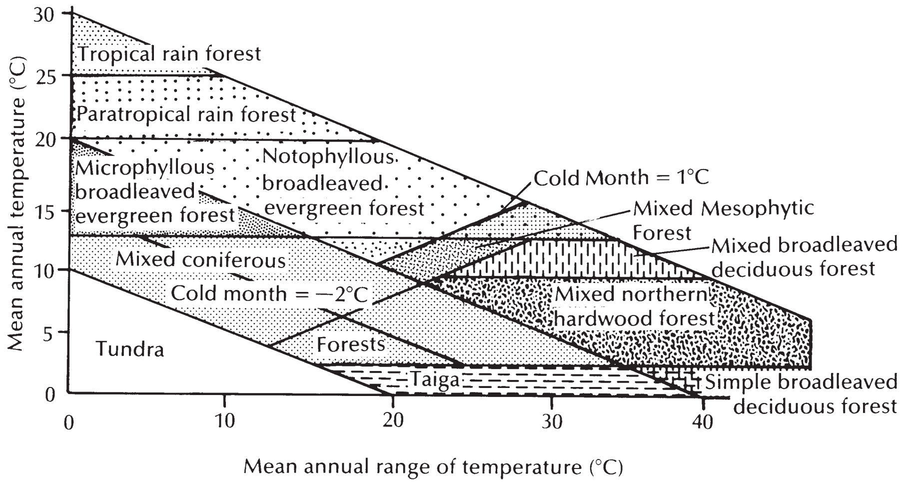

Fig. 1 Correlation of fundamental vegetational types with temperature regimes.

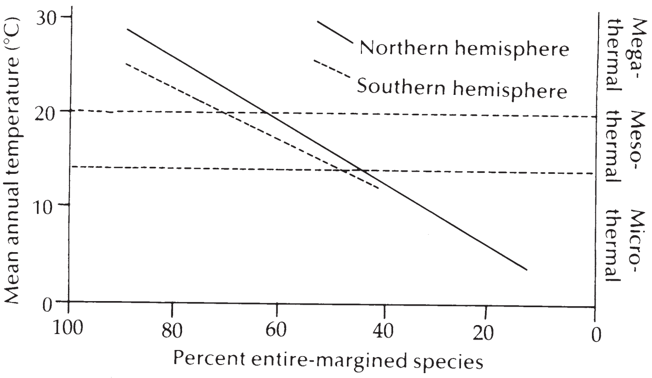

Fig. 2 Correlation of ratio of non-entire (toothed) to entire (smooth) margined leaves with mean annual temperature.

enhance drainage of surface water from the leaf and thus retard the growth of epiphytes.

Leaf texture. Leathery (*coriaceous*) leaves typically are evergreen and predominate in megathermal and mesothermal vegetation (see Fig. 2). Thin (*chartaceous*) leaves are typically deciduous and are most common in microthermal climax or successional mesothermal vegetation.

Leaf shape. Stream-side vegetation contains a high proportion of narrow (*stenophyllous*) leaves. Lobed or compound leaves (also associated with deciduousness) occur with greatest frequency in successional vegetation or understorey communities, and therefore warn of bias in the climate signal. Thick cylindrical leaves in any plant group are evidence of aridity, growth in saline water, or an inefficient vascular system.

Leaf cuticles. In all terrestrial plant groups thick cuticles with numerous trichomes (hairs) are characteristic of plants adapted to desiccating conditions (drought or salinity). Sunken stomata, particularly if overarched by papillae, and low stomatal density are also indicative of water stress. Conversely, thin, smooth cuticles suggest water-rich conditions.

Wood anatomy

Manoxylic (parenchymatous) *wood* (e.g. modern relict cycads) is frost-sensitive, while *pycnoxylic* (mostly composed of secondary xylem) *wood* (conifers and angiosperms) is usually frost-resistant.

Tree rings. In situations where climatic conditions vary frequently, pycnoxylic wood produces rings as a consequence of variations in growth rate. Rings may be produced on an annual basis where temperature, light, or water availability fluctuates on a yearly cycle, or less regularly in environments with more erratic variations in growth conditions (e.g. sporadic droughts).

Annual rings consist of early (spring) wood with large cell lumina and thin cell walls that grade into late (summer) wood, in which the lumina are smaller and the walls thicker. Wide rings generally reflect benign conditions, but ring width is also a function of position within the tree (position within the trunk, or trunk versus branch) (Creber & Chaloner 1985). High early wood–late wood ratios indicate a high rate of spring and summer growth followed by rapid onset of dormancy. At high latitudes this may be controlled by light rather than temperature.

Inter-annual variations in ring width are described using a statistic known as *mean sensitivity*:

$$\mathrm{ms} = \frac{1}{n-1}\sum_{t=1}^{t=n-1}\left|\frac{2(X_{t+1}-X_t)}{X_{t+1}+X_t}\right|,$$

where X_t is a ring width, X_{t+1} is the width of the adjacent younger ring, and n is the number of rings so measured in a sequence. Woods with a mean sensitivity of < 0.3 are termed *complacent* and indicate uniform growing conditions from year to year. *Sensitive* woods (ms > 0.3) are typical of trees growing at the edge of their range and/or in variable environments.

Intra-annual variation is marked by *false rings*. Unlike true rings these often do not form complete circles as seen in cross-section, and may be gradational to normal (usually early) wood on both concave and convex sides. False rings reflect temporary trauma within the growing season caused by waterlogging of roots, low temperatures, or severe insect attack, for example. *Frost rings* are characterized by cell wall disruption due to freezing of cell contents. Pycnoxylic wood is known from the Late Devonian to the present.

In angiosperm woods average vessel diameter divided by the frequency of vessels per mm^2 in cross-section estimates the susceptibility of a tree to air embolism (formation of air bubbles and damage to conductive elements) caused by transpirational stress or freezing. As with leaves, the reliability of the climate signal in wood increases with sample size and taphonomic understanding.

NLR methods

Plant reproductive organs have little inherent climatic signal but climate may be deduced from extrapolation of the tolerances of their NLRs. Following Axelrod & Bailey (1969), four steps are required in NLR analysis:

1 NLR of all taxa in an assemblage should be identified to modern genus level.
2 NLR determinations should also be attempted at species level (because generic tolerances are too broad).
3 The average MAT and average mean annual range of temperature (MAR) are estimated based on habit 'preferences' of modern NLRs.
4 The effective temperature (average temperature at the beginning and end of a period free from frost or chill) and equability of the palaeoclimate are calculated using the average MAT and MAR.

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4.19.2 Temperature from Oxygen Isotope Ratios

T. F. ANDERSON

Introduction

Oxygen isotope ratios ($^{18}O:^{16}O$) of well preserved marine calcareous fossils are indicative of the temperature of ancient ocean waters. This approach is based on the fact that the difference in $^{18}O:^{16}O$ ratios between calcium carbonate and the water from which it precipitates is a function of temperature. Oxygen isotope ratios are expressed in the δ notation:

$$\delta^{18}O = \left[\frac{(^{18}O{:}^{16}O)\text{ sample} - (^{18}O{:}^{16}O)\text{ standard}}{(^{18}O{:}^{16}O)\text{ standard}}\right] \times 10^3. \quad (1)$$

Units are per mil or parts per thousand. The standard material for carbonates is PDB, a late Cretaceous belemnite from the Pee Dee Formation of South Carolina; for water, the standard is SMOW, i.e. standard mean ocean water (see Anderson & Arthur 1983). Oxygen isotope palaeotemperatures for calcite can be calculated from:

$$T°\text{C} = 16.0 - 4.14\Delta + 0.13\Delta^2, \quad (2)$$

where $\Delta = \delta^{18}O$ calcite (vs. PDB) $- \delta^{18}O$ water (vs. SMOW) (Anderson & Arthur 1983). Thus, $\delta^{18}O$ of calcite increases as temperature decreases. Palaeotemperature estimates can be made with an uncertainty of ± 0.5°C, because $\delta^{18}O$ values are measured to a precision of 0.1 per mil.

Factors other than analytical precision control the uncertainty in isotopic palaeotemperatures:

1 The manner in which isotopic fractionation between biogenic calcium carbonate and water varies with temperature must be known. Equation (2) applies to inorganic precipitation of pure calcite at isotopic equilibrium and to a number of low-magnesium calcite fossil groups including bivalves, belemnites, brachiopods, and planktic foraminifera. Slightly different equations apply to preserved aragonite and high-magnesium calcite shells (Anderson & Arthur 1983). In addition, physiological effects during shell secretion in some organisms result in departures from equilibrium fractionation; notable examples are corals and echinoids.
2 It is necessary to estimate the $\delta^{18}O$ of the water in which the shell grew. In the hydrologic cycle, evaporation preferentially removes $H_2{}^{16}O$ from water, while precipitation and runoff returns $H_2{}^{16}O$. Local variation in the hydrologic balance of ocean waters of normal salinity can produce small variations in $\delta^{18}O$. (The range for modern seawater is 2.5 per mil.) This effect is normally ignored in estimating isotopic palaeotemperatures because hydrologic data on ancient ocean water is lacking. Also, because $H_2{}^{16}O$ is preferentially stored in polar icecaps and continental ice sheets, oceans are enriched in ^{18}O during glacial epochs relative to nonglacial epochs. For example, the growth and decay of continental ice

sheets during the Late Quaternary produced excursions of at least 1 per mil between glacial and interglacial oceans. The effect of Palaeozoic glaciations on the $\delta^{18}O$ of contemporaneous seawater was probably similar.

3 Reliable isotopic palaeotemperatures can be obtained only from those fossils that have been preserved from diagenetic alteration. Cemented or partially recrystallized fossils will generally give erroneous palaeotemperatures, because secondary carbonates reflect the temperature and isotopic composition of diagenetic solutions.

Isotopic palaeotemperatures from the Cenozoic and Late Cretaceous

The most continuous record of marine temperature variations for the past 100 million years has been constructed from isotopic analyses of well preserved foraminifera in deep-sea sediments. Diagenetic alteration of foraminiferal tests is minor and relatively easy to determine microscopically. In addition, the effects of continents on the temperature and $\delta^{18}O$ of ocean water in the pelagic realm is minimal.

The Quaternary oxygen isotope record of foraminifera shows oscillations with periods of about 10^5 years between $\delta^{18}O$ maxima during glacials and $\delta^{18}O$ minima during interglacials (see Savin 1977, fig. 8; Anderson & Arthur 1983). Although the direction of these isotope shifts is qualitatively compatible with temperature changes, it is now generally accepted that the amplitude of Quaternary $\delta^{18}O$ oscillation reflects changes in continental ice volumes more than changes in seawater temperatures.

Marine temperatures for the Tertiary and Late Cretaceous have been estimated from isotopic data on Deep Sea Drilling Project cores. Composite oxygen isotope records for planktic and benthic foraminifera from subtropical sites in the North Pacific illustrate the major features of palaeoclimatic changes over the past 130 million years (Fig. 1). The planktic record reflects temperature and $\delta^{18}O$ variations in low-latitude surface waters; the benthic record reflects conditions at the high-latitude source regions of deep-water masses. The data suggest general cooling in the Pacific over the past 100 million years. Temperatures of subtropical surface waters were evidently warmer in the Albian/ Cenomanian and the Eocene than in intervening times. Temperature trends in deep waters are correlated with those of surface waters from the Middle Cretaceous through the Early Tertiary. However, bottom waters during this interval (especially during the Cretaceous) were considerably warmer than at present. In other words, the latitudinal contrast in ocean temperatures had increased during the Tertiary, resulting principally from apparent cooling at high latitudes. Abrupt positive shifts in the Tertiary benthic $\delta^{18}O$ trend probably reflect the initiation (Eocene–Oligocene) and rapid expansion (Middle Miocene) of the Antarctic icecap, as well as a decrease in high latitude surface temperatures.

Palaeotemperature trends from shallow-marine bivalves from northwest Europe (Fig. 2) are similar to those for Pacific low-latitude surface waters (Fig. 1), suggesting that global palaeoclimatic changes were not obscured by the influence of continents on the temperature and $\delta^{18}O$ of nearshore seawater. In contrast to the deep-sea record, the isotopic data from bivalves suggest that the shallow

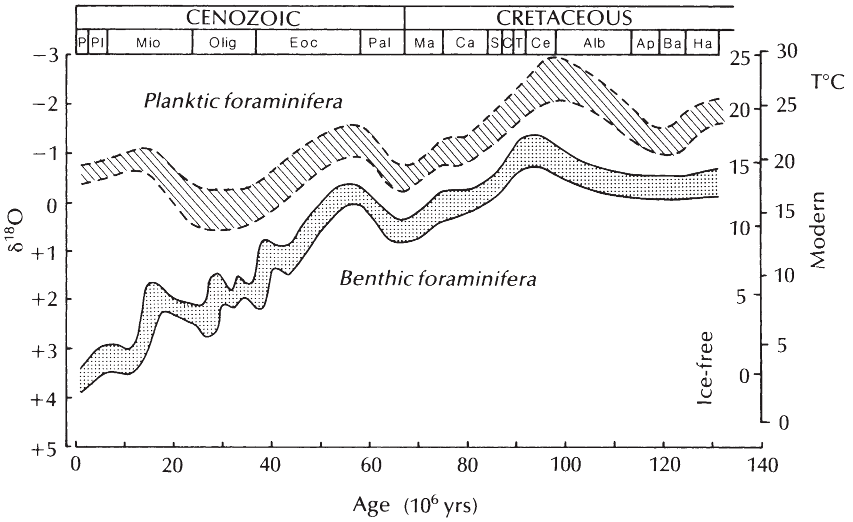

Fig. 1 Oxygen isotope record of foraminifera from the central North Pacific for the past 130 million years. $\delta^{18}O$ scale is shown on the left vertical axis; the corresponding temperature scales for modern and ice-free oceans ($\delta^{18}O$ = O and −1 per mil respectively) are shown on the right vertical axis. (Reproduced, with permission, from the *Annual Review of Earth and Planetary Sciences*, Vol. 5 © 1977 by Annual Reviews Inc.)

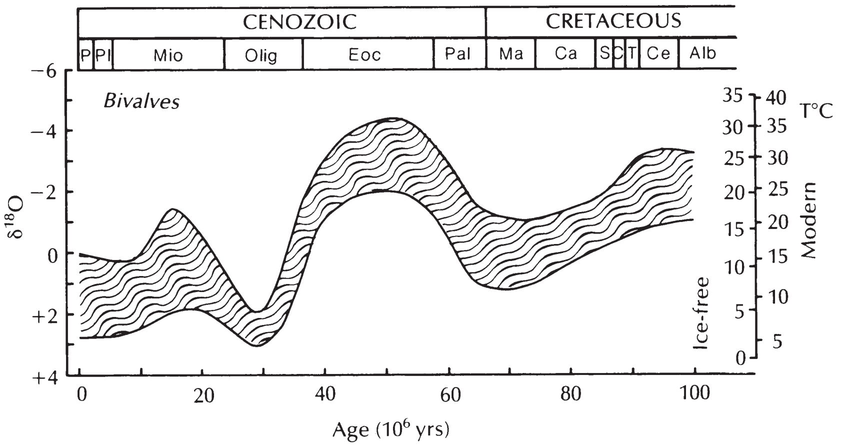

Fig. 2 Oxygen isotope record of shallow-marine bivalves from northwest Europe for the past 100 million years. $\delta^{18}O$ and temperature scales are the same as Fig. 1. (Data from Buchardt 1977 and Burdett, J. & Arthur, M. pers. comm. 1987.)

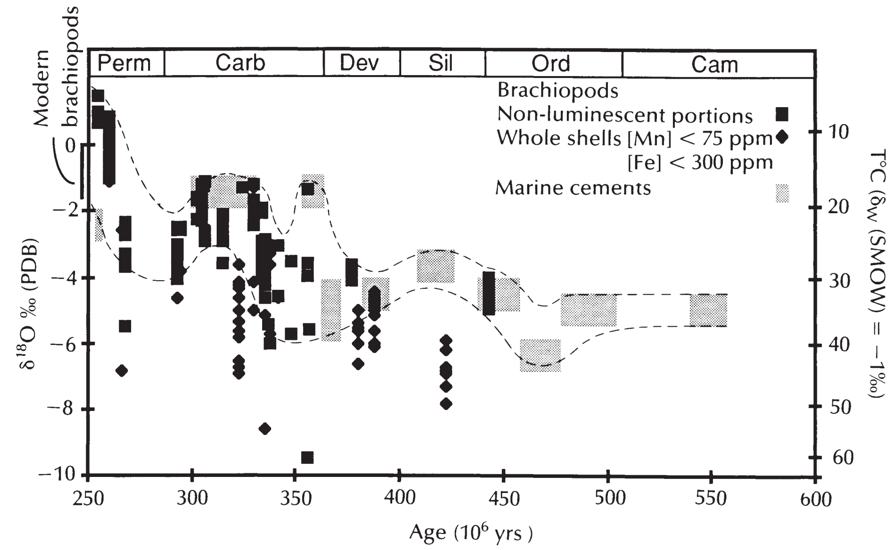

Fig. 3 Oxygen isotope record for Palaeozoic brachiopods and marine cements. The temperature scale (right vertical axis) is for ice-free oceans. (After Popp *et al.* 1986, by permission of the Geological Society of America, and Veizer *et al.* 1986.)

oceans of northwest Europe were significantly warmer during the Eocene than during the Middle Cretaceous.

Isotopic palaeotemperatures from the Palaeozoic

Isotopic palaeotemperature determinations on Palaeozoic fauna are limited necessarily to shallow-marine taxa. The most serious problem with Palaeozoic fossils is the preservation of the original isotopic signal through early diagenesis and long-term burial. Several recent studies have suggested that trace element compositions and microscopic textural characteristics can be used to identify isotopic preservation in fossil brachiopods (Popp *et al.* 1986; Veizer *et al.* 1986). Specifically, portions of brachiopods which are not cathode luminescent and whole brachiopod shells with low Mn and Fe contents have probably suffered only minimum diagenetic alteration. Data on well-preserved brachiopods from a range of locations, supplemented with estimates for primary marine cements, indicate that $\delta^{18}O$ values increased irregularly during the Palaeozoic, with a major positive shift from the Devonian to the Carboniferous (Fig. 3). The extent to which this and similar $\delta^{18}O$ age trends for cherts and sedimentary phosphates represent decreasing temperatures or increasing $\delta^{18}O$ of ocean water is a major controversy in stable isotope geochemistry. The resolution of this controversy will have a profound impact on our interpretation of surface temperature variations and hydrosphere–lithosphere interactions through time (Anderson & Arthur 1983; Veizer *et al.* 1986).

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4.19.3 Salinity from Faunal Analysis and Geochemistry

J. D. HUDSON

Introduction

Salinity is one of the main controls on the distribution of the aquatic biota, and the estimation of palaeosalinities has concerned many palaeoecologists. Most work has involved benthic invertebrates with calcium carbonate hard parts, although palynology has important applications. Fossil occurrences of particular taxa or assemblages may be compared to modern distributions. Alternatively, fossils can be analysed geochemically, as convenient samplers of the waters they inhabited. Sedimentological evidence also should be sought.

The usual result of such studies is an empirical estimate of the palaeosalinity, or range of salinities, experienced by the organisms, and is generally expressed in parts per thousand or in the 'Venice System' (Fig. 1). The recognition of fully-marine faunas is generally not controversial; nor, in Mesozoic and Cenozoic rocks, is that of freshwater lake faunas. Most palaeoenvironmental interest thus centres on the brackish water and hypersaline faunas of estuaries and other coastal environments, and of saline lakes.

Most brackish systems are labile, and the range and rate of salinity change may have as great an effect as mean salinity. Water bodies whose salinity varies are commonly also variable in temperature, depth, food supply, etc., and are often underlain by soft, organic-rich substrates. Therefore effects on biotic distribution caused directly by salinity are hard to disentangle from those which are due to other controlling factors.

Besides palaeoenvironmental interpretation, more fundamental questions concern: the mechanism(s) by which salinity control operates; whether there is a special brackish water fauna as opposed to merely a reduced-marine one; the evolutionary origin of brackish water faunas; and the relationship of brackish water faunas to the invasion of freshwaters or land by various groups of organisms. On the long time-scale, there is also the possibility that the composition of seawater itself may have changed. Palaeontology supplies essential historical data bearing on these biological and geochemical questions.

Faunal analysis

The normal palaeoecological precautions about working with *in situ* assemblages obviously apply; in particular, because salinity in estuaries and lagoons can vary so rapidly, the importance of finely-controlled collecting cannot be overstressed. Even so, some time-averaging of fine-scale variation inevitably occurs.

Many higher taxa of plants and animals today are effectively marine-stenohaline and their occurrence, especially in combination, can be used to infer fully marine salinity: *viz.* corals, cephalopods, echinoderms, bryozoans, articulate brachiopods, planktic and larger benthic foraminifera, and many calcareous red and green algae. Most of these, however, include some partially euryhaline forms extending into polyhaline waters. Only a small number of higher taxa thus account for most of the modern brackish and freshwater shelled fauna, i.e. bivalves, gastropods, ostracodes, smaller benthic foraminifera, and charophyte algae. Non-calcified arthropods are important but seldom preserved except as trace fossils (conchostracans being an exception). Many 'fish' are and have been euryhaline, although often also migratory and subject to vagaries of preservation. Even among these groups, few lower taxa have given rise to genera or species tolerant of mesohaline or more dilute waters. Most freshwater taxa are strictly stenohaline.

It follows from these considerations that brackish and freshwater faunas are of low taxonomic diver-

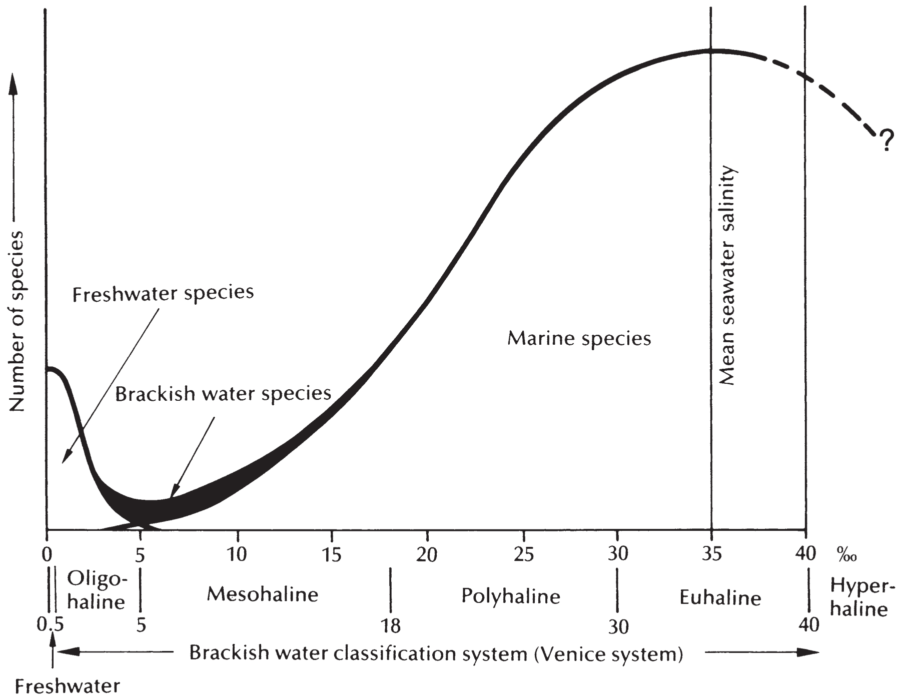

Fig. 1 Modified Remane diagram showing the relationship of species diversity–salinity. The vertical axis indicates that marine species are more numerous than freshwater ones. No precise quantitative significance is intended.

sity and comprise distinctive taxa. Few taxa are specifically adapted to brackish water and most of these are not normally capable of fossilization. They occur along with the more euryhaline members of the marine fauna and in mesohaline waters the latter generally dominate. A few freshwater forms penetrate oligohaline waters. Thus the diversity minimum is generally identified at 5–9‰ salinity, as first recognized by Remane in the Baltic Sea (Fig. 1). The reasons for this minimum have been much debated. It now appears that it does not correspond to a particularly sharp change in ionic ratios in most estuarine or lagoonal settings. A change from (Na^+, Cl^-) to (Ca^{2+}, HCO_3^-) dominated chemistry does, however, occur in more dilute waters in some areas and creates a sharp distinction between marine-derived brackish and non-marine ostracode faunas (Forester & Brouwers 1985). In inland lakes, ionic ratios, more than total salinity, control ostracode distributions (Forester & Brouwers 1983).

Brackish waters are often very productive because nutrients introduced from the land and estuarine circulation, with inflow of enriched subsurface seawater, can turn estuaries into nutrient traps. This combination of high fertility with physiological stress gives brackish water faunas their well known character of containing few species but many individuals. The species tend to be morphologically 'generalized' and the individuals small. This is both because the species are opportunists, *r*-selected for rapid exploitation of unstable resources and therefore commonly of small adult size, and because populations may contain many juveniles.

The faunas of hypersaline lagoons have some similarities to those of brackish lagoons, and the same major groups are involved. However, the lower taxa are generally different (e.g. miliolid rather than rotaliid foraminifera), and so are the sedimentary facies associations. Saline continental lakes may have different chemistry from seawater and have special faunas. Large inland seas of marine origin, such as the Caspian Sea, are also special cases.

Geochemistry

The trace element content of carbonate and phosphate shells must be related to that of the water their bearers inhabited, but there are many chemical, physiological, and diagenetic complications in applying this relationship in fossils. Relationships between the strontium : calcium ratio, for example, and salinity have been established for particular marine taxa and regions, but cannot as yet be generalized. In simple lacustrine settings the strontium: calcium ratio of ostracode shells correlates with salinity (Chivas *et al.* 1985). The distribution of the stable isotopes of carbon and oxygen, while also not free of complications, has been of more general utility (Dodd & Stanton 1981). The ^{18}O:^{16}O ratio in seawater has been rather constant ($\delta^{18}O_{SMOW}$ =

-1 to 0‰; Section 4.19.2), at least since the Late Palaeozoic. Meteoric water is variably ^{18}O depleted ($\delta^{18}O = -3$‰ in the humid sub-tropics, -50‰ in polar ice). Dissolved bicarbonate in seawater is relatively ^{13}C rich ($\delta^{13}C_{PDB} = 0$ to 3‰); river and lake bicarbonate generally contains carbon derived from the oxidation of plant material, and is thus variably ^{12}C enriched ($\delta^{13}C = -5$ to -12‰). In a simple river estuary, therefore, salinity, $\delta^{18}O$, and $\delta^{13}C$ are all linearly correlated, and the isotopic variations are reflected in the shells of molluscs living along the estuary (Mook 1971). (Temperature also affects $\delta^{18}O$, as discussed in Section 4.19.2, but seawater–freshwater mixing in a small area generally outweighs the temperature effect.)

These principles can be applied to well-preserved fossils. The best criterion of isotopic preservation is the retention of original aragonite in molluscs. Complications include the fact that $\delta^{18}O$ can be increased by evaporation of freshwater as well as by mixing, so that low-salinity water can attain positive $\delta^{18}O$ values, as in the Florida Everglades (Lloyd 1964). Humid-region lakes generally have negative $\delta^{18}O$ and $\delta^{13}C$ values in fossils; arid-zone lakes can be variable in both ratios. Especially in the Palaeozoic, time-related changes have occurred in the $\delta^{13}C$ and $\delta^{18}O$ of even fully-marine carbonates, making salinity-related changes harder to detect.

Conclusions

By using a combination of facies analysis, diversity studies, and taxonomic uniformitarianism, brackish water faunas of marginal-marine environments can be recognized with some assurance. In Cenozoic and even Mesozoic rocks faunal assemblages can be assigned to specific salinity ranges (e.g. Fürsich & Werner, 1986). Where fossils are well preserved, isotopic analyses provide further quantification. In Palaeozoic rocks, taxonomic uniformitarianism is at best doubtful, and variations in the isotopic composition of ocean water may have occurred. We have the prospect of studying the origin and evolution of the brackish and freshwater fauna that we know today, which goes back at least to the Mesozoic. It is uncertain whether Palaeozoic brackish water taxa (e.g. in the Carboniferous Coal Measures) are the direct ancestors of the modern taxa. We may eventually elucidate the fundamental controls on the nature and history of these successive faunas (Gray 1988).

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4.19.4 Oxygen Levels from Biofacies and Trace Fossils

D. J. BOTTJER & C. E. SAVRDA

Introduction

Marine strata deposited in environments characterized by low levels of bottom-water oxygenation are common in the Phanerozoic stratigraphic record. These strata are important as petroleum source beds and as the common host rock for many fossil-Lagerstätten, such as the Cambrian Burgess Shale (Section 3.11.2) and the Jurassic Posidonienschiefer (Section 3.11.6). Such strata also act as important indicators of both long- and short-term fluctuations in levels of oxygenation and, hence, circulation rate in the Earth's oceans. These factors have produced a need for continued refinement of biofacies models that permit the reconstruction of palaeo-oxygenation of ancient basin bottom-waters.

Early attempts to provide a framework for reconstruction of palaeo-oxygen levels employed a uniformitarian approach, through analysis of faunas and sediment fabric across oxygen gradients in Recent marine basins (Byers 1977). These studies divided such environments into aerobic (more than 1.0 ml/L O_2), dysaerobic (0.1–1.0 ml/L O_2) and anaerobic (less than 0.1 ml/L O_2) zones (Fig. 1A). In turn, these marine zones have been used to define oxygen-related biofacies in ancient strata (Byers 1977). Aerobic biofacies have been recognized on the basis of a thoroughly bioturbated sedimentary fabric and diverse assemblages of relatively large, heavily calcified body fossils. Dysaerobic biofacies, also characterized by bioturbated sediments, have been defined on the basis of the occurrence of low diversity assemblages of small, less heavily calcified body fossils or the absence of body fossils altogether. Anaerobic biofacies have been delineated on the basis of the preservation of primary varve-like lamination and the absence of *in situ* macrobenthic body fossils. Anaerobic strata may, however, contain well preserved remains of nektic or epiplanktic invertebrates and vertebrates.

This oxygen-related biofacies model has been significantly refined and expanded through additional studies of both modern environments and the stratigraphic record (Savrda & Bottjer 1986, 1987). Major refinements include: (1) the addition of two other potentially useful biofacies, the anoxic and exaerobic biofacies; and (2) the development of a sensitive trace fossil model for reconstructing palaeo-oxygen levels *within* the broad dysaerobic realm.

Development of the biofacies model

As originally defined, anaerobic environments may contain extremely low concentrations of dissolved oxygen. Despite the exclusion of bioturbating macrobenthic organisms, these environments may host preservable benthic microfauna, such as foraminifera and other soft-bodied components, that may result in microbioturbation (a subtle incomplete disruption of primary lamination). In contrast, anoxic biofacies represent environments totally devoid of oxygen. Anoxic biofacies, although they may be characterized by similar allochthonous faunal elements, may be distinguished from anaerobic biofacies by the absence of *in situ* benthic microfossils and microbioturbation (Fig. 1A).

Early oxygen-related biofacies models postulated a decrease in organism size and degree of calcification, as well as a drastic reduction in the relative percentage of fauna possessing calcified skeletons, as oxygen levels decrease toward the dysaerobic–anaerobic boundary (Fig. 1A). Application of these earlier models led to the interpretation that all macroinvertebrate fossils found in laminated strata were planktic, nektic, or epiplanktic. However, more recent studies (e.g. Savrda & Bottjer 1987) of modern marine environments have demonstrated that large, well calcified macrobenthic invertebrates may occur in the lower ranges of the dysaerobic zone. In addition, subsequent studies of ancient strata suggest that some shelled epibenthic organisms may have lived on the sea floor in environments where substrates were sufficiently oxygen-deficient to exclude more active, bioturbating infauna (e.g. Savrda & Bottjer 1987). In portions of the Monterey Formation (Miocene, California) the bivalve *Anadara montereyana* occurs *in situ* almost exclusively in strata deposited at the dysaerobic–anaerobic boundary. Based on this occurrence, Savrda & Bottjer (1987) proposed a new oxygen-related biofacies, the *exaerobic zone*. They further postulated that these bivalves may have favoured such oxygen-deficient environments because of a symbiotic association with sulphur-oxidizing bacteria, although other (as yet undiscovered) processes may also be responsible for producing this phenomenon. By considering variations in basin configuration and palaeoceanographic conditions, deposition under exaerobic conditions may also explain the occurrence of other epibenthic faunal elements (principally bivalve molluscs and brachiopods) in laminated, unbioturbated strata that are transitional between laminated strata which lack *in situ* body fossils, and bioturbated dysaerobic strata, in a wide variety of Phanerozoic marine sequences.

The use of trace fossils

In the biofacies model, general sedimentary fabric plays a crucial role in determining the boundary between the anaerobic (or exaerobic) and dysaerobic zones. Recent studies have shown that discrete trace fossils can be incorporated into a model for determining palaeo-oxygen levels within the dysaerobic biofacies (e.g. Savrda & Bottjer 1986). The trace fossil model involves the synthesis of ichnological criteria that are based on trends in diversity, burrow diameter, and vertical extent of biogenic structures, all of which decrease with reduced oxygen availability in bottom-waters (Fig. 1A). These trends are analysed along with cross-cutting relationships of

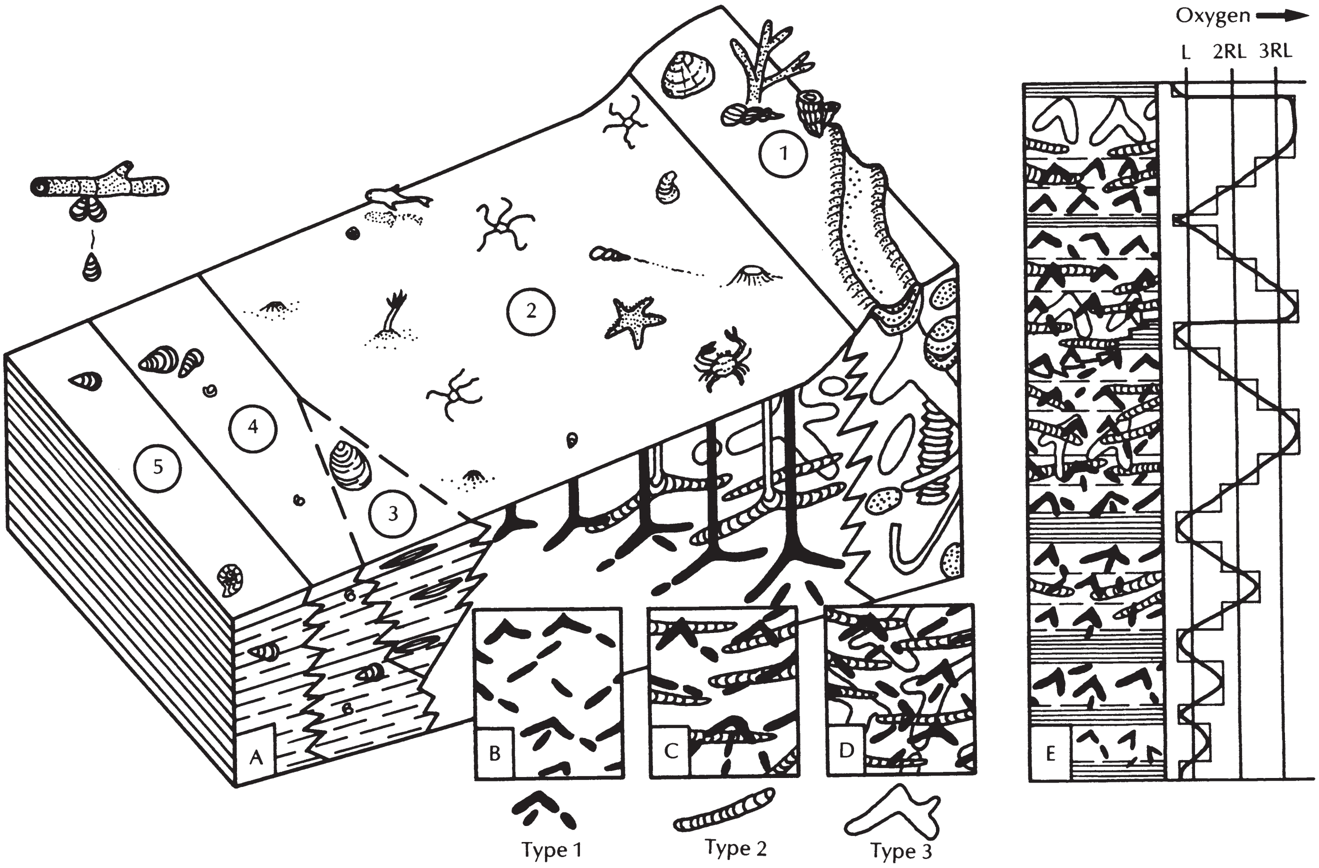

Fig. 1 A, Schematic representation of five oxygen-related biofacies described in the text. In order of decreasing levels of oxygenation, these are: (1) *aerobic*; (2) *dysaerobic*; (3) *exaerobic*; (4) *anaerobic*; and (5) *anoxic* biofacies. Presence and extent of the exaerobic zone depends on basin configuration and palaeoceanographic conditions (see Savrda & Bottjer 1987). Note reduction of diversity, burrow diameter, and vertical extent of biogenic structures with decreasing oxygenation within the dysaerobic zone. B–D, Schematic illustration of trace fossil assemblages and cross-cutting relationships expected in strata deposited at various points along the dysaerobic oxygenation gradient. E, Schematic illustration of the construction of palaeo-oxygenation curves for strata deposited in dysaerobic environments employing the trace fossil tiering model detailed by Savrda & Bottjer (1986), with permission from Macmillan Magazines Ltd.

trace fossils, which allows the recognition of tiering relationships (Section 1.7.1). The model permits the delineation of oxygen-related ichnocoenosis (ORI) units, or units of strata that were deposited under similar levels of bottom-water oxygenation (Fig. 1B–D). When applied in detailed vertical sequence analyses, the trace fossil approach can be used to construct interpreted oxygenation curves that reflect rates and magnitudes of temporal change in redox conditions (Fig. 1E) (see Savrda & Bottjer 1986, 1987, for examples from the Cretaceous Niobrara Formation of Colorado and the Miocene Monterey Formation of California). Considering the preponderance of the dysaerobic biofacies in the stratigraphic record, trace fossils are thus, at our current level of understanding, the best evidence available for evaluating ancient oxygen-deficient environments. However, continued work on geochemistry and macroinvertebrate body fossils is needed to reveal additional insights into relationships between biota and oxygen levels in marine environments through the Phanerozoic.

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4.19.5 Depth from Trace and Body Fossils

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Depth as such is unlikely to have limited a fossil organism's distribution during life. However, because many critical limiting factors are in some way related to depth, their combined effect may restrict the occurrence of particular organisms to a certain bathymetric range. Ecologically, the important parameters are food supply, light penetration, substrate mobility, rate of sedimentation, temperature, salinity, and dissolved oxygen. Geologically, the useful parameter is depth. Indications of depth may be obtained from the overall characteristics of a fossil assemblage and its mode of preservation; from a detailed study of particular taxa, especially if they are still extant; by considering the balance of benthic and pelagic groups; or by the identification of ichnofacies.

Inner versus outer shelf depths may often be inferred from the dominant fossil groups in an assemblage. Molluscan-dominated inner shelf assemblages, often with *Lingula*, may be contrasted with bryozoan/brachiopod-dominated outer shelf assemblages, often with ahermatypic corals or crinoids. Only one fossil group, however, definitively indicates shallow water — the benthic algae. Since they are dependent upon sunlight, they define the photic zone. The depth limit of the photic zone depends principally upon latitude and water turbidity. Today in the clear waters of the tropics it lies at 250 m, rising to 185 m on seamounts at 47°N, and to 90 m on oceanic plateaux at 59°N. Shelf areas like the North Sea have photic limits of 22–45 m, though this shallows to less than 1 m in estuaries.

Calcareous green algae assimilate most strongly in the red part of the spectrum and are therefore restricted to shallower water than the red algae, which are adapted to blue-green wavelengths. Rhodoliths are thus found on the shelf edge in the tropics, whereas dasyclads always indicate water only a few metres deep. Algae are noticeably absent from some carbonate facies, as for example from the basinal pioneering stages of stromatoporoid mounds in the Belgian Devonian; from Carboniferous mud mounds of the Waulsortian type (Lees *et al.* 1985); and from the Danian coral banks of southern Sweden, which grew in depths of 50–100 m.

Endolithic algal borings also show bathymetric zonation. Different types characterize particular depths, and these are well preserved in shelly shelf assemblages from the Silurian of New York State and the Miocene of North Carolina, for example

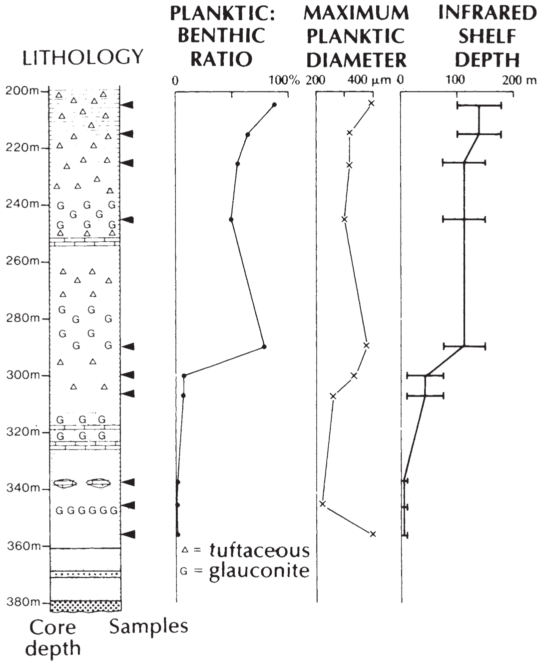

Fig. 1 Planktic: benthic foraminifera ratios and maximum planktic diameter used to indicate increasing depth during the Late Palaeocene–Middle Eocene. Sample from Deep Sea Drilling Project, Site 404, Rockall Plateau, northeast Atlantic. (Data from Murray 1979.)

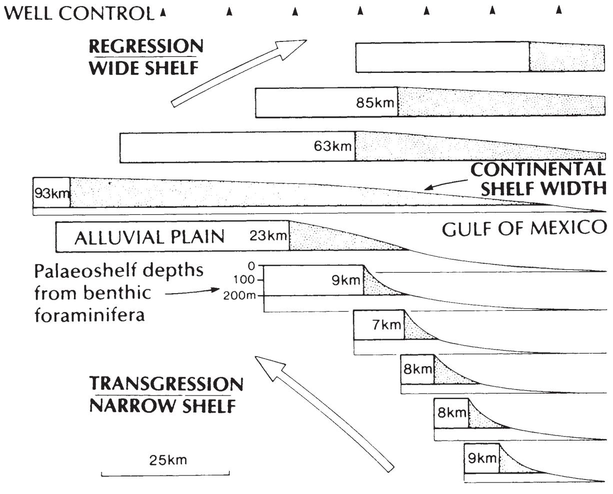

Fig. 2 Diversity of benthic foraminifera plotted at 100 m intervals through the Oligocene Anahuac Formation, subsurface Texas; reveals change in shelf gradient. (Data from Walton *in* Imbrie & Newell 1964.)

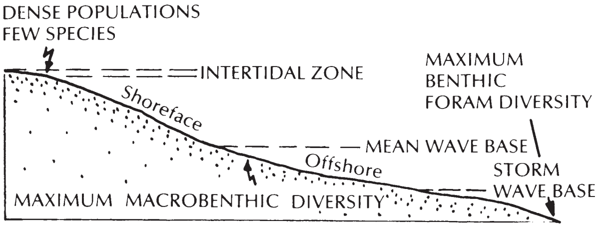

Fig. 3 Typical position of belts of maximum faunal diversity on modern depositional shelves in relation to critical physical parameters. (Data from Dörjes *in* Frey 1975 and Walton *in* Imbrie & Newell 1964.)

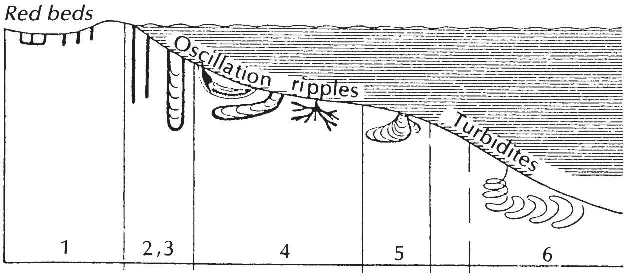

Fig. 4 The six universal depth-related ichnofacies of Seilacher *in* Hallam (1967), known from the Cambrian to the Recent: (1) *Scoyenia*; (2) *Skolithos*; (3) *Glossifungites*; (4) *Cruziana*; (5) *Zoophycos*; and (6) *Nereites*.

(Golubić *et al. in* Frey 1975). Shell-boring algae may be fed upon by gastropods which leave diagnostic grazing patterns. These occur on ammonites from certain Cretaceous shales, indicating a depth of no more than 30 m for their deposition.

Pelagic organisms, such as coccoliths, diatoms, radiolarians, pteropods, and graptolites, are rare in shallow water but are often abundant in outer shelf or bathyal settings. Planktic : benthic ratios provide a sensitive measure of outer shelf depths, in conjunction with maximum foraminiferal test size (Fig. 1).

Extrapolation of known present-day ranges for particular taxa is perhaps the commonest empirical method of interpreting palaeodepth. Outstanding syntheses using benthic foraminifera (Natland *in* Ladd 1957) and molluscs (Woodring *in* Ladd 1957) have plotted the fluctuating Tertiary water depths in the highly active Los Angeles and Ventura strike-slip basins. Latitude and faunal province must first be taken into account because organisms are temperature- rather than depth-dependent and classically exhibit 'tropical submergence'. The method has obvious pitfalls if the living taxon has been poorly sampled or is less common than in the fossil record, as with many ahermatypic corals (Wells *in* Hallam 1967).

Mapping belts of maximum faunal diversity may give useful depth indications. With microfauna this occurs just inside the shelf edge, a fact which has enabled changes in shelf gradient through the Oligocene of the Gulf of Mexico coast to be plotted (Fig. 2). With modern macrofauna it occurs just below mean wave base, at surprisingly shallow depths, even in macrotidal shelf seas (16 m for the southern North Sea: Dörjes *in* Frey 1975). This seems at variance with the situation in Silurian brachiopod-dominated fossil assemblages, where greatest diversity (admittedly of preserved species only) apparently occurs nearer the shelf edge.

Studying the taphonomy of a fossil assemblage may resolve such matters, since taphonomy is strongly depth-sensitive (see Section 3.5). Distinct boundaries between animal communities occur at mean wave base and storm wave base (Dörjes *in* Frey 1975; Fig. 3). Inshore of mean wave base the preservation of skeletal remains and trace fossils is controlled by hydrographic energy. Offshore, fossils are largely *in situ* and preservation is controlled by benthic productivity, except where interrupted by storm events.

The problem of possible reworking is avoided by using trace fossils as depth indicators. Because of their long time range, depth comparisons can be made between strata of radically different age using Seilacher's universal ichnofacies concept (Fig. 4). This has also proved of great value in broad-scale basin analysis, enabling Palaeozoic subsidence patterns in the Oslo and Central Appalachian basins to be compared (Seilacher *in* Hallam 1967). The six ichnofacies do not always occur in the expected bathymetric zone (see discussion in Frey & Pemberton 1984). *Zoophycos*, for example, occurs in shallower water in the Carboniferous than in the Mesozoic; and *Skolithos* has been recorded from proximal submarine fan facies. These anomalies occur because depth itself is not the limiting factor. Instead a combination of ecologically more significant parameters, in this instance levels of dissolved oxygen and substrate mobility, which do not always decrease with depth, determine distribution.

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