Geoscience Canada

PALEOSCENE 12. Benthic Macrofossils as Paleoenvironmental Indicators in Marine Siliciclastic Facies

Ron K. Pickerill and Pat J. Brenchley

See table of contents

Explore this journal

Cite this article
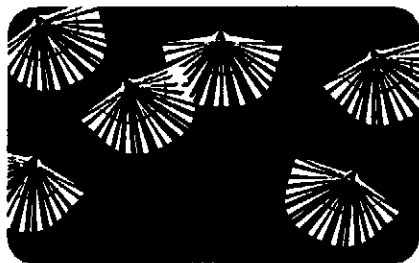
PALEOSCENE 12.
Benthic macrofossils as paleoenvironmental indicators in marine siliciclastic facies

Ron K. Pickerill
Department of Geology
University of New Brunswick
Fredericton, New Brunswick E3B 5A3

Pat J. Brenchley
Department of Earth Sciences
University of Liverpool
Liverpool L69 3BX United Kingdom

INTRODUCTION
Fossils commonly play an important role in environmental analysis and can be utilized to distinguish important variables, such as salinity and oxygen levels, substrate consistency, *etc.*, that are not readily recognizable by traditional sedimentological approaches. The significance of fossils as paleoenvironmental indicators does, however, vary greatly according to the sedimentary facies being considered. In some facies, there are distinctive bedding characteristics and sedimentary structures that constrain the likely depositional environment quite closely, but even so, increased resolution can, in most circumstances, be significantly improved by examination of contained faunas. More importantly, in other facies, particularly the more pelitic ones, sedimentological evidence is more problematic and fossils are of utmost importance in paleoenvironmental analysis. At the simplest level, the importance of fossils can be in distinguishing marine from non-marine strata, shallow marine from deep shelf, and shelf from slope and basinal environments. Although these are extremely broad distinctions, anyone who has worked on the paleoenvironmental interpretation of Precambrian sequences will have wished for a few fossils to help constrain environmental interpretations made solely on sedimentological observations.

A pervasive problem with the use of fossils as paleoenvironmental indicators is that uniformitarian principles are of limited value. The distribution of modern faunas amongst different environments can be used in de-

tailed paleoenvironmental analysis only for sediments deposited in the past few million years, as few modern species existed much beyond the Pliocene. The CLIMAP programme (mapping the climatic patterns for various times during the Quaternary using the distribution of foraminifera in conjunction with stable oxygen isotopic studies, *see* Cline and Hays, 1976) is an excellent example of taxonomic uniformitarianism, which is based on the proposition that the ecology of present organisms is the key to those of the near-recent past (Dodd and Stanton, 1981). However, it is widely appreciated that the confidence and applicability with which modern biotic distributions can be used decrease backward through the Phanerozoic. Progressively, fossil species *per se* cannot be utilized specifically as paleoenvironmental indicators and, instead, interpretations must be based on such considerations as the state of preservation and overall taxonomic composition of assemblages, the functional morphology of their constituent species, faunal diversity and abundance, *etc.* Even at higher taxonomic levels, many organisms have changed their habitat through time. For example, many benthic (bottom-dwelling) stalked crinoids, common within Paleozoic and Mesozoic shallow water paleoenvironments, have subsequently migrated to the deep sea (Hallam, 1984) and therefore strict application of the taxonomic uniformitarian approach would be misleading.

In this brief review, we concern ourselves mainly with the commoner macroscopic shelled fossils (*i.e.*, those seen without the use of a microscope) preserved in Phanerozoic siliciclastic facies deposited in marine environments. The geological history and paleoenvironmental distribution of terrestrial faunas have recently been elegantly reviewed by Gray (1988) and there is little need for repetition. We emphasize macrofossils as they are easily observed and collected by the non-specialist. Because of space limitations we do not discuss the paleoenvironmental distribution of microfossils in any detail and texts such as Haq and Boersma (1978), Brasier (1980) and Bignot (1985) should be consulted for general paleoenvironmental considerations of such groups. Additionally, we emphasize that this contribution stresses benthic as distinct from pelagic, *i.e.*, nektic (free-swimming), planktic (drifting) or epiplanktic (attached to floating objects, organic or inorganic, = pseudoplanktic of Wignall and Simms (1990)) organisms, because benthic organisms provide a more realistic assessment of the paleoenvironment in which strata accumulate. We will attempt to discuss the role that analysis of the functional morphology of benthic macrofossils can play in deciphering paleoenvironments, demonstrate how the taphonomy of shell concentrations reflects the hydrodynamics of the sedimentary environment, and show how community or benthic assem-

blage analysis has contributed to paleoenvironmental and paleogeographic reconstructions and record bathymetric changes in siliciclastic sedimentary sequences. Additionally, we will discuss how faunal diversity and biomass can be utilized as an aid in paleoenvironmental analysis and finally how macrofossils can be employed in the identification of specific aspects of the paleoenvironment.

FUNCTIONAL MORPHOLOGY
The study of functional morphology (or adaptive functional morphology) in assessing paleoenvironments relies on the fact that the construction and behaviour of living organisms are well suited or adapted to the natural circumstances in which they live. Consequently, detailed morphological analysis of benthic macrofossils can be an important predictive tool in paleoenvironmental analysis. As outlined by Dodd and Stanton (1981), three methods can be utilized to study the functional morphology of a fossil organism. These are: (1) If the fossil belongs to an extant species or is closely related to a living species, the relationship of morphology to function can be observed directly. This is the method of *homology*. (2) The function of the morphologic feature in the fossil may be explained by *analogy* to similar morphologies in extant organisms that are not closely related to the fossil. (3) The function of the morphologic feature may be indirectly determined through use of the *paradigm* approach which first proposes a likely function for a structure (*e.g.*, ribbing on a shell) and then compares that structure with the "ideal structure" for performing the function, which might be determined by mathematical modelling or an analysis of engineering design. The closer the similarity between the actual and the ideal, the more likely it is that the function has been correctly identified (Rudwick, 1964).

Morphological adaptations to environmental factors are shown in most fossil groups. For example, Stanley (1970, 1972) showed how the form of bivalves reflects their mode of life and indicates whether they are epifaunal or infaunal (respectively living on or within the substrate), whether they are deep or shallow burrowers, and, in some circumstances, whether they are adapted to fast burrowing. An adaptation to rapid burrowing is commonly shown amongst bivalves that live in mobile substrates. A deep burrowing mode of life is found amongst bivalves that live in unstable nearshore environments, including shifting sand substrates and intertidal areas where exposure is a problem. A study of Corallian (= Oxfordian, Jurassic), mainly carbonate, environments by Fürsich (1976) has shown that the proportion of bivalves with different modes of life varied between environments. In an analysis of Silurian brachiopods, Fürsich and Hurst (1974) showed how features such as strength of

ribbing, size of pedicle opening and shape of the pedicle valve may reflect degree of turbulence and nature of the substrate. A comprehensive examination of Cretaceous brachiopods from Denmark by Surlyk (1972) provides an excellent example of the principles, methodology and importance of functional morphology to paleoenvironmental analysis. Other references to the application of functional analysis amongst various groups are given in Table 1.

TAPHONOMY

Paleoecology is the study of the relationship of ancient organisms to their planetary environment, and how these organisms functioned within their habitat and toward each other (Copper, 1988). Since the appearance of important summaries by, for example, Hedgpeth (1957), Ladd (1957), Schäfer (1962, 1972), Ager (1963), Imbrie and Newell (1964) and Hecker (1965), a plethora of publications on the paleoenvironmental distribution and paleoecology of single species (paleoautecology) or mixed populations (paleosynecology) of benthic marine organisms has appeared in geological literature. For many years, a major concern of paleontologists was the recognition of whether or not the preserved biotas were *in situ* (synonymous with autochthonous, life assemblages, biocoenoses of various authors) and therefore clearly a reflection of the environment in which they lived, whether they were transported (synonymous with allochthonous, death assemblages, thanatocoenoses) and therefore indicative of the environment in which they finally accumulated, or whether they reflected a situation between these two extremes and were parautochthonous (disturbed neighborhood) assemblages representing essentially *in situ*, but locally reworked, organisms. Within marine siliciclastic strata, particularly siltstones and sandstones, it is only under exceptional conditions that *in situ* faunas are preserved and, instead, most have been transported and mixed to differing degrees by various sedimentological and biological processes. At the simplest level, it is therefore important that an evaluation of the degree of transportation and mixing of the macrobenthos must be undertaken in any paleoecological analysis. Such an analysis is part of the science of "taphonomy", which, according to Efremov (1940), who coined the term, is the "science of the laws of burial" and typically involves a recognition of both information loss and information gain (see Thomas, 1986; Wilson, 1988; Donovan, 1991, for reviews). Information loss occurs through a range of biostratinomic processes (biostratinomy is preservational history) such as decay of soft parts, transportation and fragmentation of shell material, and secondary post-burial processes such as disturbance by burrowers and diagenetic modification, so that the preserved fossil assemblage may be a poor

reflection of the original biocoenosis. On the other hand, there can be information gain, particularly where the manner of preservation provides valuable evidence about the depositional environment, and it is this aspect which will now be considered.

Fossils commonly occur in shell concentrations that may have a predominantly biological origin (in carbonate substrates, reefs are an extreme example), as sedimentary accumulations, or may be formed by a combination of biological and hydrodynamic processes. Each type of accumulation may be subsequently modified or transformed by diagenesis (see Kidwell, 1986; Kidwell et al., 1986, for reviews of the classification of shell concentrations). The degree and manner of reworking of shells provide valuable evidence about the hydrodynamic conditions and, in some situations, the frequency of events and rates of sedimentation at the site

of deposition. The diagenesis, particularly the presence and type of pyrite, may add additional evidence of environmental conditions, particularly in low energy, oxygen-poor, situations (Brett and Baird, 1986).

The nature of a fossil concentration can be defined by a range of preservational features, the most important of which are: (1) orientation of fossils, including life orientation; (2) relative degree of articulation; (3) degree of fragmentation; (4) proportion of different elements of a skeleton, for example pedicle to brachial valve ratio of brachiopods, left or right valves of bivalves; (5) convex up to convex down ratio of shells; (6) degree of abrasion, corrosion or bioerosion of skeletons; (7) type of shell fillings or coatings; (8) evidence for early dissolution of skeletons; and (9) any unusual feature of preservation (Brett and Speyer, 1990). Fossil concentrations that have consistent preser-

Table 1 Selected references to studies of the adaptive functional morphology of various macroinvertebrate groups (modified from Dodd and Stanton, 1981, 1990).

FOSSIL GROUP	REFERENCE
Sponges	Bidder, 1923
	Stearn, 1984
Coelenterata (Corals)	Philcox, 1971
	Stearn and Riding, 1973
	Hubbard, 1974
	Graus and Macintyre, 1976
	Kershaw, 1984
Bryozoa	Condra and Elias, 1944
	McKinney, 1977
	Rider and Cowan, 1977
Brachiopods	Rudwick, 1961
	Ager, 1967
	Grant, 1972
	Fürsich and Hurst, 1974
Molluscs	Trueman, 1964
	Jefferies and Minton, 1965
	Stanley, 1970
	Carter, 1972
	Westermann, 1973
	Chamberlain and Westermann, 1976
	Linsley, 1978
	Peel, 1978
	Skelton, 1979
	Savazzi, 1989
Arthropods	Clarkson, 1969
	Benson, 1975
	Campbell, 1975
	Schmalfuss, 1981
	Jaanusson, 1984
Echinoderms	Lane and Breimer, 1974
	Smith, 1978
	Welch, 1978
	Seilacher, 1979
	Stanton et al., 1979
	Smith, 1984

vational properties can be referred to particular taphonomic facies or taphofacies (Speyer and Brett, 1986; Brett and Speyer, 1990), which, briefly defined, consist of suites of sedimentary strata characterized by particular combinations of preservational features of the contained fossils (Brett and Baird, 1986). For example, the different levels of four taphonomic parameters, namely, (1) disarticulation ratio, (2) reorientation and sorting, (3) fragmentation, and (4) corrosion/abrasion (= corrasion), were used by Speyer and Brett (1988) to define seven taphofacies related to differences in turbulence, sedimentation rate and oxygen levels (Figure 1). The highest disarticulation ratios, best sorting, highest fragmentation and highest corrasion levels defined taphofacies 1 and were related to extremely high turbulence, low sedimentation rate and high oxygen levels. At the other extreme, taphofacies 7 showed low levels of the four parameters, suggesting low turbulence and relatively lower oxygen, but higher overall sedimentation rates (Figure 1). Between these two extremes, taphofacies 2 to 6 exhibited variable levels of the four parameters, reflecting different levels of turbulence, oxygen and sedimentation rate. The concept of taphofacies does, however, need to be applied with caution, because in some instances where there has been rapid

transportation and deposition, several aspects of shell preservation, such as dissolution, breakage and abrasion, are more a reflection of the environment in which the shells initially accumulated than of their final environment of deposition. The hydrodynamics of the latter are likely to be reflected in the size sorting, fabric and orientation of the shells (Davies et al., 1989). Additionally, of course, individual species of most major groups will possess, to varying degrees, different morphologies (e.g., heavy/strongly hinged versus delicate/weakly hinged, or variations thereof, brachiopods) and therefore will exhibit variable responses to similar hydrodynamic regimes. As Brett and Speyer (1990) have suggested, the concept of taphofacies requires further testing, but it may provide a useful framework for environmental interpretation, bearing in mind the intrinsic complexity of natural systems.

One of the clearest relationships between the nature of shell concentrations and the hydrodynamics of the environment occurs on wave-dominated shelves (Norris, 1986). In such environments, it is possible to recognize three general zones: (1) a nearshore zone above fair weather wave base, approximately equivalent to the shoreface (~5-15 m water depth); (2) the generally muddy shelf between fair weather and storm wave base

(~5 m to a maximum of 200 m water depth, but more commonly ~5-100 m); and (3) the shelf below storm wave base, where ecological assemblages predominate (~50-200+ m water depth) (Norris, 1986). In the nearshore zone (Zone 1), sequences are generally sandy, sedimentary structures are commonly well preserved and shells are likely to be repeatedly reworked and belong to taphofacies 1. Shell concentrations may occur as cross-stratified shell beds formed by nearshore currents, as concentrations in topographic lows between dunes, giant wave ripples, sand waves (cf. Wilson, 1986) and other bedforms (Figure 2a1), or on storm affected shores they may accumulate in the swales in amalgamated hummocky cross-stratified sequences (Figure 2b1).

The value of shell concentrations is greater in shelf environments of Zones 2 and 3 where the background sediment is mud and environmentally significant information is contained in shell accumulations. Where shelves are affected by storms, shells may be concentrated by current or wave activity (Figures 2a2–2a5 and Figure 3) and two types of storm influenced beds can be recognized: a first type in which there is little sediment transport, but strong wave winnowing, and a second type in which there is a substantial degree of offshore transport of
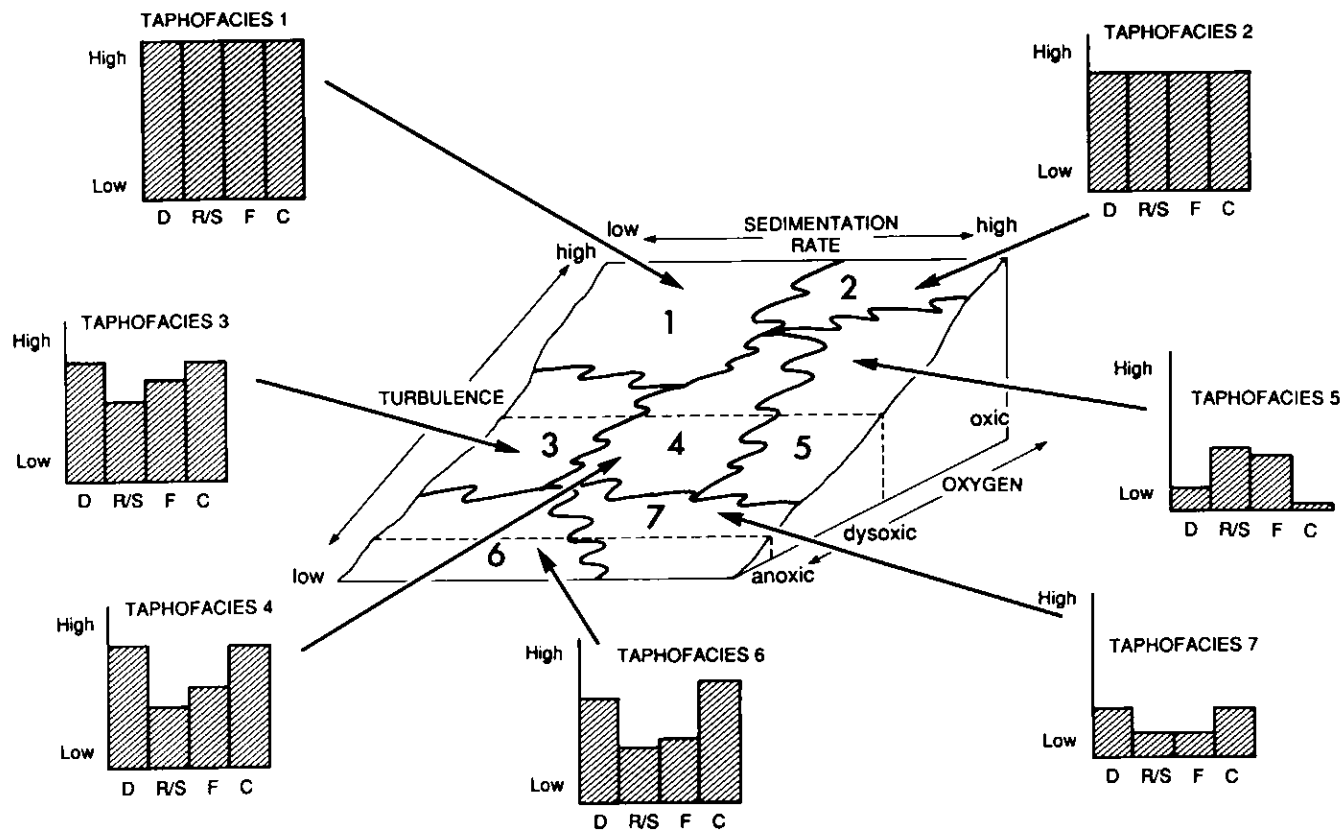

Figure 1 Generalized taphofacies recognized from Paleozoic shelf sequences, where seven distinct taphofacies are differentiated on the basis of shell disarticulation (D), reorientation and sorting (R/S), fragmentation (F) and corrasion = corrosion/abrasion (C). Generalized environmental conditions of individual taphofacies, as reflected by parameters of sedimentation rate, turbulence and oxygenation, are indicated accordingly. (Modified from Speyer and Brett, 1988; Brett and Speyer, 1990).

sand that is subsequently reworked by storm waves (Figures 2b2 and 2b3).

Beds of the first type vary according to the degree of wave winnowing and resuspension. In shoreface and inner shelf regions, storm waves are capable of eroding down a decimetre or more and the resuspended sediment is commonly deposited as a crudely graded bed (Kumar and Sanders, 1976; Kreisa, 1981; Kreisa and Bambach, 1982; Aigner, 1982) that may have a basal concentration of shells (Figure 2a2). In the more offshore shelf regions, Miller et al. (1988) and Parsons et al. (1988), working with Devonian shelf sequences, identified shell concentrations with an overlying mud blanket (cf. Figure 4) which showed an onshore to offshore gradient of decreasing thickness and complexity reflecting the waning influence of storm waves (Figures 2a3–2a5). Mid-shelf shell beds were referred to as complex shell beds, with commonly erosional bases and tops typically possessing some articulated shells (Figure 2a3). Internally, there are thin discontinuous mud layers suggestive of repeated episodes of accretion and winnowing. The implication is that these beds may have accumulated over a long period, that there may have been a physical mixing of shells from different periods of accumulation and therefore that the assemblages were "time-averaged". Time-averaging, the mixing of skeletal elements of non-contemporane-

ous populations, or communities, by sedimentological, biological or rarely diagenetic factors, is becoming increasingly recognized as a substantial influence on the structure of faunal groupings. Fürsich and Aberhan (1990) have recently provided a concise review of the causes, recognition and significance of time-averaging in various marine environments and Table 2 summarizes their main conclusions. Further offshore, such beds may be blanketed by several centimetres of rapidly deposited muds and shell-beds become simpler (Figure 2a4) and generally consist of an erosional base covered by a layer of finely comminuted shell debris followed by well-preserved, commonly articulated, shells toward the top. Finally, even further offshore, the shell beds consist of pavements and stringers with commonly articulated shells lying one deep on bedding planes (Figure 2a5). As the shell beds become progressively thinner offshore, the overlying mud blanket thins too. The offshore shell pavements appear to represent ecological beds which have been little modified by deep storm waves. Generally, along the same onshore to offshore gradient, as shell beds become thinner and the effects of storm waves wane, shells within the intervening muddy sediments are more likely to be articulated (Figure 5).

Beds of the second type are sandstones that typically possess hummocky cross-

stratification reflecting the ability of storm waves to rework sand on the sea floor. Shell concentrations usually occur as a basal lag to the sandstone bed or as a coquina filling scours on the base (Figure 6) and reflect vigorous wave activity. Such fossil concentrations may be similar in taxonomic composition to those in the adjacent muds (Watkins, 1979; Cherns, 1988; Brenchley and Pickerill, 1991) suggesting winnowing of nearby sediments, or they may show a quite different composition (Pickerill and Hurst, 1983) indicating substantial transport. It is clear that where fossils are being used for the study of ancient benthic assemblages or communities, coquinas at the base of storm sandstones should be used with caution.

In environments of Zone 3, below storm wave base, shells tend to be dispersed, articulated and are generally sparse. In these deep shelf environments, the development of pyrite in the sediment and in association with fossils may give valuable information about sediment geochemistry and oxygen levels. In general, in anoxic environments, pyrite is randomly dispersed and fossils are not preferentially pyritized (see Oxygen). In dysaerobic settings, pyrite is abundant and may be nodular, tabular or fill fossil cavities, such as ammonites, to produce steinkerns (Brett and Baird, 1986; Fisher and Hudson, 1987). In aerobic environments, authigenic pyrite is likely to be rare.
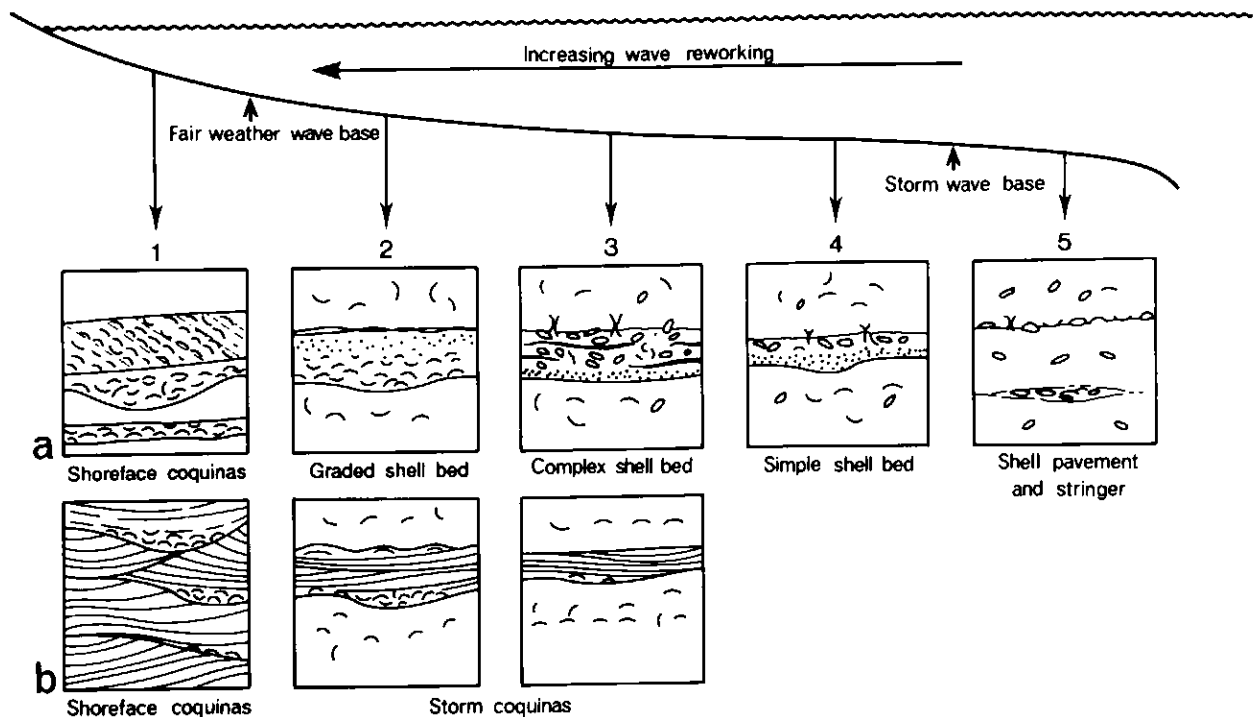

Figure 2 Shell accumulations related to storm processes across a shelf.

(a) Predominantly in situ reworking of shell material with little addition of sediment. (a1) Cross-stratified current-reworked shell bed, and wave-reworked shells in an erosional hollow. (a2) A graded nearshore shell bed. (a3) A complex shell bed with mud partings, reflecting multiple storm events. (a4) A simple storm bed with bioclastic material at base and in situ preservation of articulated brachiopods, trilobites, etc. (a5) Shell pavements and stringers representing only slight reworking of living shell assemblages.

(b) Shell accumulations in association with sand deposited during storm events. (b1) Shell coquinas in the swales of hummocky cross-stratification. (b2) and (b3) Shell concentrations at the base of storm sandstone beds which internally have hummocky cross-stratification.

Table 2   Predictive model of the relative abundance and significance of various types of time-averaging in contrasting marine environments, where A = abundant, C = common, O = occurs, R = rare and c = continuous, d = discontinuous, vl = very low, l = low, m = medium, h = high and vh = very high (modified from Fürsich and Aberhan, 1990).

	BEACH	ESTUARY	TIDAL FLAT	DELTA	LAGOONS, BAYS	SUBTIDAL BARS	NEARSHORE SHELF	OFFSHORE SHELF	DEEP SEA
Energy levels	h	l-h	l-h	l-h	l	h	m-h	l	l
Net sedimentation rates	l-m	m-h	l-h	l-vh	m-h	l	m-h	l-m	vl
No time-averaging	-	R	R	O	O	R	O	R	-
Allochthonous time-averaging	A	C	C	O	-	O	O	-	-
Autochthonous time-averaging short(<10⁴ yrs)	-	Rd	Rd	Oc/d	Oc	-	Od	Oc	Rc
long (>10⁴ yrs)	-	-	-	-	-	Rd	Rc	Oc	Cc

Figure 3 (left) Erosively based, fine-grained sandstone layer containing abundant disarticulated brachiopod shells interlayered with bioturbated muddy siltstones from the Siluro-Devonian Arisaig Group (Stonehouse Formation) of northeastern Nova Scotia. This particular shell concentration resulted from deposition by storm activity on a shelf in an area between fair weather and storm wave base. Bar scale = 15 cm.
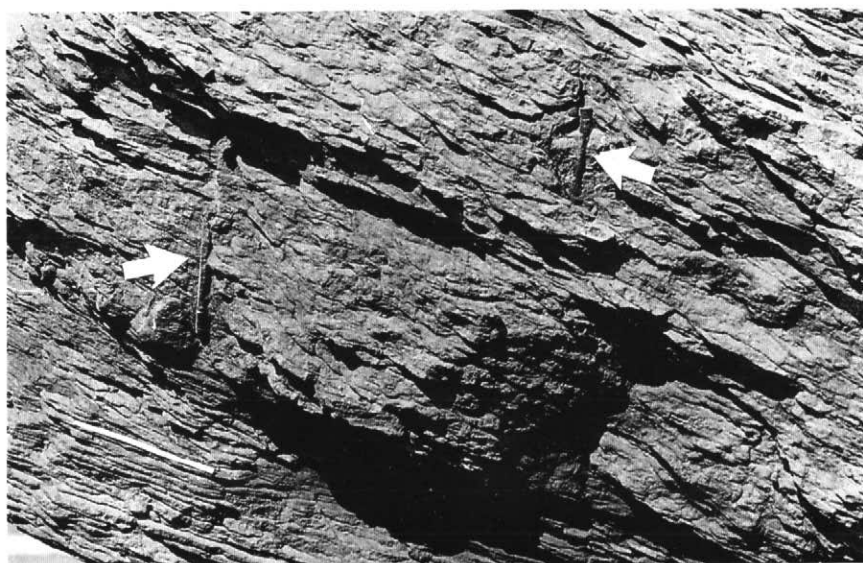
Figure 4 (left) Cleaved mudstones preserving two sub-vertically oriented crinoid stems (arrowed) from the shallow marine Siluro-Devonian Arisaig Group (Moydart Formation) of northeastern Nova Scotia. The fabric dipping from left to right represents the fracture cleavage. These crinoids are preserved in situ and suggest that a relatively thick mudstone blanket was deposited rapidly, thereby preventing disarticulation and reworking of the stems by wave and current activity. Bar scale = 5 cm.

Although we have emphasized the importance of taphofacies in the diagnosis of shelf regimes, taphonomy may yield important environmental information in a wide range of other environments. For example, a study of Cretaceous lagoonal sediments (Fürsich and Kirkland, 1986) showed how the taphonomy of shell beds reflected the energy conditions of the lagoon. Shell bed distribution, faunal distribution and faunal diversity all showed similar vertical changes in the sequence, reflecting changes in sedimentation rate, intensity of storm reworking and the salinity of the lagoon.

COMMUNITY/BENTHIC ASSEMBLAGE PALEOECOLOGY

A community (fossil community, paleocommunity, biofacies) refers to assemblages of organisms inferred to represent a distinct biological entity and normally related to a specific (paleo)environment. In the fossil record, a community is commonly represented only by remains of skeletized organisms because soft-bodied components, which can be an important constituent of such faunal groupings, are generally not preserved (see Lawrence, 1968). As a result, such faunal groupings have been referred to as associations rather than communities in both the fossil record (e.g., Watkins, 1979; Hurst and Pickerill, 1986) and Recent environments (e.g., Persson, 1982), though there is still no general agreement on the nomenclature. Several texts (e.g., Valentine, 1973; Parker, 1975; Scott and West, 1976; Boucot, 1981) have addressed such nomenclatural debates, but, for the purposes of this contribution, we refer to such groupings as communities.

Communities are normally recognized by rigorous sampling of the faunal elements followed by application, in increasing complexity, of univariate, bivariate or multivarate numerical analysis which, as recently summarized by Jones (1988) and Harper and Ryan (1990), can now easily be undertaken utilizing microcomputers. A vast array of benthic marine communities (and associations) have now been described from marine Phanerozoic siliciclastic sequences (e.g., Boucot, 1975; McKerrow, 1978; Gray et al., 1981). Typically, though not universally, these communities have been named after a group, genus or species characteristic of the particular community or after the habitat they occupied. The resultant proliferation of community names, particularly those described from Paleozoic strata, from where many pioneering studies were undertaken with respect to ancient sequences, prompted Boucot (1975) to conceive the term Benthic Assemblage (B.A.) for a group of communities that occurred repeatedly in different parts of a region and in the same position relative to shoreline. Boucot (1975) recognized six benthic assemblages, simply referred to as B.A.1 to B.A.6 inclusive (Figure

7), that he regarded as highly correlated to water depth (but which, he suggested, were also probably temperature controlled) and each of which contained different communities depending upon other environmental controls.

The pioneering work by Petersen (1913, 1915), who suggested that modern marine animals on level bottom clastic substrates of the Baltic Sea are distributed into several communities along an onshore to offshore gradient, provided a uniformitarian basis for paleoecological investigations into the environmental distribution of ancient marine communities. Thorson (1957) developed

Petersen's work and suggested that it was possible to distinguish broadly similar, though not taxonomically identical, parallel communities on a global scale. In contrast, other authors have emphasized the variability and patchiness of communities that may be strongly influenced by substrate (Bloom et al., 1972; Flint, 1981, amongst others). These different viewpoints are echoed in paleoecological studies, some of which emphasize the depth-related nature of benthic communities (e.g., Ziegler, 1965; Ziegler et al., 1968; Noble, 1976), whereas other workers note the complexity of ecosystems and urge restraint in emphasizing

Figure 5 *Articulated brachiopod shells preserved in situ within generally massive mottled silty mudstones of the Siluro-Devonian Arisaig Group (Moydart Formation) of northeastern Nova Scotia. Bar scale = 5 cm.*
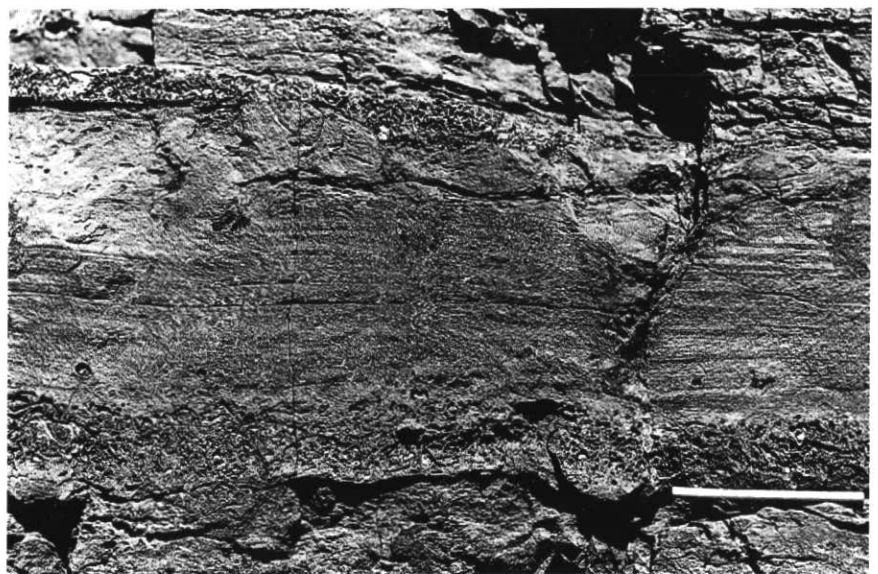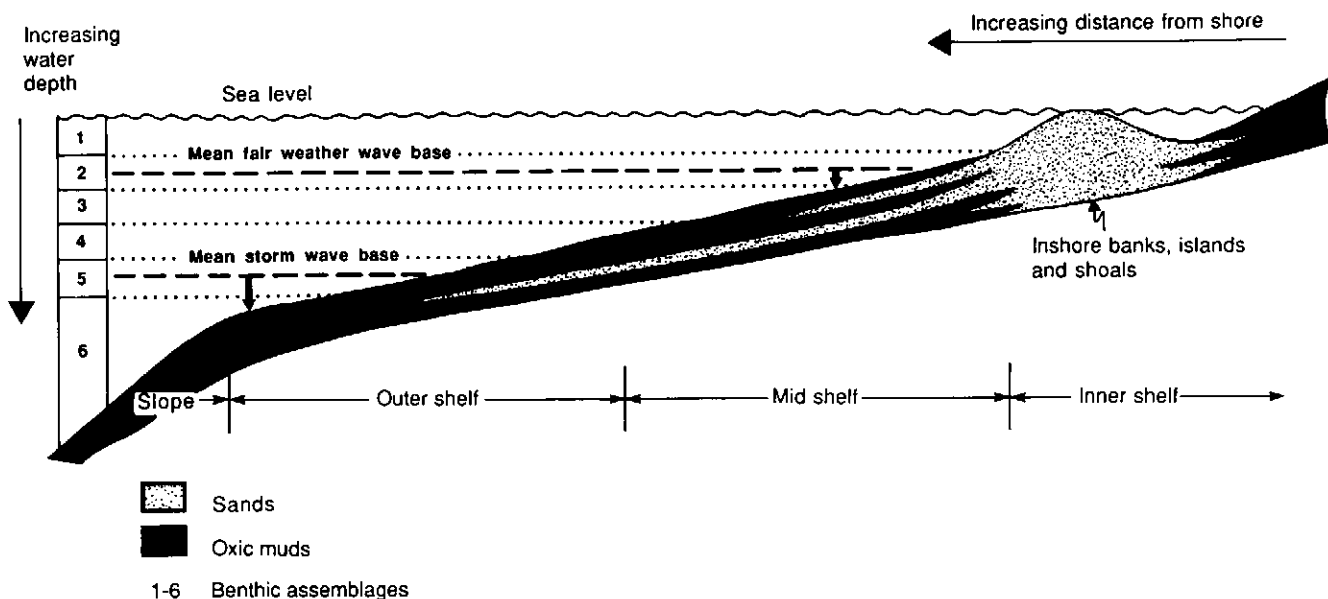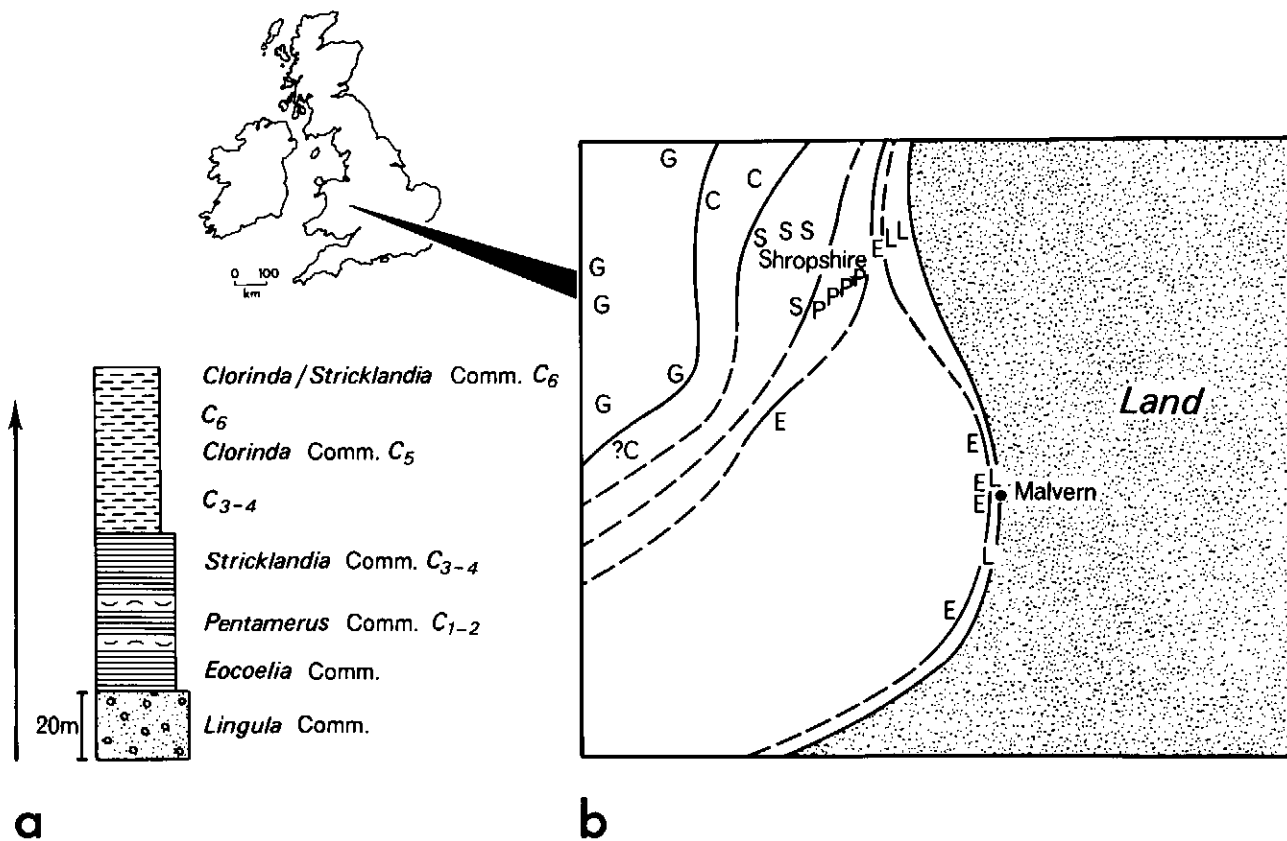

Figure 6 *Storm-influenced sandstone bed with a basal coquina infilling and directly overlying a scoured basal surface from the Siluro-Devonian Arisaig Group (Moydart Formation) of northeastern Nova Scotia. Bar scale = 5 cm.*

Increasing
water
depth

Increasing distance from shore

Sea level

Mean fair weather wave base

Mean storm wave base

Inshore banks, islands
and shoals

Slope → |← —————— Outer shelf —————— | —————— Mid shelf —————— | —— Inner shelf ——→

Sands

Oxic muds

1-6   Benthic assemblages

Figure 7 *Schematic representation of the depth-related Benthic Assemblages (B.A.) 1 to 6 of Boucot (1975) across a shoreline to slope profile. We have chosen an arbitrary water depth of ca. 100 m for mean severe storm wave base, though we do recognize it can be deeper as indicated by the solid arrow. Thus, we place mean severe storm wave base within B.A. 5 (cf. Baarli, 1988) whereas others (e.g., Möller, 1989) have placed it at the B.A. 4-5 transition. Eckert and Brett (1989) also note that severe storms would extend to B.A. 5, and that the "average" storm would affect B.A.3 and B.A.4 assemblages. Mean fair weather wave base is arbitrarily placed in a water depth of 5-15 m following Walker (1984a). Water depth estimates for B.A. 1-6 are difficult to assess realistically; however, those by Johnson (1987) are reasonable and are: B.A. 1, 0-10 m; B.A. 2, 10-30 m; B.A. 3, 30-60 m; B.A. 4, 60-90 m; B.A. 5, 90-120 m; B.A. 6, >120 m. The photic zone is placed at the lower boundary of B.A. 3 by Boucot (1975) and between B.A. 4 and 5 by Johnson (1987), Johnson et al. (1989) and Eckert and Brett (1989). Note that the position of the shelf break and the shelf width may vary considerably from 18 m to 915 m and from a few to more than 1000 km, respectively (Bouma et al., 1982). The interplay of shelf morphology, meteorological regime, magnitude of fluid energy, latitude, etc., will also determine mean storm and fair weather wave base.*

Clorinda / Stricklandia Comm. C_6

C_6

Clorinda Comm. C_5

C_{3-4}

Stricklandia Comm. C_{3-4}

Pentamerus Comm. C_{1-2}

Eocoelia Comm.

Lingula Comm.

20m

a

b

Figure 8 (a) *A schematic representation of the upper Llandovery succession on the Midland Platform, England. The upper Llandovery is divided into informal stratigraphic units C1 to C6. The beds with a Lingula community and an Eocoelia community at the base are not precisely dated. The community succession reflects progressive deepening from the base of the sequence to C5, with possibly slight shallowing into a mixed Clorinda/Stricklandia community at the top.*
(b) *A paleogeographic map for C1 times, showing the progressive distribution of a nearshore Lingula community to increasingly deeper Eocoelia (E), Pentamerus (P) and Stricklandia (S) communities and to a Clorinda community (C) at or near the platform edge. Graptolites (G) occur on the slope and inner margins of the basin floor.*

the simple correlation of community distribution with depth (e.g., Benedict and Walker, 1978; Watkins, 1979; Pickerill and Hurst, 1983).

The problem with adopting paleocommunities as environmental indicators is that the environmental position of each paleocommunity has to be initially correctly identified before it can be used as a paleoenvironmental guide elsewhere. The relationship between communities and environment is best established in transgressive or regressive sequences where, according to Walther's Law, the vertical succession of facies and faunas reflects the horizontal distribution of facies and biofacies at the time of deposition. This methodology is well exemplified by Ziegler's (1965) study of upper Llandovery communities in the Welsh Borderland of Great Britain, where communities are arranged in a regular vertical sequence in the transgressive Llandovery rocks and had a similar horizontal distribution across the Llandovery shelf in any one period of time (Figure 8). The pattern of community distribution identified by Ziegler (1965) and co-workers (Cocks, 1967; Ziegler et al., 1968) was relatively simple and was interpreted as being depth related. Other researchers, working in the Ordovician or in post-Llandovery time, more commonly recognized more complex community patterns (Bowen et al., 1974; Pickerill and Brenchley, 1979; Brenchley and Cocks, 1982) that were broadly depth related, but were also influenced by local facies variations. The variability of faunas, even within a single environment, has been noted by Cherns (1988), who emphasized the role of opportunistic species in dominating some assemblages and so increasing the heterogeneity of the community.

Based on their correlation with particular depth zones, the Llandovery communities have been widely used to identify depth changes in vertical sequences and to construct bathymetric curves for the Llandovery. On this basis, several deepening and shallowing cycles have been identified that appear to be of the same age on different plates (recorded in USA, Norway, China, etc.) and hence may be interpreted as eustatic (Rong et al., 1984; Johnson et al., 1985; Baarli, 1988). Until recently, the Ziegler model of depth-related communities had not been tested in any detail with respect to the sedimentological record. However, Baarli (1988) plotted independently communities and proximity trends for storm sandstones from the Silurian of Norway and found a good correlation.

Detailed studies of faunal change in the relatively uniform dark grey shale facies of the Devonian Hamilton Group (New York State) have been successful in identifying progressive faunal changes and periodic shifts that are interpreted as symmetrical deepening and shallowing cycles that are

recognizable basinwide (Brett et al., 1986). Depth changes indicated by the variations in diversity and taxonomic composition are supported by changes in the taphonomic nature of the shell concentrations (see Taphonomy).

Faunal gradients on a horizontal scale of tens of kilometres and a vertical scale of metres to tens of metres have been studied by Cisne and Rabe (1978) using gradient analysis. They suggested that, where communities intergrade along an onshore to offshore profile or in a vertical section, it is better to relate them to a continuous scale of

similarity (e.g., gradient analysis) rather than partition them arbitrarily into communities. In this study of faunas from the Ordovician Trenton Group of New York State, a good correlation between sections was effected by bentonites, and the relative abundance of different brachiopods and trilobites was shown to change laterally at each stratigraphic level (Figure 9a). The progressive shifts in faunal composition and faunal abundance were measured by gradient analysis using a variety of ordinations. The polar ordination position shown in Figure 9b is a method for ordinating samples on a scale of
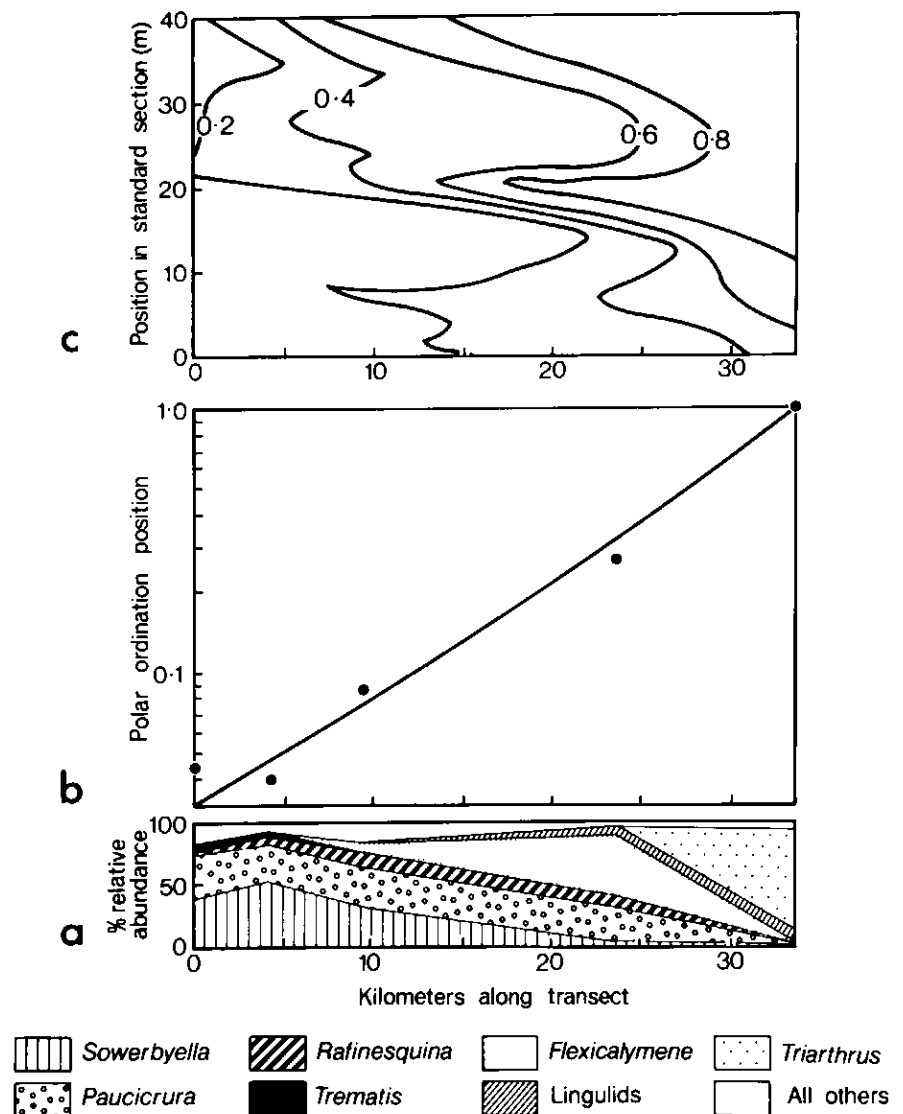

Figure 9 (a) Relative abundance of taxa along a time parallel transect, established using a bentonite marker horizon down a Middle Ordovician slope (Trenton Group, central New York, USA).

(b) Polar ordination position of points along the transect based on gradient analysis. The ordination curve is derived by direct polar ordination of samples with respect to replicate samples at each end of the transect (R = 0.0 km upslope and R = 33.6 km downslope). The ordination position reflects position along the depth gradient.

(c) Isocoene ("equal commonality") diagram for part of the Trenton Group, New York. The horizontal axis is the downslope transect, the vertical axis represents a standard vertical section through the sequence. The solid lines are positions of equal ordination values. Low ordination values represent upslope faunas; high values, deeper downslope faunas. The curves show the changing distribution of faunas in space and time, from which depth changes can be inferred (for further details, see Cisne and Rabe, 1978).
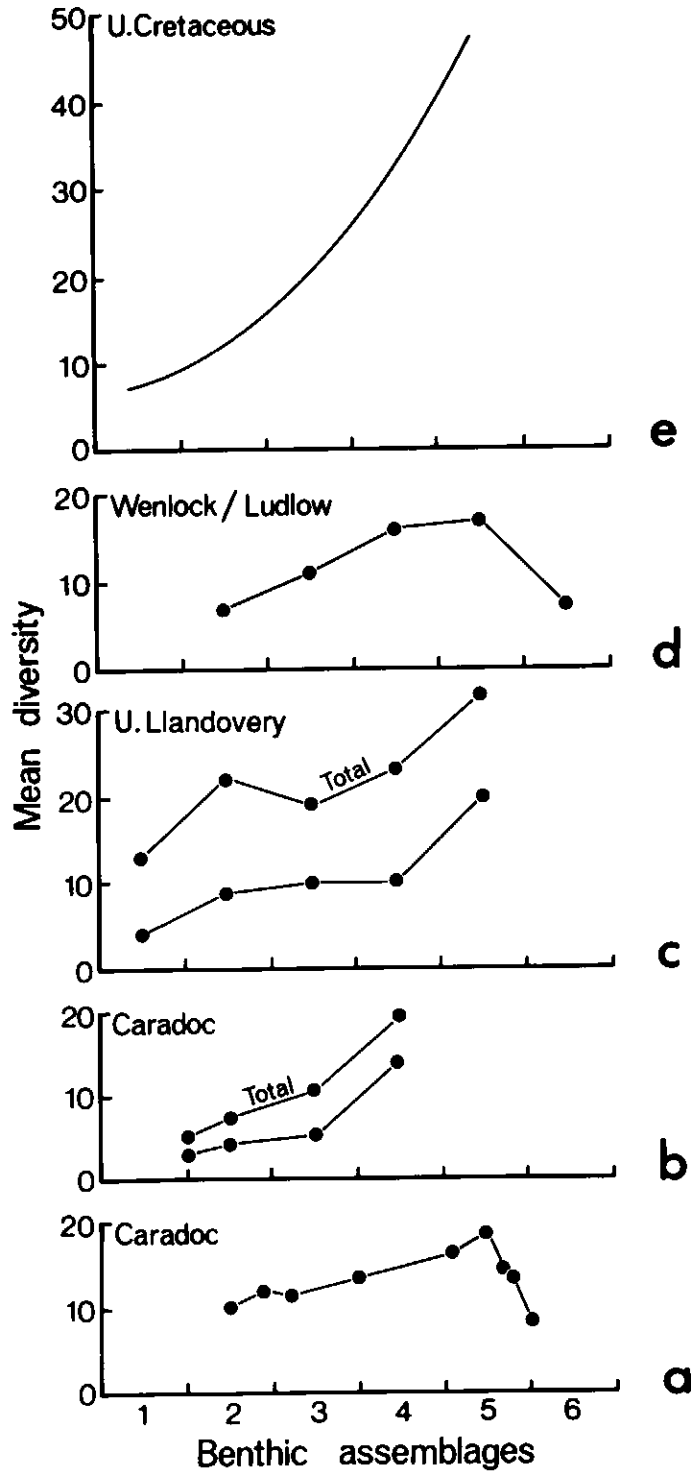
Figure 10 *Variation in diversity, measured as number of species in benthic assemblages across ancient shelves.*

(a) *Brachiopod diversity in the Caradoc (Hurst, 1979).*

(b) *Brachiopod and total diversity in the Caradoc (Pickerill and Brenchley, 1979).*

(c) *Brachiopod and total diversity in the upper Llandovery (Cocks and McKerrow, 1984).*

(d) *Brachiopod diversity in the Wenlock/Ludlow (Calef and Hancock, 1974).*

(e) *Total macrofaunal diversity in Campanian to Maastrichtian sequences of Seymour Island, Antarctica (Macellari, 1988). The data of Macellari were not referred to benthic assemblages, so have been drawn as a smooth curve for the range of the diversity data which came from a spectrum of nearshore to offshore environments.*

0 to 100 according to their similarity values relative to two endpoint members (*see* Cisne and Rabe, 1978, p. 354). Polar ordination values derived from faunas at several stratigraphic levels are shown in Figure 9c, which demonstrates both the lateral gradients and the shifts of these gradients with time that define deepening and shallowing cycles. It can be seen that, in favorable circumstances, gradient analysis is a powerful tool for the investigation of vertical and lateral faunal change and the position of faunas within that spectrum.

The epifaunal benthic faunas of the Paleozoic seem to provide a clearer relationship between depth and community type than the mollusc-dominated faunas of the Mesozoic and Tertiary that appear to be more influenced by the nature of the substrate (*e.g.*, Hallam, 1976; Fürsich, 1976). Nevertheless, there are taxonomic differences between nearshore and offshore communities (*e.g.*, Hallam, 1976) and the overall increase in diversity from nearshore to the deep shelf widely recognized in the Paleozoic seems to hold for the Mesozoic (Macellari, 1988).

DIVERSITY AND BIOMASS GRADIENTS IN BENTHIC FAUNAS

In spite of the variability of ecosystems, it is possible to identify general gradients in benthic assemblage or community characteristics along a nearshore to offshore transect. One important cross-shelf gradient is that of faunal diversity. Diversity is the number of species forming a community and living in a particular area of the shelf. Unfortunately, the total population is never completely sampled by either the marine biologist or the paleontologist, and the number of species in a collected sample is seriously affected by sample size, *i.e.*, larger samples will generally have more species than smaller ones. Various corrections for sample size have been used in paleontological studies, but one commonly used diversity index is

$$D = \frac{S-1}{\log N} ,$$

where S = number of species in the sample and N = number of specimens. Magurran (1988) has provided a useful summary of the extensive literature on the measurement of diversity and on other indices that have been proposed, their properties, and their relative measurements.

In siliciclastic strata, several studies of Ordovician and Silurian benthic communities, particularly the brachiopod component, have demonstrated a progressive increase in diversity across the shelf and then a rapid decrease at the shelf margin (Figure 10). The shape of the diversity curve depends upon the taxonomic group studied, though detailed data are not generally available. Peak diversity amongst rugose corals appears to be in the mid-shelf region, while the diversity of trilobites remains high at least to the shelf edge (Ludvigsen, 1975,

1978). A similar trend has not been widely identified in the Mesozoic, but Macellari (1988) showed a broadly similar diversity change in Late Cretaceous siliciclastic sediments (Figure 10). Onshore to offshore diversity trends are interpreted to be a response to progressively more stable environments in an offshore direction (Sanders, 1968). According to this interpretation, diversity should remain high into deep-basin water rather than decreasing sharply at the shelf edge as it does in the Paleozoic. It has been shown that modern faunas do have a high diversity to depths as great as 4500 m, but although diversity starts to decrease at depths greater than 2000-3000 m, they have a low abundance (*i.e.*, number of individuals) and biomass (Sanders and Hessler, 1969), probably because nutrients are in small supply. Nutrient supply may have been a more severe limiting factor in the past and there is evidence that many groups have colonized deeper water environments later in their evolutionary history (Jablonski et al., 1983).

Diversity not only changes with depth but also with latitude. In general, species, genera and family diversity decrease from the tropics to the polar regions (Fischer, 1960; Stehli, 1968), though there may be considerable deviations from this simple pattern. Although exceptions do exist, the presence of low diversity shelf faunas in successions lacking limestones is an indication that the sediment may have been deposited in high latitudes.

In general, biomass (the amount of living material in a particular area, stated in terms of the weight or volume of organisms per unit area or of the volume of the environment) exhibits a decrease with distance offshore and with water depth, to show very low values in abyssal waters (see Levinton, 1982, p. 384). The main exception to this pattern is the rich and varied faunas found around volcanic vents and "smokers" in deep water over mid-oceanic ridges. The distribution of biomass in marine waters is reflected amongst fossil assemblages by fossil-rich benthic faunas from nearshore zones. The distribution of faunas in nearshore facies can, however, be patchy because very mobile substrates, particularly those associated with migrating dunes, are typically almost devoid of living organisms (Wilson, 1986). Biomass remains relatively high in hospitable environments out to the mid-shelf, whence it declines with depth so that outer shelf faunas tend to be sparse even though they may be highly diverse.

IDENTIFICATION OF SPECIFIC ASPECTS OF THE ENVIRONMENT

The distribution of species in the ecosystem is controlled by many physical and biotic parameters and Hedgpeth (1957), Boucot (1981), Gall (1983) and Robertson (1989), amongst others, have provided reviews of several of these environmental factors. Nor-

mally, the controls are complex and a species will live within certain ranges of the absolute values of many of these parameters and will also be affected by biological interaction with other species (*e.g.*, Tevesz and McCall, 1983). A wide range of physical parameters controls the environmental distribution of a species. Where a particular parameter starts to approach or exceed the limits of tolerance of the species it is said to be a "limiting factor". In general, it is difficult to isolate any one influence on the distribution of a species or community, but in special circumstances one constraint may be paramount. In these circumstances, certain species or species associations may help to identify particular, usually extreme, conditions, such as those found in hypersaline or dysaerobic environments.

Some environmental parameters, such as turbulence and substrate, can be evaluated from field observations. Turbulence is an extremely important environmental parameter with respect to the distribution of species or communities, as reflected in Boucot's (1975) subdivision of (particularly) B.A.1 to B.A.3 inclusive into "quiet water" and "rough water" assemblages. Substrate, and its overall characteristics, is also an important limiting factor, though its exact role in determining species or community distributions is imperfectly understood in most instances and has been disputed by both marine ecologists and paleoecologists (*see* McCall and Tevesz, 1982; Brenchley and Pickerill, 1991).

Other limiting factors cannot be easily inferred from direct observation, but can be assessed by careful analysis of macrobenthos (or traces of their activity) in marine siliciclastic facies. We consider the more important of these to be light, salinity, oxygen, temperature, sedimentation rates and water depth, each of which is considered below.

Light
Light is an extremely important environmental parameter as it controls primary productivity and hence the availability of organic matter to the food chain. In present-day seas, the depth to which light penetrates the water column, the photic (or euphotic) zone, depends principally on latitude and turbidity. In 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 (Farrow, 1990). Light is obviously a physical parameter that is extremely difficult for the paleontologist to estimate and all that can be assessed realistically is whether or not faunas inhabited the photic as distinct from the subphotic (or aphotic) zone (Boucot, 1981).

Although more rarely observed in siliciclastic strata compared to their carbonate equivalents, the following may be regarded as indicative of the photic zone:

(i) The presence of benthic marine algae as a result of their primary requirement of light as an energy source for photosynthesis. Calcareous green algae (*e.g.*, dasyclads) absorb more strongly in the red part of the spectrum than red algae (rhodoliths), which are adapted to blue-green wavelengths; the former are therefore indicative of bathymetrically shallower conditions within the photic zone (Farrow, 1990).

(ii) The presence of endolithic microborings as a result of symbiotic algal infestation of calcareous exoskeletons. Marine-boring algae normally flourish in extremely shallow waters of the littoral zone. In progressively deeper waters, the abundance and diversity of algal microborings markedly decrease, until the compensation depth of algae (depth at which photosynthesis equals respiration, *i.e.*, lower level of the photic zone) is approached. Within the photic zone, endolithic algal microborings may also exhibit bathymetric zonation, different types characterizing particular water depths (Golubic et al., 1975). Useful reviews of algal microborings are provided by Bromley (1970), Golubic et al. (1975) and Kobluk and Kahle (1978).

(iii) The presence on the surface of shells of distinctive grazing patterns produced by organisms feeding on photosynthetic algae infesting those shells. These grazing marks have been given specific ichnogeneric names which include *Gnathichnus* Bromley, produced by regular echinoids, and *Radulichnus* Voigt, produced by gastropods or chitons (*see* Bromley, 1975; Voigt, 1977).

(iv) The presence of colour patterns (dots, stripes, concentric banding, zig-zags), which are very common in calcified marine organisms in today's oceans and are essentially restricted to the photic zone (Boucot, 1981; Blodgett et al., 1988), particularly, though not exclusively, in tropical marine waters. Such patterns have been recorded from many invertebrate phyla from Mesozoic and Cenozoic sequences, but also from Paleozoic strata, as recently reviewed by Kobluk and Mapes (1989).

We emphasize that, particularly in siliciclastic facies, these features are not universally developed and their exclusion does not necessarily indicate formation of strata in the subphotic zone. Being rather uncommon in siliciclastic sequences, it is the presence of one or more of these features rather than their absence that is more important and indicative of photic zone conditions.

Salinity
Evidence for salinity levels tending toward hypersalinity at one extreme or brackish water at the other (*see* Figure 11 for a classification of salinity levels) comes from comparison with modern coastal faunas or from shell geochemistry. Most marine animals are marine stenohaline, in other words, they are restricted to a narrow salinity range. Such groups as corals, cephalopods, articulate brachiopods, echinoderms, bryozoans, and

planktic and larger benthic foraminifers are rarely found outside normal marine waters and when found fossilized together are good indicators of normal marine salinities. Brackish waters are virtually universally inhabited by faunas dominated by bivalves, gastropods, ostracodes and smaller benthic foraminifers and characteristically exhibit low diversities. The members of a brackish fauna are typically normal marine species that are euryhaline (have a broad salinity tolerance) and so can tolerate brackish water, though are not confined to it. The identification of brackish water conditions from fossil assemblages must therefore be made with some caution because low diversity marine faunas, though common in areas of reduced salinities, can also occupy some nearshore environments with normal marine salinities (Barnes, 1989). Relatively few animals have adapted to a freshwater environment, but those that have are typically stenohaline. Most Mesozoic and Tertiary freshwater faunas are broadly similar taxonomically to modern equivalents. Lagoonal and estuarine brackish environments are commonly nutrient-rich and faunas can be very abundant. Because these nearshore environments are very variable geographically and temporally, the preserved facies commonly reflect different environments with different salinity levels, and faunal sampling needs to be closely spaced.

Faunal evidence of brackish or fresh water can be supported by stable isotope data

using unaltered shell material, based on the assumption that the shell carbonate was precipitated in equilibrium with the ambient water (see Dodd and Stanton, 1990, for a review). $^{18}O/^{16}O$ values in normal seawater are relatively constant (-1‰ to 0‰), but will deviate from zero in brackish or hypersaline waters. In general, meteoric water is depleted in ^{18}O (-3‰ in humid sub-tropics) so $^{18}O/^{16}O$ values in brackish water are low; however, this generalization must be treated with some caution because evaporation of fresh water can preferentially remove ^{16}O and hence increase the $^{18}O/^{16}O$ ratio in some humid freshwater lakes. Dissolved bicarbonate in seawater is normally ^{13}C rich relative to ^{12}C. Bicarbonate in rivers and lakes usually contains bicarbonate derived from ^{12}C-rich organic material so brackish waters and fresh waters tend to have a low $^{13}C/^{12}C$ ratio (Mook, 1971).

The taxonomic uniformitarian approach to paleosalinities appears to be broadly valid in post-Paleozoic time, but should be applied with extreme caution to Paleozoic faunas. The isotopic composition of Paleozoic seawater may have been different (Hudson, 1990), so the stable isotopic composition of shell material can only be used with caution.

Oxygen

Ecologists have particularly emphasized the importance of oxygen availability with respect to the distribution of marine benthic organisms. Unfortunately, there is no direct method to measure oxygen levels immedi-

ately above or below the sediment-water interface in the ancient record. Generalities can, however, be made by employing faunal and ichnofaunal data, providing these data are employed in conjunction with sedimentological observations. The oxygen content of seawater varies between 0 mL•L^{-1} and 8.5 mL•L^{-1}, being mainly in the range of 1 mL•L^{-1} to 6 mL•L^{-1} (Thompson et al., 1985). Currently, five oxygen-related zones or biofacies are recognized in both modern and ancient marine sequences. These, and their diagnostic characteristics, are (see Rhoads and Morse, 1971; Byers, 1977; Savrda and Bottjer, 1986, 1987, 1989; Bottjer and Savrda, 1990):

Aerobic (> 1.0 mL•L^{-1} O$_2$). Contains diverse assemblages of relatively large calcified body fossils and strata are intensely bioturbated by infaunal biota.

Dysaerobic (0.2-1.0 mL•L^{-1} O$_2$). Contains low diversity assemblages of small, less heavily calcified body fossils or, toward lower O$_2$ values, benthic faunas may be absent. Trace fossils or bioturbation are typically present.

Exaerobic (0.1-0.2 mL•L^{-1} O$_2$). Recently defined by Savrda and Bottjer (1987) for strata deposited transitional to the dysaerobic/anaerobic boundary. Characterized by laminated, non-bioturbated strata with anomalous occurrences of shelly faunas.

Anaerobic (<0.1 mL•L^{-1} O$_2$). Macrobenthos absent, though benthic microfauna such as foraminifera may be present in addition to subtle microbioturbation of essentially varve-like primary lamination.

Anoxic (no O$_2$). No in situ macrobenthos or microbenthos, no bioturbation, delicate varve-like primary lamination preserved.

Strata deposited in anaerobic or anoxic conditions will therefore contain no in situ macrobenthos, no megascopic bioturbation or trace fossils and will be delicately laminated. Such strata, typically, but not universally, black shales, may, however, possess preserved remains of nektic, planktic and epiplanktic fossils or benthic organisms introduced by sediment gravity flows. Interestingly, Wignall and Simms (1990) have recently reviewed Phanerozoic pseudoplankton reported from black shale sequences and have re-interpreted many examples as truly benthic forms that were opportunistic colonists, exploiting slightly and temporarily increased oxygen levels within generally anoxic environments. Such occurrences may therefore be indicative of exaerobic or largely dysaerobic conditions. Characteristically, anaerobic or anoxic sediments will possess high free carbon, pyrite and organic material (Boucot, 1981), as well as elevated authigenic uranium values (Wignall and Myers, 1988). Anoxic biofacies may be distinguished from anaerobic biofacies by the absence in the former of in situ microfossils and microbioturbation (Bottjer and Savrda, 1990). At the opposite end of the spectrum, aerobic biofacies will be charac-
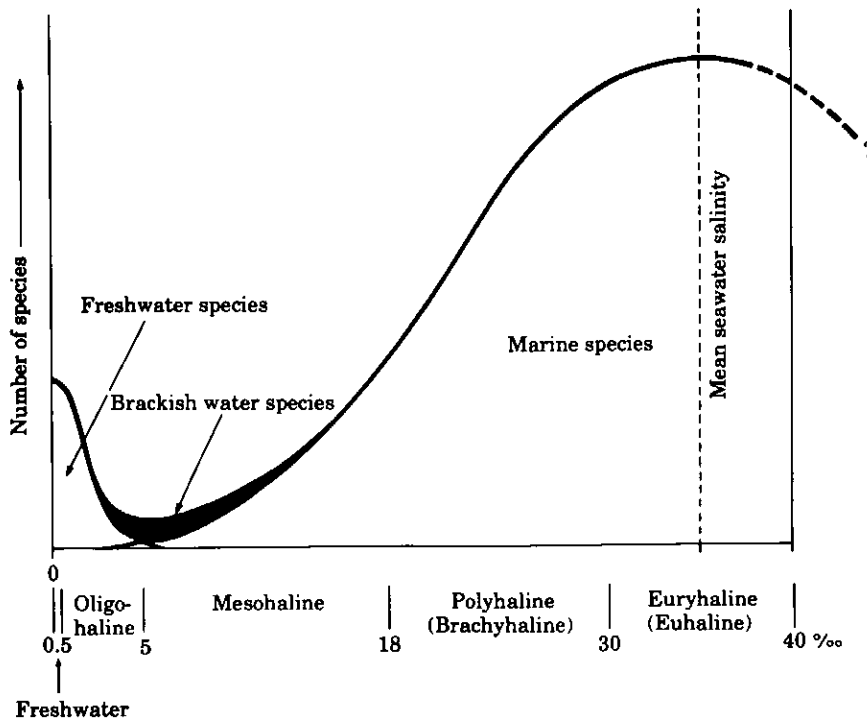
Figure 11 *Classification of salinity levels and generalized relationship of species diversity with respect to salinity. Note that brackish and freshwater faunas are of low taxonomic diversity and the diversity of marine species increases as salinity values increase and peaks at average seawater salinity levels (modified from Hudson, 1990).*

terized by abundant and diverse epifaunas and infaunas and both bioturbation and discrete ichnofaunas will be common. Bioturbation may be so intense that primary sedimentary fabrics are completely destroyed and the sediment is effectively homogenized.

The presence or absence of macrobenthos and biogenic structures, particularly in fine-grained siliciclastic strata, can therefore be a definitive indicator of paleo-oxygen levels as, respectively, aerobic or anaerobic/anoxic. The recognition of dysaerobic biofacies in the ancient record is, however, more problematic. Dysaerobic biofacies, when originally defined by Rhoads and Morse (1971), were believed to be dominated by soft-bodied infaunal organisms of low species richness capable of producing extensive bioturbation, in addition to low diversity assemblages of poorly calcified organisms. However, based on a modern study of macrobenthos from offshore central California, Thompson et al. (1985) demonstrated the presence of calcareous faunas associated with highly bioturbated sediments deposited in waters with oxygen levels down to 0.3 mL•L^{-1}. Between 0.1 mL•L^{-1} and 0.3 mL•L^{-1} dissolved oxygen occurred in a zone possessing soft-bodied infaunal organisms, consistent with the proposal of Rhoads and Morse (1971). Thus, while it still remains true that, under decreasing oxygen conditions in the dysaerobic biofacies, a gradual reduction in species richness, biomass and body size will occur concomitant with the gradual disappearance of calcified organisms (Rhoads and Morse, 1971; Thompson et al., 1985), the absolute values of dissolved oxygen with respect to these patterns still remain to be more accurately defined. Furthermore, data provided by Thompson et al. (1985) suggest that employing characteristics of the macrobenthos alone to recognize dysaerobic biofacies in the ancient record must be undertaken with caution.

An attractive alternative approach has been provided by Savrda and Bottjer (1987, 1989) who, based on the original predictions by Rhoads (1975), have utilized various aspects of ichnology to evaluate the relative degree of oxygenation within the dysaerobic biofacies (see also Bromley and Ekdale, 1984; Jordan, 1985). Utilizing both modern and ancient settings in clastic sequences, these authors have demonstrated that trace fossil diversity, burrow size and penetration depth all decrease with decreasing levels of oxygen concentration. This approach is particularly useful in vertical successions as it can be employed to demonstrate both long- and short-term temporal fluctuations in oxygen levels, which are commonplace in both basinal and relatively shallow-water epeiric seas (Wignall and Myers, 1988). Further research is, however, required with respect to these particular aspects of ichnology, as similar patterns of decreased size and diversity of trace fossils have also been correlated to

reduced salinity rather than oxygen concentrations (Hakes, 1985).

Finally, the exaerobic zone or biofacies of Savrda and Bottjer (1987) is an extremely subtle subdivision of the redox continuum and, in most instances, may well be difficult to recognize in the ancient record. It may, however, provide a reasonable explanation for the occurrence of calcified organisms in laminated, non-bioturbated strata that are interlayered with lithofacies indicative of temporally fluctuating anaerobic and dysaerobic conditions (see Savrda and Bottjer, 1987, fig. 1, p. 54).

Temperature

Factors influencing the vertical, geographic and temporal distribution and variation of temperature in today's oceans are extremely complex (e.g., Kennett, 1982) and presumably were equally so in the past. The influence of temperature on a particular species is equally as complex and affects organisms in a variety of ways, such as inducing death at different values and affecting reproduction, larval success and competition (Boucot, 1981). An approximate index of paleotemperature can be made utilizing the relative diversity of macrobenthic faunas occurring within a typical marine assemblage. For example, Parker (1964) found from five to ten times the number of species on tropical level bottoms than were found on cold climate bottoms. More accurate and realistic estimates of paleotemperatures can be made by utilizing well-preserved calcified organisms and determining the $^{18}O/^{16}O$ ratios. Such ratios are based on the premise that the difference in $^{18}O/^{16}O$ ratios of calcium carbonate and the water from which it precipitates is a function of temperature. There are,

however, many difficulties and assumptions involved in such procedures (Savin, 1977, Shackleton, 1984; Anderson, 1990). The $^{18}O/^{16}O$ ratio of seawater has probably changed over Phanerozoic time (Hudson, 1989; Anderson, 1990) and has certainly fluctuated markedly during glacial to interglacial intervals. The latter is more a result of changing ice volume and the resultant change in ocean water composition than it is a result of temperature change (Shackleton and Opdyke, 1973). Further, cemented or partially recrystallized fossils will give erroneous values because secondary carbonates reflect the temperature and isotopic composition of diagenetic solutions. Dodd and Stanton (1981) have provided a number of criteria that can be utilized to detect such alteration. As also noted by Parker (1979), it is important to have some knowledge of the paleoautecology of the organisms being studied as, for example, it would be erroneous to base average paleotemperatures on forms that might have been fresh water, brackish, or more intertidal than subtidal in habitat. Consequently, a significant degree of controversy still remains concerning interpretation of oxygen isotope data and there are several areas of uncertainty, so that even specialists cannot agree with each other (Shackleton, 1984).

Despite the inherent difficulties, a vast literature has now accumulated on paleotemperatures, particularly from Tertiary and Late Cretaceous siliciclastics from Deep Sea Drilling Project cores, utilizing isotopic data obtained from both planktic and benthic foraminifera. As noted by Anderson (1990), diagenetic alteration of foraminiferal tests is minor and relatively easy to determine microscopically and therefore these taxa are
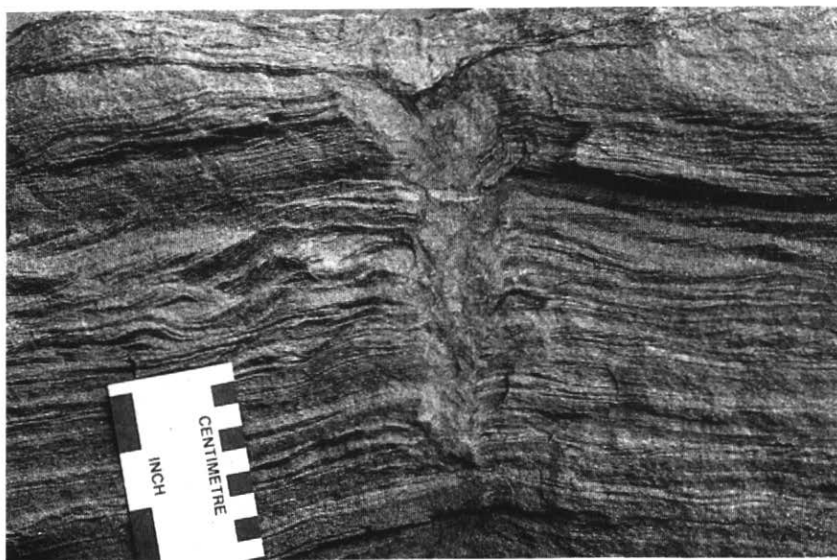
Figure 12 Example of an "escape structure" or Fugichnion from a tempestite in the Carboniferous Albert Formation of New Brunswick. As with many other previously described or figured Fugichnia, this structure is interpreted as having been produced by a bivalve migrating vertically in response to rapid sedimentation.

ideally suited for isotopic analysis. Paleo-temperature estimates have also been made utilizing a variety of macrofaunas, most commonly molluscs (particularly belemnites and bivalves) and brachiopods (see Dodd and Stanton, 1981, table 3.2, p. 172).

Sedimentation Rates

There has been increasing awareness in recent years that rates of deposition are both variable and episodic and that there are frequent hiatuses in sedimentary successions. Nevertheless, it is usually difficult to be precise about either sedimentation rates or the amount of time unrepresented by sediment at an hiatus. The recognition that many sandstone beds in shelf sequences can be interpreted as tempestites, deposited from storm-generated flows, has identified these units as being rapidly deposited, probably over a period of hours to days. It is the intervening mud intervals that are more difficult to evaluate. The analysis of shell concentrates (see Taphonomy) has provided a qualitative basis for recognizing rapidly accumulated beds from complex beds repeatedly winnowed over "a long period of time". Various authors have reported fossils that seem to have been partly buried in mud within their own lifetime (Figure 4), and Parsons et al. (1988) provide interesting evidence that rapidly deposited mud blankets are common. On the other hand, slow sedimentation rates are reflected by shell material that is bored or encrusted post mortem by other organisms or has associated authigenic glaucony (sensu Odin and Matter, 1981), phosphate or iron minerals.

Relative sedimentation rates can also be broadly assessed by examination of the degree of disturbance of primary sedimentary fabrics by organism activity, i.e., bioturbation. The relative degree of bioturbation has been classified by Droser and Bottjer (1986) in terms of ichnofabrics (bioturbate textures) varying on a scale from one, non-bioturbated, to six, completely bioturbated. In general, increased bioturbation reflects progressively slower sedimentation rates, but the reverse may not hold true, because other environmental parameters, such as low oxygen levels, may preclude habitation by benthic faunas so that even though sedimentation rates may be slow there will be no bioturbation. Extremely high rates of deposition can be inferred by the presence of "escape structures" or Fugichnia (see Ekdale et al., 1984), which are generally interpreted as structures formed by the upward movement of infaunal organisms in response to rapid burial (Figure 12).

Water Depth

The depth of deposition of marine siliciclastic facies has always held great interest for sedimentologists and paleontologists, and a variety of approaches, including both macrofaunal and ichnological studies, has been utilized in order to provide an assessment (e.g., Hallam, 1967). For benthic organisms,

water depth is a passive factor and is unlikely to have limited their distribution during life. Nevertheless, other critical "limiting factors", such as wave energy, light and temperature, commonly exhibit a broad correlation with depth and therefore, in a broad sense, qualitative and even semi-quantitative estimates of water depth can be made by utilizing benthic macrofossils. Caution must, however, be exercised in employing single species or types of organisms, extinct or extant, as many taxa have a broad bathymetric distribution (Figure 13) and are restricted in their occurrence by one or several limiting factors rather than water depth per se. As an example (and there are many others), in the 1950s and 1960s, in situ infaunal lingulid brachiopods were considered by both ecologists and paleoecologists as indicative of intertidal or shallow subtidal conditions. Subsequent research, however, in both Recent (e.g., Emig et al., 1978) and ancient (e.g., Cherns, 1979; Pickerill et al., 1984) successions has extended their bathymetric range to include outer shelf, slope and even basinal environments.

A more attractive approach to estimating paleobathymetry is the utilization of communities or benthic assemblages whose semi-quantitative depth ranges are indicated in Figure 7. As discussed previously, however, taphonomic information must initially be carefully assessed, and application of the community or benthic assemblage paradigm must then proceed with care. For example, following careful sedimentological and taphonomic analysis, Pickerill and Hurst (1983) described faunal associations that elsewhere are more typical of Benthic Assemblage 1, occurring seaward and in presumed deeper water than faunas of Benthic Assemblage 2 from the Llandovery (Silurian) of Nova Scotia.

An alternative approach was provided by Seilacher (1964, 1967), who, as reviewed by Frey and Pemberton (1984), formulated a series of spatially and temporally recurring and broadly depth-related ichnofacies, each named after a characteristic trace fossil genus (ichnogenus). Since the original research by Seilacher, nine, and possibly ten (see Lockley et al., 1987), recurring ichnofacies are now recognized (Frey et al., 1990; Bromley and Asgaard, 1991). In the marine realm, seven ichnofacies typify soft or firm substrates and, providing caution is exercised, can serve as broad paleobathymetric indicators. These are (see Frey and Pemberton, 1984; Frey et al., 1990; Bromley and Asgaard, 1991):

Psilonichnus ichnofacies (supralittoral to moderate- or low-energy marine). Typically, a coastal, low diversity, but variable density, assemblage of vertical suspension- or deposit-feeding burrows produced essentially by crustaceans As noted by Bromley and Asgaard (1991), however, this ichnofacies is ecological and its usefulness as a paleo-

environmental indicator has yet to be fully tested.

Glossifungites ichnofacies (firm, unlithified omission surfaces, commonly littoral and shallow sublittoral, but bathymetrically variable and more dependent on the presence of firm substrates). Low density, vertical cylindrical, U-shaped or protrusive spreiten-bearing burrows.

Skolithos ichnofacies (littoral to infralittoral). Low diversity, but commonly high density, vertical or U-shaped dwelling burrows produced essentially by suspension feeders. The ichnofacies characterizes environments of high hydrodynamic energy and low environmental predictability.

Cruziana ichnofacies (infralittoral to shallow circalittoral). High diversity and abundant, vertical and horizontal feeding and grazing traces produced by vagile deposit feeders in lower energy and more stable and predictable environments.

Zoophycos ichnofacies (circalittoral to bathyal). Low diversity, commonly high density, grazing and feeding traces produced by deposit feeders resulting in relatively deep horizontal, vertical to inclined spreiten structures. The ichnofacies develops in soft substrates in environmentally stable situations.

Nereites ichnofacies (bathyal to abyssal). High diversity, low density assemblages of geometrically complex horizontal grazing traces and patterned feeding-dwelling structures produced by deposit feeders, scavengers or harvesters.

Arenicolites ichnofacies (infralittoral to bathyal). High density, low diversity, vertical or U-shaped burrows produced by pioneering opportunists in event beds (storm or turbidite sands) in normally incongruous environments. This ichnofacies was recently defined by Bromley and Asgaard (1991), who discuss differences from the taxonomically similar Skolithos ichnofacies.

Although these ichnofacies are broadly applicable in assessing water depth, most ichnologists now agree that they are best viewed in the context of actual depositional conditions or environmental gradients where they occur (Frey et al., 1990) and are not necessarily universally related to paleobathymetry (Bromley and Asgaard, 1991). Therefore, one should not be surprised to find nearshore or shallow-water ichnofacies in offshore or deeper water strata (e.g., Crimes, 1977), and vice versa (e.g., Bjerstedt, 1988), if these accumulated under conditions otherwise like those preferred by the trace-making organisms (Frey et al., 1990) and other environmental parameters (e.g., substrate consistency, hydrodynamic regime, salinity, etc.) were of more critical importance than water depth per se. Nevertheless, the relative scale of bathymetry has proven useful in numerous applications and the ichnofacies concept works well in most situations.

CONCLUDING REMARKS

Paleoenvironmental analysis of marine silici-clastic strata is ideally best achieved by consideration of all sedimentological, geochemical, paleontological and ichnological data and the spatial and temporal distribution of these data within the particular rocks under consideration. The quality and availability of these data do, however, vary considerably in siliciclastics so that, for example, it is not uncommon to encounter successions that are devoid or virtually devoid of benthic macrofossils and interpretations must be made utilizing alternative information. Conversely, however, in other situations, macrofossils are common or abundant and, as previously discussed, can provide important details on several aspects of the paleoenvironment.

In the previous sections, we have attempted to outline the kind of information that macroinvertebrate fossils can yield about the environment. In this final section, we propose a broad methodology for analyzing fossiliferous beds in siliciclastic sequences and how particular environments might potentially be identified. Prior to any detailed analysis of fossil assemblages, it is important to appreciate their actual position within a siliciclastic lithofacies sequence and the nature of the particular lithofacies in which they occur. This involves the standard procedures of facies analysis as described in detail elsewhere (e.g., see Walker, 1984b; Anderton, 1985). In extremely favourable circumstances, the lithofacies will yield reasonably unequivocal evidence of the depositional environment; however, where the lithofacies do not yield diagnostic evidence, hopefully fossils may provide important information regarding environmental interpretations.

Normally, the first consideration is that of the taphonomy of the assemblage, as it is important to determine whether the fossils are in situ life assemblages, disturbed neighbourhood assemblages, or substantially transported assemblages. The nature of the shell concentration (the taphofacies) will provide important information about the hydrodynamics of the environment, rates of accumulation, etc.

The second important consideration is the identification of the component taxa within the assemblage. The more precise the identifications are (ideally to species level), the more information can be extracted from the assemblage. Nevertheless, quite crude tax-
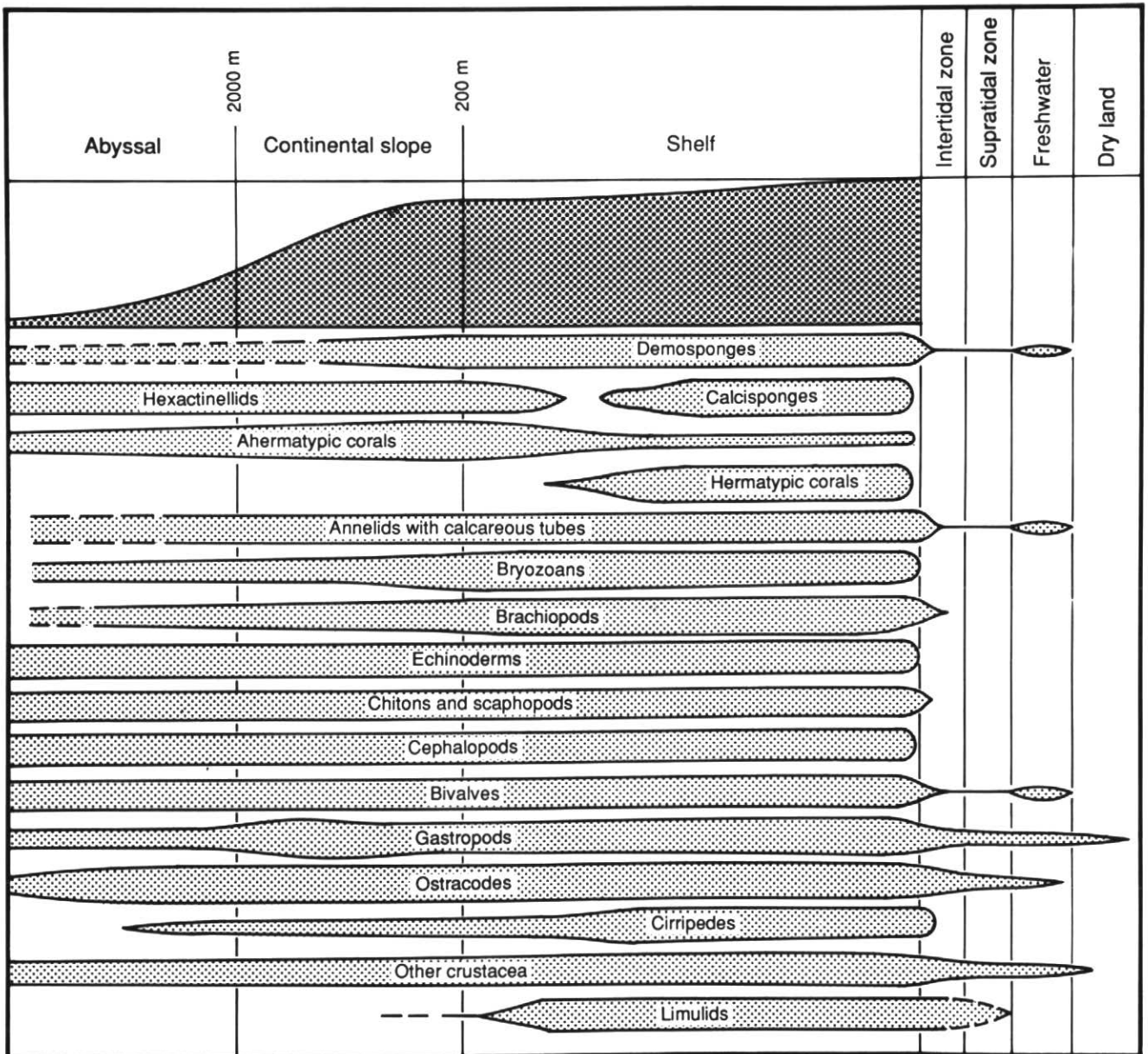

Figure 13 Bathymetric distribution of present-day macroinvertebrates. (Modified from Heckel, 1972).

onomy can also yield useful information and the taxonomic composition of the assemblage can be analysed in different ways:

(1) It can be utilized to define or recognize a particular community. If other comparable community studies have been completed on rocks of a similar age, the defined community may well identify a particular benthic assemblage and hence its relative location on the shelf.

(2) The dominance of particular groups of taxa may also be significant. For example, spire-bearing spiriferoid and atrypoid brachiopods characteristically occur in offshore environments in the Ordovician and Silurian; an abundance of attached bivalves suggests the availability of hard substrates; deposit-feeding nuculoid bivalves most commonly occur in offshore muddy facies, etc.

(3) The overall taxonomic diversity of the assemblage can be utilized to suggest the relative environmental position on the shelf. The data are best treated as both total diversity, and diversity corrected for assemblage size.

(4) A qualitative assessment of abundance can also prove to be useful. It is best to consider the abundance of fossils in a few metres of sediment (vertically) rather than in a single layer, as shells probably accumulated in the latter as a result of current or wave concentration.

Other observations may also be significant. For example, if the shells have encrusting epifauna, they probably lay for some considerable time on the sea floor; crinoids preserved in vertical position suggest high sedimentation rates, etc. It is important to carefully observe the nature of the fossils themselves, particularly in in situ life assemblages, because they may provide evidence of the animals' reaction to the environment. For example, corals may show episodic growth, reflecting times of normal growth interrupted by episodes of rapid sedimentation.

Taking a broad view, in marine conditions, benthic macrofaunas change progressively from the shoreline across the shelf into slope and basinal environments and can be partitioned into several broad bands occupied by their distinctive faunas — the benthic assemblages of Boucot (1975 and Figure 7). These onshore to offshore gradients can be analysed by qualitative or quantitative gradient and diversity analyses, by recognition of taphofacies, by traditional community paleoecology, and through ichnology. Particular end-member environments (e.g., hypersaline) can sometimes be recognized by their distinctive faunas.

Nearshore shoreface and inner shelf zones are the most spatially heterogeneous, with many environments and sub-environments producing a wide range of facies. Typically, the lithofacies and their characteristic sedimentary structures provide the best evidence for paleoenvironmental interpretation though fossil concentrations and ichnofacies may offer complementary evidence.

Faunas are, however, commonly of major importance in identifying fresh water or brackish water in coastal areas. It is in the middle and outer shelf regions that macrofossils play a major part in environmental analyses. Here, used in conjunction with sedimentological evidence, such as proximality indices of storm sandstones, macrofossil remains and ichnofossils allow a broad bathymetric subdivision of the shelf, summarized in Table 3 (see p. 134-135). In vertical successions (e.g., Easthouse and Driese, 1988), this may even provide a basis for recognizing deepening and shallowing cycles and correlation between them. Faunas are also beginning to provide important evidence of changes in sedimentation rate and the location of hiatuses in sedimentary sequences.

The prevalence of cyclicity on a range of scales from small-scale cycles (~1-5 m thick) (Goodwin and Anderson, 1985) to seismostratigraphic sequences (tens to hundreds of metres thick) (Vail et al., 1977) are now being widely recognized. Although cycle boundaries and changing bathymetry within cycles are commonly reflected by facies changes, important information about sea-level change may also be provided by paleontological evidence. Communities and changes in their diversity may help to identify the shape of the bathymetric curve, as in a study of cycles in the Rochester Shale (Devonian) where sea-level change was shown to be symmetrically deep-shallow-deep (Miller et al., 1988). Shell concentrations may play an important role in sequence stratigraphy, where they help to define hiatuses. Shell concentrations may in particular help to locate the boundary of a sequence when they occur as transgressive lag deposits at the base of a coarsening-upward cycle or they may occur as a thin bone bed or shell concentrate in the "condensed section" formed later in the transgressive phase when sea level reaches its maximum flooding surface (Kidwell, 1989). Paleontology might be expected to be particularly helpful in sequence stratigraphy in the more offshore parts of the cycles, where the lithological definition of cyclic sequences is less clearly expressed. Here, careful community paleoecology and taphonomic studies should be helpful in defining bathymetric trends and hiatal surfaces. Historically, paleoecology has been underutilized in environmental analysis, so we hope this brief review will encourage others to use paleoecological information in conjunction with sedimentology for a full environmental interpretation of sedimentary sequences.

ACKNOWLEDGEMENTS

REFERENCES

Ager, D.V., 1963, Principles of palaeoecology: McGraw-Hill, New York, 371 p.

Ager, D.V., 1967, Brachiopod palaeoecology: Earth-Science Reviews, v. 3, p. 157-179.

Aigner, T., 1982, Calcareous Tempestites: Storm dominated stratification in Upper Muschelkalk Limestones (Middle Trias, SW Germany), in Einsele, G. and Seilacher, A., eds., Cyclic and Event Stratification: Springer-Verlag, Berlin, p. 180-198.

Anderson, T.F., 1990, Temperature from Oxygen Isotope Ratios, in Briggs, D.E.G. and Crowther, P.R., eds., Palaeobiology, A Synthesis: Blackwell Scientific Publications, London, p. 403-406.

Anderton, R., 1985, Clastic facies models and facies analogues, in Brenchley, P.J. and Williams, B.P.J., eds., Sedimentology: Recent Developments and Applied Aspects: Geological Society of London, Special Publication No. 18, Blackwell Scientific Publications, London, p. 31-47.

Baarli, B.G., 1988, Bathymetric co-ordination of proximality trends and level bottom communities: a case study from the Lower Silurian of Norway: Palaios, v. 3, p. 577-587.

Barnes, R.S.K., 1989, What, if anything, is a brackish-water fauna?: Royal Society of Edinburgh, Transactions, Earth Sciences, v. 80, p. 235-240.

Benedict, G.L. and Walker, K.L., 1978, Paleobathymetric analysis in Paleozoic sequences and its geodynamic significance: American Journal of Science, v. 278, p. 579-607.

Benson, R.H., 1975, Morphologic stability in Ostracod, in Swain, F.M., ed., Biology and Paleobiology of Ostracoda: Bulletins of American Paleontology, v. 65, p. 11-46.

Bidder, G.P., 1923, The relation of the form of a sponge to its currents: Quarterly Journal of the Microscopical Society, v. 67, p. 293-325.

Bignot, G., 1985, Elements of micropalaeontology: Graham and Trotman, London, 217 p.

Bjerstedt, T.W., 1988, Multivariate Analyses of Trace Fossil Distribution from an Early Mississippian Oxygen-Deficient Basin, Central Appalachians: Palaios, v. 3, p. 53-68.

Blodgett, R.B., Boucot, A.J. and Williams, W.F., 1988, New occurrences of color patterns in Devonian articulate brachiopods: Journal of Paleontology, v. 62, p. 46-51.

Bloom, S.A., Simon, J.L. and Hunter, V.D., 1972, Animal-sediment relations and community analysis of a Florida estuary: Marine Biology, v. 13, p. 43-56.

Bottjer, D.J. and Savrda, C.E., 1990, Oxygen Levels from Biofacies and Trace Fossils, in Briggs, D.E.G. and Crowther, P.R., eds., Palaeobiology, A Synthesis: Blackwell Scientific Publications, London, p. 408-410.

Table 3   Summary of general lithologic, taphonomic, macroinvertebrate and ichnologic characteristics
of brackish lagoonal, shoreface, shelf and slope and basinal siliciclastic environments.

BRACKISH LAGOONAL ENVIRONMENTS

Context	Commonly associated with terrestrial, barrier bar, estuarine, marsh or shallow marine shoreface facies (*see* Reinson, 1984).
Lithology	Typically shales though siltstones, sandstones and less commonly coarser grained sediments may be introduced by tidal or storm processes in flood-tidal deltas and washover fans.
Taphonomy	Dispersed *in situ* or disturbed neighborhood assemblages typically (though not universally, *e.g.*, Land, 1972) as thin shell concentrations. Tidal and storm processes may introduce allochthonous assemblages from shoreface and inner shelf environments.
Taxonomy/Diversity	*In situ* faunas typically restricted and of low diversity; usually ostracodes, bivalves and gastropods.
Abundance	Variable, commonly low in thin shell accumulations, but high in thick, typically monospecific, shell beds.
Ichnology	Imperfectly described; low diversity assemblages of the *Psilonichnus, Glossifungites, Cruziana* and *Zoophycos* ichnofacies may each occur depending on energy and salinity levels, grain size, substrate consistency and specific depositional environment within the lagoon.

SHOREFACE ENVIRONMENTS

Context	Nearshore and associated beach facies, distinguished from inner shelf deposits by a change in gradient from a gently sloping shallow subtidal tract of variable width to the virtually level inner shelf (McGubbin, 1982). Shoreface facies commonly cap upward-coarsening shallow marine cycles.
Lithology	Typically sandstones with locally developed mudstones (Howard and Frey, 1984). Sandstones exhibit planar- or cross-stratification formed by wave, tidal or wind-forced currents, or hummocky cross-stratification formed by combined flow.
Taphonomy	Allochthonous shell concentrations that may occur as coquinas, on bedding planes or as lags in cross-stratified foresets.
Taxonomy/Diversity	Paleozoic assemblages characterized by brachiopods, bivalves and gastropods. Mesozoic/Cenozoic assemblages characterized by varied bivalves (including deep burrowers, attached forms) and gastropods. Taxa affected by substrate mobility (*e.g.*, corals) are rare. *In situ* faunas rare. Diversity, though still generally low, can be elevated by introduction of allochthonous faunas by storm, tidal and wave activity.
Abundance	Generally low; however, in more subdued shoreface environments shells may be relatively common in coquinas. Cenozoic strata typically possess more abundant remains.
Ichnology	Typically *Skolithos*, more rarely *Psilonichnus* and *Cruziana*, ichnofacies depending on substrate mobility and subtle gradients in hydrologic, sedimentologic and ecologic parameters. Diversity typically low.

INNER (SHALLOW) SHELF ENVIRONMENTS

Context	Facies subject to normal fair weather waves and tidal processes, commonly occurring below shoreface sandstones and above mid-shelf sequences in coarsening-upward cycles.
Lithology	Sandstones dominate, but may occur in equal abundance with interbedded shales. Storm-influenced facies exhibit hummocky cross-stratification; tidal facies may exhibit herringbone cross-stratification, sigmoidal cross-stratification or mud drapes.
Taphonomy	Allochthonous or disturbed neighborhood assemblages at the base of storm sandstones, typically as coquinas. Tidally influenced sandstones commonly exhibit transported assemblages or shell lags distributed along foresets. Shales possess disarticulated and dispersed shells and bedding plane assemblages. *In situ* faunas rare or absent.
Taxonomy/Diversity	Paleozoic strata dominated by moderately but variably diverse assemblages of brachiopods, particularly orthoids and strophomenoids; Mesozoic/Cenozoic strata typically possess variable infaunal and epifaunal bivalves. Representatives of other benthic macroinvertebrates may occur.
Abundance	Generally moderate, but high in coquinas. Faunas can, however, be generally sparse where a freshwater influence is established, as, for example, in inner shelf environments in front of deltas.
Ichnology	Typically moderate to high diversity assemblages of the *Cruziana* and/or *Skolithos* ichnofacies. Mudstones commonly intensely bioturbated and possess trace fossils typical of the *Cruziana* ichnofacies; associated sandstones contain representatives of the *Skolithos* ichnofacies providing substrate mobility does not result in their destruction.

Table 3,   continued

MIDDLE SHELF ENVIRONMENTS

Context	Commonly form portions of upward-coarsening sequences, but may also form part of a predominantly mudstone sequence. Below fair weather wave base, above storm wave base.
Lithology	Mudstones, typically intensely bioturbated, and interbedded sandstone tempestites with hummocky cross-stratification being common.
Taphonomy	Mudstones may contain *in situ* clumped or dispersed shells that are still commonly articulated, or as thin stringers or locally reworked disturbed neighborhood assemblages. Sandstones commonly contain allochthonous lag assemblages or coquinas that are taxonomically similar or dissimilar to those assemblages within the associated mudstones.
Taxonomy/Diversity	Paleozoic strata possess high diversity assemblages dominated by brachiopods represented by several orders. Crinoids, bryozoans, corals, trilobites and gastropods also common. Mesozoic/Cenozoic strata dominated by varied infaunal and epifaunal bivalve assemblages with gastropods, echinoderms, bryozoans and less commonly brachiopods also present.
Abundance	Generally high.
Ichnology	Similar to inner shelf environments with high diversity assemblages typical of the *Arenicolites* ichnofacies in sandstones, typically as opportunists following storm activity, and intense bioturbation by members of the *Cruziana* ichnofacies in associated mudstones.

OUTER (DEEP) SHELF ENVIRONMENTS

Context	Mudrock-dominated sequences in association with shallow shelf or slope/basin environments. Below or above storm wave base.
Lithology	Bioturbated mudstones with uncommon, and where present typically thin, distal siltstone or sandstone tempestites.
Taphonomy	*In situ* dispersed, articulated faunas predominate. Thin stringers and bedding plane assemblages also common; disturbed neighborhood assemblages may occur. Distal tempestites may contain allochthonous shells, though not commonly.
Taxonomy/Diversity	Paleozoic strata dominated by brachiopods and trilobites; Mesozoic/Cenozoic strata by bivalves, particularly infaunal species — nuculoids are very common. Other groups also occur but in lower numbers. Pelagic forms (*e.g.*, graptolites (Paleozoic), ammonites, belemnites (Mesozoic)) also commonly present. Diversity variable depending on parameters such as nutrients, oxygen levels, *etc.*, but can be high, then typically markedly decreases at the shelf edge.
Abundance	Typically low.
Ichnology	Discrete ichnotaxa commonly difficult to recognize as a result of intense bioturbation. Representatives of *Cruziana, Zoophycos* or rarely *Nereites* ichnofacies may predominate depending on specific environmental conditions. Bioturbation intense though diversity commonly low to moderate.

SLOPE AND BASIN ENVIRONMENTS

Context	Mudrock-dominated sequences with associated sediment gravity flows, particularly, but not exclusively, turbidites. Submarine canyons and associated fans commonly occur in association with slope and continental rise sequences. Contourites also common on slope and continental rise environments (reviewed *in* Stow and Piper, 1984).
Lithology	Pelagic and hemipelagic mudstones, turbiditic sandstones, and siltstones. Canyons and fans typically possess coarser grained lithofacies.
Taphonomy	Autochthonous faunas, typically dispersed and articulated, in pelagic/hemipelogic mudstones. Allochthonous faunas introduced particularly by turbidity currents.
Taxonomy/Diversity	Dominated by pelagic macroinvertebrates (*e.g.*, Paleozoic — trilobites, graptolites, nautiloids; Mesozoic — ammonites, belemnites). *In situ* forms include Paleozoic trilobites, hyolithids, *etc.* and Mesozoic/Cenozoic bivalves, gastropods and crinoids. Other groups may occur but are uncommon. Diversity is low.
Abundance	Very low, but can be higher in sediment gravity flow deposits.
Ichnology	Variable, with representatives of the *Skolithos, Arenicolites* and/or *Glossifungites* ichnofacies commonly occurring in association with well-oxygenated submarine canyons and fans, *Zoophycos* ichnofacies with slopes with restricted circulation or low oxygen levels and the *Nereites* ichnofacies in more stable, classical flysch-like settings in generally quiet, but oxygenated waters.

Boucot, A.J., 1975, Evolution and Extinction Rate Controls: Elsevier, Amsterdam, 427 p.

Boucot, A.J., 1981, Principles of Benthic Marine Paleoecology: Academic Press, New York, 463 p.

Bouma, A.H., Berryhill, H.L., Knebel, H.J. and Brenner, R.L., 1982, Continental slopes, in Scholle, P.A. and Spearing, D., eds., Sandstone Depositional Environments: American Association of Petroleum Geologists, Memoir 31, p. 281-327.

Bowen, Z.P., Rhoads, D.C. and McAlester, A.L., 1974, Marine benthic communities in the Upper Devonian of New York: Lethaia, v. 7, p. 93-120.

Brasier, M.D., 1980, Microfossils: Allen and Unwin, London, 193 p.

Brenchley, P.J. and Cocks, L.R.M., 1982, Ecological associations in a regressive sequence: the latest Ordovician of the Oslo-Asker District, Norway: Palaeontology, v. 25, p. 783-815.

Brenchley, P.J. and Pickerill, R.K., 1991, Animal-sediment relations in the Ordovician and Silurian of the Welsh Basin: Proceedings of the Geological Association, v. 101, in press.

Brett, C.E. and Baird, G.C., 1986, Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation: Palaios, v. 1, p. 207-227.

Brett, C.E. and Speyer, S.E., 1990, Taphofacies, in Briggs, D.E.G. and Crowther, P.R., eds., Palaeobiology, A Synthesis: Blackwell Scientific Publications, London, p. 258-263.

Brett, C.E., Speyer, S.E. and Baird, G.C., 1986, Storm-generated sedimentary units: tempestite proximality and event stratification in the Middle Devonian Hamilton Group of New York, in Brett, C.E., ed., Dynamic Stratigraphy and Depositional Environments of the Hamilton Group (Middle Devonian) in New York State; Part I: New York State Museum, v. 457, p. 129-156.

Bromley, R.G., 1970, Borings as trace fossils and Entobia cretacea Portlock, as an example, in Crimes, T.P. and Harper, J.C., eds., Trace Fossils: Geological Journal, Special Issue 3, Seel House Press, Liverpool, p 49-90.

Bromley, R.G., 1975, Comparative analysis of fossil and recent echinoid bioerosion: Palaeontology, v. 18, p. 725-739.

Bromley, R.G. and Asgaard, U., 1991, Ichnofacies: a mixture of taphofacies and biofacies. Lethaia, v. 24, p. 153-163.

Bromley, R.G. and Ekdale, A.A., 1984, Chondrites: a trace fossil indicator of anoxia in sediments: Science, v. 224, p. 872-874.

Byers, C.W., 1977, Biofacies patterns in euxinic basins: a general model, in Cook, H.E. and Enos, P., eds., Deep-Water Carbonate Environments: Society of Economic Paleontologists and Mineralogists, Special Publication 25, p. 1-27.

Calef, C.E. and Hancock, A.J., 1974, Wenlock and Ludlow marine communities in Wales and the Welsh Borderland: Palaeontology, v. 17, p. 779-810.

Campbell, K.S.W., 1975, The functional morphology of Cryptolithus: Fossils and Strata, v. 4, p. 65-86.

Carter, R.M., 1972, Adaptations of British chalk bivalvia: Journal of Paleontology, v. 46, p. 325-340.

Chamberlain, J.A. and Westermann, E.G., 1976, Hydrodynamic properties of cephalopod shell ornament: Paleobiology, v. 2, p. 316-331.

Cherns, L., 1979, The environmental significance of Lingula in the Ludlow Series of the Welsh Borderland and Wales: Lethaia, v. 12, p. 35-46.

Cherns, L., 1988, Faunal and facies dynamics in the Upper Silurian of the Anglo-Welsh Basin: Palaeontology, v. 31, p. 451-502.

Cisne, J.L. and Rabe, B.D., 1978, Coenocorrelation: gradient analysis of fossil communities and its applications in stratigraphy: Lethaia, v. 11, p. 341-364.

Clarkson, E.N.K., 1969, A functional study of the odontopleurid trilobite Leonaspis deflexa (Lake): Lethaia, v. 2, p. 329-344.

Cline, R.M. and Hays, J.D., 1976, eds., Late Quaternary paleoceanography and paleoclimatology: Geological Society of America, Memoir 145, 464 p.

Cocks, L.R.M., 1967, Depth patterns in Silurian marine communities: Marine Geology, v. 5, p. 379-382.

Cocks, L.R.M. and McKerrow, W.S., 1984, Review of the distribution of the commoner animals in Lower Silurian marine benthic communities: Palaeontology, v. 27, p. 663-670.

Condra, G.E. and Elias, M.K., 1944, Study and revision of Archimedes (Hall): Geological Society of America, Special Paper 53, 243 p.

Copper, P., 1988, Paleoecology: paleoecosystems, paleocommunities: Geoscience Canada, v. 15, p. 199-208.

Crimes, T.P., 1977, Trace fossils of an Eocene deep-sea sand fan, northern Spain, in Crimes, T.P. and Harper, J.C., eds., Trace Fossils 2: Geological Journal, Special Issue 9, Seel House Press, Liverpool, p. 71-90.

Davies, D.J., Powell, E.N. and Stanton, R.J., Jr., 1989, Taphonomic signature as a function of taphonomic process: shells and shell beds in a hurricane-influenced inlet on the Texas coast: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 72, p. 317-356.

Dodd, J.R. and Stanton, R.J., Jr., 1981, Paleoecology, concepts and applications: Wiley, New York, 559 p.

Dodd, J.R. and Stanton, R.J., Jr., 1990, Paleoecology, Concepts and Applications, Second Edition: Wiley, New York, 502 p.

Donovan, S.K., 1991, ed., The Processes of Fossilization: Belhaven Press, London, 303 p.

Droser, M.L. and Bottjer, D.J., 1986, A semiquantitative field classification of ichnofabric: Journal of Sedimentary Petrology, v. 56, p. 558-559.

Easthouse, K.A. and Driese, S.G., 1988, Paleobathymetry of a Silurian Shelf System: Application of Proximality Trends and Trace Fossil Distributions: Palaios, v. 3, p. 473-486.

Eckert, B.-Y. and Brett, C.E., 1989, Bathymetry and paleoecology of Silurian benthic assemblages, Late Llandoverian, New York State: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 74, p. 297-326.

Efremov, I.A., 1940, Taphonomy, a new branch of paleontology: Akademiya Nauk SSSR Byulleten, Seriya Biologicheskaya, v. 3, p. 405-413. [in Russian, with English translation in Pan American Geologist, v. 74, p. 81-93]

Ekdale, A.A., Bromley, R.G. and Pemberton, S.G, 1984, Ichnology. The Use of Trace Fossils in Sedimentology and Stratigraphy: Society of Economic Paleontologists and Mineralogists, Short Course 15, 317 p.

Emig, C.C., Gall, J.-C., Pajaud, D. and Plaziat, J.-C., 1978, Réflexions critique sur l'écologie et la systématique des Lingules actuelles et fossiles: Geobios, v. 11, p. 573-609.

Farrow, G.E., 1990, Depth from Trace and Body Fossils, in Briggs, D.E.G. and Crowther, P.R., eds., Palaeobiology, A Synthesis: Blackwell Scientific Publications, London, p. 411-413.

Fischer, A.G., 1960, Latitudinal variations in organic diversity: Evolution, v. 14, p. 64-81.

Fischer, I. St. J. and Hudson, J.D., 1987, Pyrite formation in Jurassic shales of contrasting biofacies, in Brooks, J. and Fleet, A.J., eds., Marine Petroleum Source Rocks: Geological Society of London, Special Publication No. 24, p. 69-78.

Flint, R.W., 1981, Gulf of Mexico outer continental shelf benthos: macrofaunal environmental relationships: Biological Oceanography, v. 1, p. 135-155.

Frey, R.W. and Pemberton, S.G., 1984, Trace Fossil Facies Models, in Walker, R.G., ed., Facies Models, Second Edition: Geoscience Canada Reprint Series 1, p. 189-207.

Frey, R.W., Pemberton, S.G. and Saunders, T.D.A., 1990, Ichnofacies and bathymetry: a passive relationship: Journal of Paleontology, v. 64, p. 155-158.

Fürsich, F.T., 1976, Fauna-substrate relationships in the Corallian of England and Normandy: Lethaia, v. 9, p. 343-356.

Fürsich, F.T. and Aberhan, F.T., 1990, Significance of time-averaging for palaeocommunity analysis: Lethaia, v. 23, p. 143-152.

Fürsich, F.T. and Hurst, J.M., 1974, Environmental factors determining the distribution of brachiopods: Palaeontology, v. 17, p. 879-900.

Fürsich, F.T. and Kirkland, J.I., 1986, Biostratinomy and paleoecology of a Cretaceous brackish lagoon: Palaios, v. 1, p. 543-560.

Gall, J.-C., 1983, Ancient Sedimentary Environments and the Habitats of Living Organisms: Springer-Verlag, Berlin, 219 p.

Golubic, S., Perkins, R.D. and Lukas, K.J., 1975, Boring microorganisms, and microborings in carbonate substrates, in Frey, R.W., ed., The Study of Trace Fossils: Springer-Verlag, Berlin, p. 229-259.

Goodwin, P.W. and Anderson, E.J., 1985, Punctuated aggradational cycles: a general hypothesis of episodic stratigraphic accumulation: Journal of Geology, v 93, p. 515-533.

Grant, R.E., 1972, The lophophore and feeding mechanism of the Productidina (Brachiopoda): Journal of Paleontology, v. 46, p. 213-249.

Graus, R.R. and Macintyre, I.G., 1976, Light control of growth form in colonial reef corals: Computer simulation: Science, v. 193, p. 895-897.

Gray, J., 1988, Evolution of the freshwater ecosystem: the fossil record: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 62, p. 1-214.

Gray, J., Boucot, A.J. and Berry, W.B.N., 1981, eds., Communities of the Past: Hutchinson Ross, Stroudsberg, Pennsylvania, 623 p.

Hakes, W.G., 1985, Trace fossils from brackish-marine shales, Upper Pennsylvanian of Kansas, U.S.A., in Curran, H.A., ed., Biogenic Structures: Their use in interpreting depositional environments: Society of Economic Paleontologists and Mineralogists, Special Publication 35, p. 21-35.

Hallam, A. 1967, ed., Depth indicators in marine sedimentary environments: Marine Geology, Special Issue, v. 5, p. 329-555.

Hallam, A., 1976, Stratigraphic distribution and ecology of European Jurassic bivalves: Lethaia, v. 9, p. 245-259.

Hallam, A., 1984, Distribution of fossil marine invertebrates in relation to climate, in Brenchley, P.J., ed., Fossils and Climate: Wiley, New York, p. 107-126.

Haq, B.U. and Boersma, A., 1978, eds, Introduction to Marine Micropaleontology: Elsevier, New York, 376 p.

Harper, D.A.T. and Ryan, P.D., 1990, Towards a statistical system for palaeontologists: Journal of the Geological Society, London, v. 147, p. 935-948.

Hecker, R.F., 1965, Introduction to Paleoecology: Elsevier, Amsterdam, 166 p.

Heckel, P.H., 1972, Recognition of ancient shallow marine environments, in Rigby, J.K. and Hamblin, W.K., eds., Recognition of Ancient Sedimentary Environments: Society of Economic Paleontologists and Mineralogists, Special Publication 16, p. 226-286.

Hedgpeth, J.W., 1957, ed., Treatise on marine ecology and paleoecology, Volume 1, Ecology: Geological Society of America, Memoir 67, 1296 p.

Howard, J.D. and Frey, R.W., 1984, Characteristic trace fossils in nearshore to offshore sequences, Upper Cretaceous of east-central Utah: Canadian Journal of Earth Sciences, v. 21, p. 200-219.

Hubbard, J.A.E.B., 1974, Coral colonies as microenvironmental indicators: Société Géologique de Belgique, Annales, v. 97, p. 143-152.

Hudson, J.D. 1989, Palaeotemperatures in the Phanerozoic: Journal of the Geological Society of London, v. 146, p. 155-160.

Hudson, J.D., 1990, Salinity from Faunal Analysis and Geochemistry, in Briggs, D.E.G. and Crowther, P.R., eds., Palaeobiology, A Synthesis: Blackwell Scientific Publications, London, p. 406-410.

Hurst, J.M., 1979, Evolution, succession and replacement in the type upper Caradoc (Ordovician) benthic faunas of England: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 27, p. 189-246.

Hurst, J.M. and Pickerill, R.K., 1986, The relationship between sedimentary facies and faunal associations in the Llandovery siliciclastic Ross Brook Formation, Arisaig, Nova Scotia: Canadian Journal of Earth Sciences, v. 23, p. 705-726.

Imbrie, J. and Newell, N., 1964, eds., Approaches to Paleoecology: Wiley, New York, 432 p.

Jaanusson, V., 1984, Functional morphology of the shell in platycope ostracods: A study of arrested evolution: Lethaia, v. 18, p. 73-84.

Jablonski, D., Sepkoski, J.J., Jr., Bottjer, D.J. and Sheehan, P.M., 1983, Onshore-offshore patterns in the evolution of Phanerozoic shelf communities: Science, v. 222, p. 1123-1125.

Jefferies, R.P.S. and Minton, P., 1965, The mode of life of two Jurassic species of Posidonia (Bivalvia): Palaeontology, v. 8, p. 158-185.

Johnson, M.E., 1987, Extent and Bathymetry of North American Platform Seas in the Early Silurian: Paleooceanography, v. 2, p. 185-211.

Johnson, M.E., Rong, J.-Y. and Fox, W.T., 1989, Comparison of Late Ordovician Epicontinental Seas and their Relative Bathymetry in North America and China: Palaios, v. 4, p. 43-50.

Johnson, M.E., Rong, J.-Y. and Yang, X.-C., 1985, Intercontinental correlation by sea-level events in the Early Silurian of North America and China (Yangtze Platform): Geological Society of America, Bulletin, v. 96, p. 1384-1397.

Jones, B., 1988, Biostatistics in Paleontology: Geoscience Canada, v. 15, p. 3-22.

Jordan, D.W., 1985, Trace fossils and depositional environments of Upper Devonian black shales, east-central Kentucky, U.S.A., in Curran, H.A., ed., Biogenic Structures: Their use in interpreting depositional environments: Society of Economic Paleontologists and Mineralogists, Special Publication 35, p. 279-298.

Kennett, J.P., 1982, Marine Geology: Prentice Hall, New Jersey, 813 p.

Kershaw, S., 1984, Patterns of stromatoporoid growth in level bottom communities: Palaeontology, v. 27, p. 113-130.

Kidwell, S.M., 1986, Models for fossil concentrations: paleobiologic implications: Paleobiology, v. 12, p. 6-24.

Kidwell, S.M., 1989, Stratigraphic condensation of marine transgressive records; origin of major shell deposits in the Miocene of Maryland: Journal of Geology, v. 97, p. 1-24.

Kidwell, S.M., Fürsich, F.T. and Aigner, T., 1986, Conceptual Framework for the Analysis and Classification of Fossil Concentrations: Palaios, v. 1, p. 228-238.

Kobluk, D.R. and Kahle, C.F., 1978, Geological significance of boring and cavity-dwelling marine algae: Bulletin of Canadian Petroleum Geology, v. 26, p. 362-379.

Kobluk, D.R. and Mapes, R.H., 1989, The Fossil Record, Function, and Possible Origins of Shell Color Patterns in Paleozoic Marine Invertebrates: Palaios, v. 4, p. 63-85.

Kreisa, R.D., 1981, Storm-generated sedimentary structures in subtidal marine facies with examples from the Middle and Upper Ordovician of southwestern Virginia: Journal of Sedimentary Petrology, v. 51, p. 823-848.

Kreisa, R.D. and Bambach, R.K., 1982, The role of storm processes in generating shell beds in Palaeozoic shelf environments, in Einsele, G. and Seilacher, A., eds., Cyclic and Event Stratification: Springer-Verlag, New York, p. 200-207.

Kumar, N. and Sanders, J.E., 1976, Characteristics of shoreface deposits: Modern and ancient: Journal of Sedimentary Petrology, v. 46, p. 145-162.

Ladd, H.S., 1957, ed., Treatise on marine ecology and paleoecology, Volume 2, Paleoecology: Geological Society of America, Memoir 67, 1077 p.

Land, C.B., Jr., 1972, Stratigraphy of Fox Hills Sandstone and associations, Rock Springs uplift and Wamsutter arch area, Sweetwater Country, Wyoming: a shoreline-estuary sandstone model for the Late Cretaceous: Colorado School of Mines, Quarterly Journal, v. 67, 69 p.

Lane, N.G. and Breimer, A., 1974, Arm types and feeding habits of Paleozoic crinoids: Koninklijke Nederlandse Akademie van Wettenshappen, Series B, v. 77, p. 32-39.

Lawrence, D.R., 1968, Taphonomy and information losses in fossil communities: Geological Society of America, Bulletin, v. 79, p. 1315-1330.

Linsley, R.M., 1978, Locomotion rates and shell form in the Gastropoda: Malacologia, v. 17, p. 193-206.

Levinton, J.S., 1982, Marine Ecology: Prentice Hall, Englewood Cliffs, New Jersey, 526 p.

Lockley, M.G., Rindsberg, A.K. and Zeiler, R.M., 1987, The paleoenvironmental significance of the nearshore Curvolithus ichnofacies: Palaios, v. 2, p. 255-262.

Ludvigsen, R., 1975, Ordovician formations and faunas, southern MacKenzie Mountains: Canadian Journal of Earth Sciences, v. 12, p. 663-697.

Ludvigsen, R., 1978, Middle Ordovician trilobite facies, southern MacKenzie Mountains: Geological Association of Canada, Special Publication 18, p. 1-37.

Macellari, C.E., 1988, Stratigraphy, sedimentology and paleoecology of Upper Cretaceous/Paleocene shelf-deltaic sediments of Seymour Is-

land, in Feldmann, R.M., ed., Geology and Paleontology of Seymour Island, Antarctic Peninsula: Geological Society of America, Memoir 169, p. 25-53.

Magurran, A.E., 1988. Ecological diversity and its measurements: Princeton University Press, Princeton, New Jersey, 179 p.

McCall, P.L. and Tevesz, T.S., 1982, eds., Animal-Sediment Relations. The Biogenic Alteration of Sediments: Plenum Press, New York, Topics in Geobiology, v. 2, 336 p.

McCubbin, D.G., 1982, Barrier-island and strand plain facies, in Scholle, P.A. and Spearing, D., eds., Sandstone Depositional Environments: American Association of Petroleum Geologists, p. 247-279.

McKerrow, W.S., 1978, ed., The Ecology of Fossils: Duckworth, London, 384 p.

McKinney, F.K., 1977, Parabaloid colony bases in Paleozoic stenolaemate bryozoans: Lethaia, v. 10, p. 209-217.

Miller, K.B., Brett, C.E. and Parsons, K.M., 1988, The paleoecologic significance of storm-generated disturbance within a Middle Devonian muddy epeiric sea: Palaios, v. 3, p. 35-52.

Möller, N.K., 1989, Facies analysis and paleogeography of the Rytteraker Formation (Lower Silurian: Oslo Region, Norway): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 69, p. 167-192.

Mook, W.G., 1971, Paleotemperatures and chlorinities from stable carbon and oxygen isotopes in shell carbonate: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 9, p. 245-263.

Noble, J.P.A., 1976, The relative significance of depth and substrate in Lower Palaeozoic community distribution: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 27, p. 167-178.

Norris, R.D., 1986, Taphonomic gradients in shelf fossil assemblages: Pliocene Purisima Formation, California: Palaios, v. 1, p. 256-270.

Odin, G.S. and Matter, A., 1981, De glauconarium originae: Sedimentology, v. 28, p. 611-641.

Parker, R.H., 1964, Zoogeography and ecology of some macro-invertebrates, particularly mollusks, in the Gulf of California and the continental slope off Mexico: Videnskabelige Meddelelser fra Dansk Nuturhistorisk Forening, v. 126, 178 p.

Parker, R.H., 1975: The study of benthic communities — a model and a review: Elsevier, Amsterdam, 279 p.

Parker, R.H., 1979, Paleotemperature and depth indicators, in Fairbridge, R.W. and Jablonski, D., eds., The Encyclopedia of Paleontology: Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, p. 581-587.

Parsons, K.M., Brett, C.E. and Miller, K.B., 1988, Taphonomy and depositional dynamics of Devonian shell-rich mudstones: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 63, p. 109-139.

Peel, J.S., 1978, Faunal succession and mode of life of Silurian gastropods in the Arisaig Group, Nova Scotia: Palaeontology, v. 21, p. 285-306.

Persson, L.A., 1982, Macrozoobenthic associations of the Hanö Bight, southern Baltic: Sarsia, v. 67, p. 93-106.

Petersen, C.G.J., 1913, Valuation of the sea II. The animal communities of the sea bottom and their importance for marine zoogeography: Reports of the Danish Biological Station, v. 21, p. 1-44.

Petersen, C.G.J., 1915, On the animal communities of the sea bottom in the Skagerrak, the Christiana Fjord and the Danish waters: Reports of the Danish Biological Station, v. 23, p. 3-28.

Philcox, M.E., 1971, Growth form and role of colonial coelenterates in reefs of the Gower Formation (Silurian), Iowa: Journal of Paleontology, v. 45, p. 338-346.

Pickerill, R.K. and Brenchley, P.J., 1979, Caradoc marine benthic communities of the south Berwyn Hills, North Wales: Palaeontology, v. 22, p. 229-264.

Pickerill, R.K., Harland, T.L. and Fillion, D., 1984, In situ lingulids from deep-water carbonates of the Middle Ordovician Table Head Group of Newfoundland and the Trenton Group of Quebec: Canadian Journal of Earth Sciences, v. 21, p. 194-199.

Pickerill, R.K. and Hurst, J.M., 1983, Sedimentary facies, depositional environments and faunal associations of the lower Llandovery (Silurian) Beechill Cove Formation, Arisaig, Nova Scotia: Canadian Journal of Earth Sciences, v. 29, p. 1761-1779.

Reinson, G.E., 1984, Barrier-island and associated strand-plain systems, in Walker, R.G., ed., Facies Models, Second Edition: Geoscience Canada Reprint Series 1, p. 119-140.

Rhoads, D.C., 1975, The paleoecologic and environmental significance of trace fossils, in Frey, R.W., ed., The Study of Trace Fossils: Springer-Verlag, Berlin, p. 147-160.

Rhoads, D.C. and Morse, J.W., 1971, Evolutionary and ecologic significance of oxygen-deficient basins: Lethaia, v. 4, p 413-428.

Rider, J. and Cowan, R., 1977, Adaptive architectural trends in encrusting Ectoprocta: Lethaia, v. 10, p. 29-41.

Robertson, J.D., 1989, Physiological constraints upon marine organisms: Royal Society of Edinburgh, Transactions, Earth Sciences, v. 80, p. 225-234.

Rong, J.-Y., Johnson, M.E. and Yang, X., 1984, Early Silurian (Llandovery) sea-level changes in the Upper Yangtze Region of central and southwestern China: Acta Palaeontologica Sinica, v. 23, p. 672-694. [in Chinese with English summary]

Rudwick, M.J.S., 1961, The feeding mechanism of the Permian brachiopod Prorichthofenia: Palaeontology, v. 3, p. 450-471.

Rudwick, M.J.S., 1964, The function of zigzag deflections in the commissure of fossil brachiopods: Palaeontology, v. 7, p. 135-171.

Sanders, H.L., 1968, Marine benthic diversity: a comparative study: American Naturalist, v. 102, p. 243-282.

Sanders, H.L. and Hessler, R.R., 1969, Ecology of the deep-sea benthos: Science, v. 163, p. 1419-1424.

Savazzi, E., 1989, Burrowing mechanisms and sculptures in Recent gastropods: Lethaia, v. 22, p. 31-48.

Savin, S.M., 1977, The history of the Earth's surface temperature during the last 100 million years: Annual Review of Earth and Planetary Sciences, v. 5, p. 319-355.

Savrda, C.E. and Bottjer, D.J., 1986, Trace-fossil models for reconstruction of paleo-oxygenation in bottom waters: Geology, v. 14, p. 3-6.

Savrda, C.E. and Bottjer, D.J., 1987, The exaerobic zone, a new oxygen-deficient biofacies: Nature, v. 327, p. 54-56.

Savrda, C.E. and Bottjer, D.J., 1989, Trace fossil model for reconstructing oxygenation histories of ancient marine bottom waters: application to Upper Cretaceous Niobrara Formation, Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 74, p. 49-74.

Schäfer, W., 1962, Actuo-Paläontologie nach Studien in der Nordsee: Kramer, Frankfort, 666 p.

Schäfer, W., 1972, Ecology and paleoecology of marine environments: University of Chicago Press, Chicago, 568 p.

Schmalfuss, H., 1981, Structure, patterns and function of cuticular terraces in trilobites: Lethaia, v. 14, p. 331-341.

Scott, R.W. and West, R.R., 1976, eds., Structure and Classification of Paleocommunities: Dowden, Hutchinson and Ross, Stroudsberg, Pennsylvania, 291 p.

Seilacher, A., 1964, Biogenic sedimentary structures, in Imbrie, J. and Newell, N.D., eds., Approaches to Paleoecology: John Wiley, New York, p. 296-316.

Seilacher, A., 1967, Bathymetry of trace fossils: Marine Geology, v. 5, p. 413-428.

Seilacher, A., 1979, Constructional morphology of sand dollars: Paleobiology, v. 5, p. 191-221.

Shackleton, N.J., 1984, Oxygen isotope evidence for Cenozoic climatic change, in Brenchley, P.J., ed., Fossils and Climate: John Wiley, New York, p. 27-34.

Shackleton, N.J. and Opdyke, N.D., 1973, Oxygen isotope and palaeomagnetic stratigraphy of equatorial Pacific core V28-238: oxygen isotope temperatures and ice volumes on a 10^5 and 10^6 year scale: Quaternary Research, v. 3, p. 305-313.

Skelton, P.W., 1979, Preserved ligament in a radiolitid rudist bivalve and its implication of mantle marginal feeding in the group: Paleobiology, v. 5, p. 90-106.

Smith, A.B., 1978, A comparative study of the lifestyle of two Jurassic irregular echinoids: Lethaia, v. 11, p. 57-66.

Smith, A.B., 1984, Echinoid palaeobiology: Allen and Unwin, London, 190 p.

Speyer, S.E. and Brett, C.E., 1986, Trilobite taphonomy and Middle Devonian taphofacies: Palaios, v. 1, p. 312-327.

Speyer, S.E. and Brett, C.E., 1988, Taphofacies models for epeiric sea environments: Middle Paleozoic examples: Palaeogeography, Palaeoclimatology, Palaeoecology,, v. 63, p. 225-262.

Stanley, S.M. 1970, Relation of shell form to life habits of the Bivalvia (Mollusca): Geological Society of America, Memoir 125, 296 p.

Stanley, S.M., 1972, Functional morphology and evolution of bysally attached bivalve mollusks: Journal of Paleontology, v. 46, p. 165-212.

Stanton, R.J., Jr., Dodd, J.R. and Alexander, R.R., 1979, Eccentricity in the clypeasteroid echinoid Dendraster: environmental significance and application in Pliocene paleoecology: Lethaia, v. 12, p. 75-87.

Stearn, C.W., 1984, Growth forms and macrostructural elements of the coralline sponges: Palaeontographica Americana, v. 54, p. 315-325.

Stearn, C.W. and Riding, R., 1973, Forms of hydrozoan-Millepora on a Recent coral reef: Lethaia, v. 6, p. 187-199.

Stehli, F.G., 1968, Taxonomic diversity gradients in pole location: The recent model, in Drake, E.T., ed., Evolution and Environment: Yale University Press, New Haven, Connecticut, p. 163-277.

Stow, D.A.V. and Piper, D.J.W., 1984, eds., Fine-Grained Sediments: Deep-Water Processes and Facies: Geological Society of London, Special Publication No. 15, 659 p.

Surlyk, F., 1972, Morphological adaptations and population structures of the Danish Chalk brachiopods (Maastrichtian, Upper Cretaceous): Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter, v. 19, 57 p.

Tevesz, M.J. and McCall, P.L., 1983, Biotic Interactions in Recent and Fossil Benthic Communities: Plenum Press, New York, Topics in Geobiology, v. 3, 837 p.

Thomas, R.D.K., 1986, prefacer, Taphonomy: ecology's loss is sedimentology's gain: Palaios, v. 1, p. 206-338.

Thompson, J.B., Mullins, H.T., Newton, C.R. and Vercoutere, T.L., 1985, Alternative biofacies model for dysaerobic communities: Lethaia, v. 18, p. 167-179.

Thorson, G., 1957, Bottom communities, in Hedgpeth, J., ed., Treatise on Marine Ecology and Paleoecology, Volume 1, Ecology: Geological Society of America, Memoir 67, p. 461-534.

Trueman, E.R., 1964, Adaptive morphology in paleoecological interpretation, in Imbrie, J. and Newell, N.D., eds., Approaches to Paleoecology: Wiley, New York, p. 45-74.

Vail, P.R., Mitchum, R.M. and Thompson, S., III, 1977, Seismic stratigraphy and global changes of sea-level, Part 3. Relative changes of sea-level from coastal onlap, in Payton, C.W., ed., Seismic stratigraphy applications to hydrocarbon exploration: American Association of Petroleum Geologists, Memoir 26, p. 63-97.

Valentine, J.W., 1973, Evolutionary Paleoecology of the Marine Biosphere: Prentice-Hall, New Jersey, 511 p.

Voigt, E., 1977, On grazing traces produced by the radula of fossil and Recent gastropods and chitons, in Crimes, T.P. and Harper, J.C., eds., Trace Fossils 2: Geological Journal, Special Issue 9, Seel House Press, Liverpool, p. 335-346.

Walker, R.G., 1984a, Shelf and shallow marine sands, in Walker, R.G., ed., Facies Models, Second Edition: Geoscience Canada Reprint Series 1, p. 141-170.

Walker, R.G., 1984b, General Introduction: Facies sequences and facies models, in Walker, R.G., ed., Facies Models, Second Edition: Geoscience Canada Reprint Series 1, p. 1-9.

Watkins, R., 1979, Benthic community organization in the Ludlow Series of the Welsh Borderland: Bulletin of the British Museum of Natural History (Geology), v. 31, p. 175-280.

Welch, J.R., 1978, Flume studies of simulated feeding and hydrodynamics of a Paleozoic stalked crinoid: Paleobiology, v. 4, p. 89-95.

Westermann, G.E.G., 1973, Strength of concave septa and depth limits of fossil cephalopods: Lethaia, v. 6, p. 383-403.

Wignall, P.B. and Myers, K.J., 1988, Interpreting benthic oxygen levels: a new approach: Geology, v. 16, p. 452-455.

Wignall, P.B. and Simms, M.J., 1990, Pseudoplankton: Palaeontology, v. 33, p. 359-378.

Wilson, J.B., 1986, Faunas of tidal current and wave-dominated continental shelves and their use in the recognition of storm deposits, in Knight, R.J. and McLean, J.R., eds., Shelf Sands and Sandstones: Canadian Society of Petroleum Geologists, Memoir 11, p. 313-326.

Wilson, M.V.H., 1988, Taphonomic processes: information loss and information gain: Geoscience Canada, v. 15, p. 131-148.

Ziegler, A.M. 1965, Silurian marine communities and their significance: Nature, v. 207, p. 270-272.

Ziegler, A.M., Cocks, L.R.M. and Bambach, R.K., 1968, The composition and structure of Lower Silurian marine communities: Lethaia, v. 1, p. 1-27.