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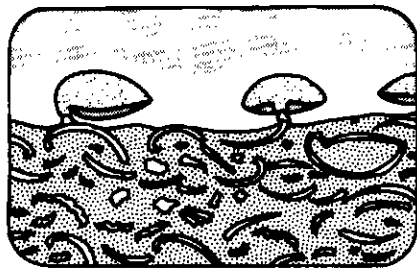
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# Articles



## PALEOSCENE 14. Organisms and Carbonate Substrates in Marine Environments

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### INTRODUCTION

Carbonate substrates are normally produced *in situ* by organisms that live above, at or below the sediment-water interface; that is, they represent a relatively self-enclosed ecosystem. During the last 3.5 billion years, there have been major cyclical variations in the global carbonate sediment budget in the oceans, and organisms have been, to a large extent, directly responsible for these variations. At the substrate level, there is a direct interplay between the planktic and nektic organisms that occupy the watermass above, and the benthic organisms that utilize the substrate as a food resource and domicile below, though these relationships depend more on grain size, nutrient in the sediment, pore chemistry, and the general nature of the substrate (texture, fabric, etc.) than it does on the mineralogical differences between the siliciclastic or calcium carbonate composition of the sedimentary grains. This synthesis is an attempt to look at both the macrocosmos and microcosmos of organisms and the carbonate substrates they occupy. It will exclude the reef and intertidal-subtidal microbial mat environments, as well as terrestrial fresh water ecosystems. Trace

fossils will be treated only in passing because of their importance to recognition of sediment cycling. Fossil organisms provide many clues to the ancient marine environment, as their distribution is limited by physico-chemical factors such as temperature, light, substrate and watermass chemistry (pH, Eh, solubles, salinity, etc.), gases (oxidizing, reducing, etc.), ambient physical energy, random or predictable catastrophic effects (tides, storms, sea level change, etc.), the nature of the substrate (hard, soft, mobile, static, smooth, rough, grain size, etc.), and biological factors, such as their own functional limitations and relationships to other organisms occupying the substrate.

### GLOBAL CARBONATE SEDIMENT DISTRIBUTION IN TIME

Calcium carbonate is the earth's most important sink for carbon (Bolin, 1970; Kitano, 1983), and carbon, in the form of organic molecules, is the key to all life on Earth. A global carbon inventory shows that limestones form ~224 million billion metric tons (bmt), organic matter ~25 bmt, and coal, oil and gas ~2.7 bmt (Poldervaart, 1955). Carbonates can be considered as minerals in which metal oxides, mostly Ca, have been neutralized by CO<sub>2</sub> (Holland, 1978). Virtually all carbonate sediments are biologically precipitated; in the early oceans, this appears to have been accomplished by photosynthetic and procaryotic cyano- and chloroxybacteria (Margulis and Stolz, 1983). In the modern world ocean, limestones are the world's most obvious and evident "savings bank" for carbon dioxide, which is absorbed and vented primarily through the ocean-atmosphere system. In the lithosphere, *i.e.*, the earth's crust and upper mantle, carbon is a scarce resource, not even figuring in the eight most abundant elements (*e.g.*, in decreasing abundance O, Si, Al, H, Na, Fe, Ca and Mg). Carbon arrives in the oceanic system mainly from the atmosphere, where it is the fourth most abundant element, ~0.003%, after N, O and the neutral gas Ar, the last of which is ~300 times more abundant. A secondary source for carbon is bicarbonate ions, produced through solution of rock materials, and swept *via* rivers into the oceans. Carbon dioxide forms a substantial amount by weight

of limestones, but even the average shale contains significant CaCO<sub>3</sub>, ~5% of its weight. The solution of limestones and breakdown of shales thereby cycles significant amounts of CO<sub>2</sub> into the atmosphere and hydrosphere. The solution and precipitation of carbonates is a crucial aspect of the oxygen-carbon dioxide, photosynthesis-respiration, biogeochemical system on this planet.

Calcium, in contrast to carbon, is relatively abundant, making up ~2% of the lithosphere. The ultimate origins of calcium (and magnesium) in the oceans are the Ca-rich silicates, particularly plagioclases and pyroxenes, available by weathering either from intrusive complexes or volcanic piles. It is surely not coincidental that calcium-rich feldspars dissolve more readily than their counterparts at the other end of the Bowen reaction spectrum. During the early Precambrian, with a reducing CO<sub>2</sub> atmosphere saturated by acid-rain clouds, and in the absence of protective soils and plant cover, combined physico-chemical weathering processes would have been very rapid. Rapid erosion rates are evident in the kilometre-thick piles of sediments accumulated at continental margins in the Precambrian. Such thick successions are rare in the Phanerozoic. Archean carbonates are exceptionally scarce; this may be related, in part, to their metamorphism, or relative carbonate solubility in an acid ocean and thus preservational scarcity, but is perhaps also a feature of undersaturation or the scarcity of carbonates in the oldest oceans (Fig. 1). It is not clear whether the Archean ocean was mildly acidic, with a pH of <7, the general belief, or strongly alkaline (a pH of 8.5 is suggested by Kempe and Kazmierczak, 1990). Archean fossils are also a rarity, and most are probably dubiofossils. Buick (1991) has pointed out that most Archean cherts, the primary places to look for microfossils, were deposited in greenstone belts, probably reflecting preservation under hot, acidic and reducing fluids. Most later cherts rich in fossils are associated with limestones precipitated in "normal" shelf sedimentary environments.

Limestones, as a storehouse of carbon, did not become common until the beginning of the Proterozoic, some 2.5 billion years ago

(Fig. 1). Since then, the oceans appear to have been saturated with respect to calcium bicarbonate (Westbroek and Dejong, 1983). The early Earth atmosphere was probably also exceptionally warm: the first 2 billion years of Earth history may have had such a runaway greenhouse effect that life would have been difficult, except for thermophile, halophile or acidophile archaeobacteria. This may have been partly balanced by the "faint young Sun paradox", since, theoretically at least, the sun's luminosity 4 billion years ago was lower (see Kasting, 1992 for a review of this question). The introduction of progressively more complex cells, especially the advancement from procaryotic eubacteria to eucaryotic cellular organisms, may have played a major role in setting climatic gradients, as well as increasing  $\text{CaCO}_3$  precipitation. The oldest glaciation events are known from Huronian sequences ~2.1 billion years ago. Photosynthesis by cyanobacteria and algae thus appears to have been a leading factor in cooling the global climate to respectable levels by removing  $\text{CO}_2$  (Schwartzmann and Volk, 1989).

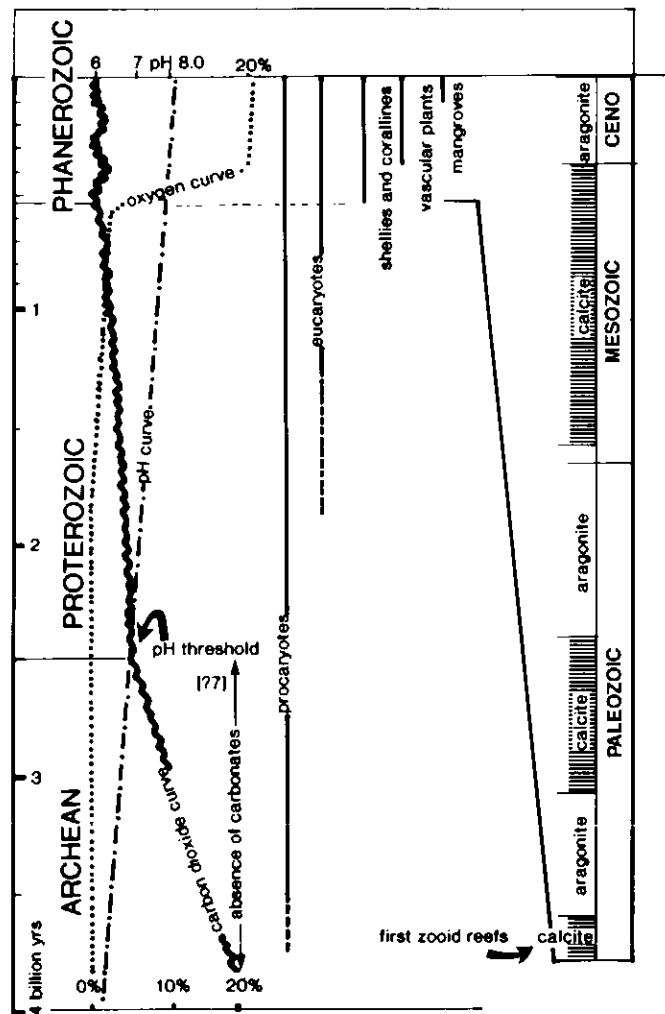
With the development of a thicker continental crust, and therewith the expansion of continental shelves of substantial width of the order of 100 km or more, early Proterozoic carbonate shelves expanded in tropical and subtropical latitudes. These carbonate shelves were richly populated by carbonate-accreting organisms, forming distinctive stromatolite communities (as microbial mats) under a reducing atmosphere and mildly acidic conditions. A model for such conditions might be Gotomeer, a restricted marine basin along the coast of Bonaire (Caribbean), where sulfate reduction leads to microbial precipitation of aragonites in very shallow, <1.5 m, hypersaline, weakly acid waters (Kobluk and Crawford, 1990). The organisms producing the Early Proterozoic microbialite microenvironments were cyanobacterial, but underneath the mat, within the substrate, there were probably sulphate-reducing bacteria which, together with the mat surface dwellers, "fixed" the chemical environment in which  $\text{CaCO}_3$  was precipitated and cemented. The ocean system attained an alkaline pH, perhaps in the order of at least 7, ~1.7-1.4 billion years ago (Holland, 1978), with the arrival of the first nucleated cells, the eucaryotes, largely in the form of 5-50 micron-sized red and green algal cells (Fig. 1). But even these, at this time, seem to have been unable to secrete  $\text{CaCO}_3$  as rigid or semi-rigid microskeletons.

Another major revolution in the development of life on the planet was for monerans (procaryotes, cells without a nucleus), protostians (single-celled or simple aggregates of eucaryotes), and animals to secrete  $\text{CaCO}_3$  within or directly around their cells, e.g., their cell walls (Pentecost and Riding, 1985). This happened with the Cambrian explosion in life forms. Oceanic pH must have

been near the present-day figure of ~8, a basic, minimal figure for the beginning of skeletal organisms, the fertilization of invertebrate eggs, and normal respiration. Not only did the invertebrates produce skeletons for the first time at the beginning of the Phanerozoic, but also the cyanobacterial monerans (e.g., taxa like *Renalcis* and *Epiphyton*), and perhaps the first agglutinated forams (protocists), which used  $\text{CaCO}_3$  as a glue to construct their walls. The arrival of sufficient carbonate ions in the oceans, reflecting saturation levels, was important not only to those organisms utilizing carbonates as skeletal components, but also to those organisms which had a phosphorus-based skeleton. The strength of a phosphatic exoskeleton depends largely on its calcium content. Calcium provides a rigid architectural framework for mechanical purposes,

such as locomotion and muscle attachment, as well as a protective mechanism, a housing to shelter organisms against the environment or predators. Curiously enough, the presence of organic phosphate inhibits calcification, especially for aragonite. Symbiotic algal zooxanthellae appear to remove it in modern corals, but phosphate oversupply may be able to kill off carbonate-producing organisms (Hallock and Schlager, 1986). Thus, there is a suggestion that even the Early Cambrian invertebrate reef-formers, the archeocyaths, were zooxanthellate in order to enhance  $\text{O}_2$  production and stimulate carbonate secretion.

The modern ocean appears to be aragonite dominated. The most abundant carbonate-secreting shelly animals (the molluscs) and coralline elements (scleractinians, hydrozoans, octocorals) that dominate the



**Figure 1** Chronological range chart of features relevant to biological carbonate production in the oceans. The oxygen-carbon dioxide balance (fluctuating) and pH balance (here assumed to be gradual and consistent) in the ocean-atmosphere system is a reflection of biological evolution. The pH 7.0 threshold is suggested to have been crossed by the end of Archean time 2500 m.y. ago, and the terminal Precambrian pH was probably near 8.0, reflecting rapid calcite deposition by invertebrates and eucaryotes, and requirements for fertilization and larval settlement. The initiation of a biologically diversified carbonate substrate began in the Middle Ordovician (Caradoc), with modern  $\text{O}_2$  content of the atmosphere by the end Devonian, arriving with the development of terrestrial forest cover.

benthos today are aragonitic, their skeletons usually dissolved or converted to calcite at death (thus decreasing their chances for preservation). This is a relatively peculiar situation. Paleozoic corals and shells, largely made of calcite, are usually much better preserved than their Cenozoic and Mesozoic counterparts. Middle Paleozoic oceans appear, therefore, in contrast, to have been calcite dominated. Why this should be so is not fully understood. Also, the present-day climate is in a relatively cold, abnormal, "icehouse" phase compared to much of the Phanerozoic. Ancient oceans, especially those of the mid-Paleozoic (Silurian to Late Devonian) and Mesozoic (mid-Triassic through Cretaceous), and thereby for most of the Phanerozoic, were commonly much warmer. Using complex data sets, based on isotope mass balance models and carbon isotopic calculations for ancient seawater, taking into account sedimentary burial of organic matter, continental weathering of silicates, carbonates and organic matter, and calculations of volcanic and metamorphic degassing, Berner (1990), independently confirmed that  $\text{CO}_2$  levels were higher during these periods, and lower in the Permian-Carboniferous and Cenozoic. It is thus possible that the aragonite-calcite balance was affected by both temperature and  $\text{CO}_2$  content of the oceans. Calcite precipitates more readily in colder waters, and dissolves more quickly in warmer, and the variation in  $\text{CO}_2$  is a possible driving cause (Palmer *et al.*, 1988; Wilkinson and Walker, 1989). The peculiar absence of calcified Late Paleozoic stromatoporoids, which were among the most abundant reef-formers in the mid-Paleozoic, has been suggested to be due to decreases in oceanic alkalinity and carbon-

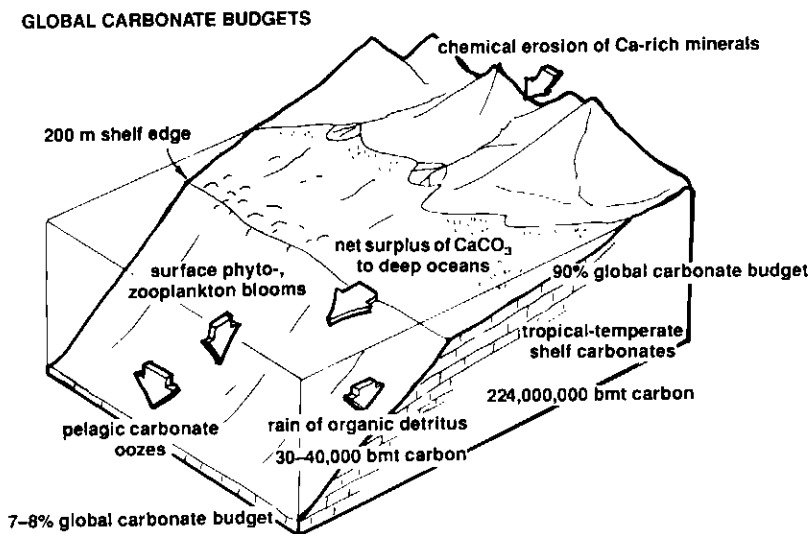
ate supersaturation (Kazmierczak and Kempe, 1990). There is, as yet, no independent evidence that oceanic alkalinity fluctuations were significant enough in the Phanerozoic to affect skeletalization, although  $\text{CO}_2$  content would have affected pH.

Are oceans steady-state biogeochemical systems over the very long term, *i.e.*, millions of years? It is increasingly evident that not only have the oceans changed progressively during geologic time, but that they have undergone cyclical variations in their chemistry, perhaps modulated or even controlled by the evolution of the earth's complex biotas. Substrates which are dominated by or consist entirely of calcium carbonate are thereby widespread, particularly in equatorial belts that favour precipitation over dissolution. The relative significance of the shelf environment versus the deep sea for volumetric abundance of calcium carbonate deposition is disputed. We know that the warmer surface waters of oceans are supersaturated with respect to carbonates, and that the deep sea is relatively undersaturated (Li *et al.*, 1969). This undersaturation, and resultant dissolution of carbonates in the deeper ocean waters, are caused by the "coca cola" effect: cold, carbonic acid,  $\text{CO}_2$  under pressure dissolves calcium carbonates. Thus, shallow shelves favour precipitation, and deeper basins, solution. Nevertheless, sufficient oxygen is available at depth to allow for the precipitation of some proportionally thin, layers of calcareous oozes (such as foram or pteropod oozes today). On the one hand, abyssal ocean regions make up ~70% of the present-day earth's surface (some  $332 \times 10^6 \text{ km}^2$ ), and on the other, shelf-slope areas make up ~7.5% ( $27 \times 10^6 \text{ km}^2$ ). The continental shelf is three times as biologically produc-

tive as the open ocean (the shelf producing organic matter at the rate of  $\sim 600 \text{ gm} \cdot \text{m}^{-2}/\text{a}$ ; Bolln, 1970). Approximately 40% of the ocean floor is covered by thin calcareous oozes, and an equivalent percentage of the shelf produces much thicker carbonate sediments. Parts of the Great Barrier Reef with full coral cover generate  $\text{CaCO}_3$  at the rate of  $10 \text{ kg} \cdot \text{m}^{-2}/\text{a}$  (Kinsey and Hopley, 1991), the Bahama Banks accumulate calcium carbonate at the rate of  $\sim 0.5 \text{ kg} \cdot \text{m}^{-2}/\text{a}$ , and the deeper ocean floor, ~1% of the latter. If these figures are reasonable approximations, continental shelves may be producing at least 12 times as much carbonate as the open ocean, and shelves are, in essence, the planetary carbonate factories (Fig. 2). Moreover, carbonate shelves and their acme, reef ecosystems, provide a net surplus of carbonate which is shed into the oceans by currents and downslope gravity transport. This points to the tropical and subtropical shelves, and the limestones they produce, as the world's largest carbon storehouses. Deep-water carbonates today provide ~8% of the total carbonate supply, and deep-water carbonates are cycled approximately eight times faster than shelf carbonates (Wilkinson and Walker, 1989). It has also been estimated that ~80% of calcium carbonate formed near-shore or in the upper ocean layers dissolves in the deep sea upon sedimentation (Gieskes, 1974). In order to explain that 60-80% of carbonate accumulation occurs today in deep waters, a very rapid, short-term flux or dissolution rate stimulated by  $\text{CO}_2$  is required.

Caldeira (1991) has ingeniously proposed that the Mesozoic-Cenozoic oceans have changed from a steady-state mode dominated by continental shelf precipitation of carbonates (Mesozoic) to a pelagic, deep-ocean carbonate precipitation phase, with a high  $\text{CO}_2$  flux (which prevails in the Cenozoic). This may have been triggered by the evolution of calcareous plankton, *e.g.*, the globigerinids and coccoliths. If this model can be pushed back in time, a similar oceanic conversion may have taken place from the mid-Paleozoic to Late Paleozoic (Fig. 1). The mid-Cambrian to mid-Ordovician oceans are also unique; zooid reefs are virtually nonexistent, and microbialite precipitation of carbonate dominated as it did in the Proterozoic. Were these Early Paleozoic oceans dominated by shelf or pelagic carbonates? Indirect evidence favouring such deep-water or cold-climate carbonates for this time needs to be discovered. The global ocean system may fluctuate between these states, pending atmospheric  $\text{CO}_2$  content and ice-house-greenhouse climates.

The residence time of calcium in the oceans is ~850,000 years (for Mg ~10 m.y.; Holland, 1978). This is one of the fastest cycling schedules for any of the major oceanic dissolved elements. Thus, river input of calcium is rapidly absorbed biologically, and



**Figure 2** Global productivity of the oceanic carbonate factories was dominated by the shelf environment (~90%), followed by the deep sea (7-8%). The balance was probably produced in the terrestrial setting. Organic matter played a significant but more readily cycled role. Figures in billions of metric tons (bmt) from Poldervaart (1955).

precipitated in the form of exoskeletal shells, endoskeletal crystal nuclei or needles, or basal skeletons. The reason for this becomes evident when we realize that the other major elements in sea salts, e.g., Na, Mg, K, Sr, Cl, play only a trivial role in biological skeletal production, although they are needed for "soft tissue" cellular processes, such as metabolism, enzyme production, growth, reproduction, biogeochemical cycle moderation (e.g., pH control), respiration and photosynthesis. Major oceanic overturns of productivity, explosive plankton radiations, and mass extinctions may play a major role in producing fluctuations in ocean chemistry through time. The living biosphere may thus control, at least theoretically, secular variations in ocean chemistry, much as predicted by Lovelock (1988). Geologists tend to favour ideas that plate tectonic processes, such as sea-floor spreading, plate collisions and subduction, mountain and plateau building, and volcanic activity or even extra-terrestrial events, have provided the mechanisms for major changes in oceanic carbonate chemistry with time. Probably geologic and paleobiologic processes are intimately intertwined.

The current carbonate output of the oceans consists of aragonite, calcite and small amounts of dolomite. The surface water of the oceans is supersaturated with respect to carbonates (Holland, 1978). The rate of carbonate production may be as high as  $13 \text{ kg} \cdot \text{m}^{-2}/\text{a}$  in modern reefs, but  $\sim 2.5 \text{ kg}$  is a shelf average (Chave *et al.*, 1972; Guillaume, 1990; Kinsey and Hopley, 1991). Reefs are net producers of carbonate, which may spill back over the shelf or down the shelf slope and, alongside mangrove ecosystems, may be major accretionary mechanisms for carbonate shelf expansion. Deep-ocean water is normally undersaturated for calcium carbonate below the carbonate compensation depth (CCD), since  $\text{CaCO}_3$  is more readily precipitated in warmer waters and more readily dissolved in cooler waters. Dolomite ( $\text{MgCa}(\text{CO}_3)_2$ ) is relatively minor because few organisms are capable of secreting dolomite, and the amounts precipitated in evaporitic environments are almost exclusively restricted to the coastal sabkha environments or alkaline lakes in desert belts. Only cyanobacteria, some algae, and fungi play any biological role in Mg precipitation, perhaps primarily in scavenging Mg from seawater in microbial mats. Also, dolomite is much less soluble under average pH conditions (why animals appear incapable of producing dolomite skeletons is a puzzle, as they can produce any of approximately 100 minerals; Lowenstam, 1981). Organisms produce nearly all carbonates today. However, abiotic precipitation of calcium carbonate, usually in the absence of light (and thereby the absence of photosynthetic processes), plays a role in the production of ooids, some aragonitic needle mounds, and in the filling of

reef cavities by various cements (Ginsburg and James, 1976). But even here, bacteria, fungi and other microbes may play some role as buffers or microenvironmental controllers, forming micron-thick films over grains or surfaces.

#### ORGANIC MATTER AND CARBONATES

Organic matter (=organic detritus) is differentiated as the non-mineral, particulate residues of disintegrated soft tissues and imported dead bacterial, phyto- and zooplankton, land plants, and animal materials incorporated into the substrate. This excludes the biological skeletal production of aragonite or calcite, which makes up the carbonate fraction of sediment (and in the case of siliceous oozes or phosphorites,  $\text{SiO}_2$  and  $\text{PO}_4$ ). Organic detritus does not include living organisms, nor nutrients. Nutrients are those constituents required by plants (Levinton, 1982). These encompass dissolved inorganic forms (such as ammonia and nitrates) and organic forms (such as amino acids, vitamins, proteins, fatty acids, carbohydrates and sugars). In marine environments, organic matter in nearshore habitats may be partly terrigenous or be produced *in situ*; in offshore habitats it is largely marine derived. Dissolved nutrients, organic matter, and living biomass occur in the ratios of 100:10:2 in sediments (Strickland, 1965). In most carbonate rocks, the organic matter which remains after dissolution of the carbonate fraction in acetic, formic or hydrochloric acids is trivial, and  $<1\%$  by weight of original sediment mass. But in some instances, as in black shales or sapropelic rocks, it can be substantial and constitute up to 100% of the sediment. Organic detritus is broken down mechanically, bacterially and *via* chemical leaching. Under appropriate conditions, when it is not recycled biologically as a food resource, organic matter may ultimately be converted to hydrocarbons.

The amount of organic matter on the sub-

strate is normally minute by comparison to the volume of carbonate muds, silts or sands. An exception may be the mangrove ecosystem; large amounts of mangrove litter are crucial to a whole range of benthic biota, even though little of this will be preserved in the geologic record (Risk and Rhodes, 1985). Abnormal concentration of organic-rich sediments in the oceans is traditionally attributed to anoxic conditions, which have both spatial and temporal variance. Reducing conditions on the sea floor inhibit scavenging and recycling of organic matter as a food resource for benthic invertebrates. Thus, conventional wisdom has dictated that sluggish, stagnant basins induce concentration of organic matter. However, a rich rain of organic plankton also stimulates microbial decay, which in turn raises the level of  $\text{CO}_2$  and  $\text{SO}_2$  in the substrate. In the Cenozoic, there are few examples of black organic-rich mud environments, the best known of which is the Black Sea. Pedersen and Calvert (1990) and Calvert and Pedersen (1991) have recently pointed out that Black Sea sediments are not particularly enriched in organic matter. They suggest, instead, that increased primary production of zoo- and phytoplankton in the surface ocean layers explains far more clearly the great abundance of organic matter in black shales at specific periods in Earth history. This may account for the abundance of widespread black shales in the Late Caradoc (Ordovician) and Cretaceous, time periods when the world's oceans do not appear to have been sluggish, and when widespread distribution of faunas over vast interior sedimentary basins suggests good circulation and reasonable oxygenation.

Organic detritus is of immediate importance to carbonate-dwelling organisms in two direct ways: as a food resource to be harvested or mined, and as a modifier of substrate chemistry. Organic matter is more abundant in the silt to mud-size fractions of sediment, where it tends to be trapped, and

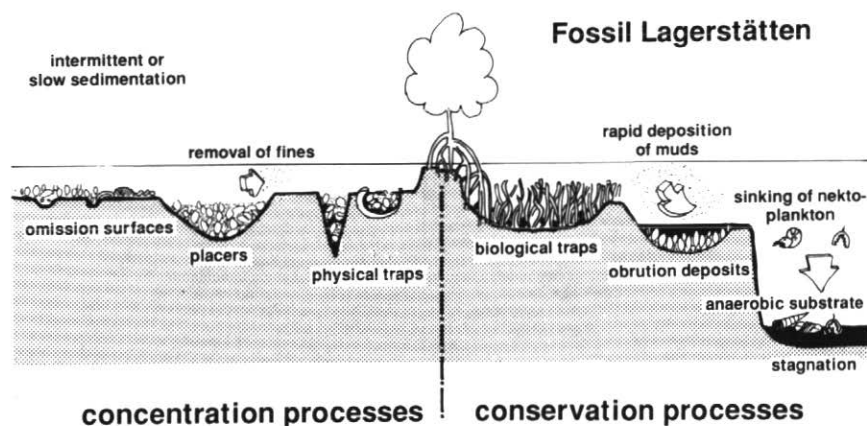


Figure 3 The biological (conservation) and physical (concentration) factors involved in the production of fossil ore deposits or Lagerstätten, as visualized in marine carbonate deposits (after Seilacher, 1970). The tree denotes the mangrove and adjacent seagrass community as biological traps.

rather scarce in sandy or conglomeratic substrates, where it is oxidized. There is a broad increase in organic matter as sediment particle size decreases, especially in siliciclastic substrates, and, hence, in clays. This increase is paralleled by a greater abundance of deposit feeders (the miners of sediment) as sediments become muddier, and a decline in the number of suspension feeders (whose feeding apparatus is clogged up by fine muddy fractions; Levinton, 1982). However, pure-clay substrates are difficult for deposit feeders to penetrate because of early compaction, greater shear strength, and minimal porosity and permeability. Deposit feeders, particularly the marine polychaetes, therefore favour muddy substrates which have some silt-sand and organic content. The same rationale may be different for calcareous muds; these appear to be readily exploitable by many deposit feeders, perhaps because they are less cohesive and more amenable to "mining".

It has long been known that bacteria produce organic coatings and films around every sedimentary particle (Levinton, 1982). Total live bacterial volume present around grains and in interstitial pore fluids is difficult to estimate. However, these bacterial films are often essential in inducing larval settlement of benthic invertebrates. Sterilized sediment tends not only to inhibit the arrival of benthic larvae, but also to limit their metamorphosis to adult sizes. Larval settlement (because of the timing of fertilization) is usually triggered to coincide with nutrient output, temperature changes and tidal effects. There is, therefore, a seasonal overprint. Larvae, especially of sessile invertebrates, must find a suitable substrate, a difficult task with a high mortality and low success rate. They are sensitive to the physical nature of the substrate (grain size, softness, topography), they often gregariously seek out their own kind (adults), and must detect chemical or bacterial clues to their habitat.

#### LAGERSTÄTTEN IN CARBONATE SUCCESSIONS

Fossil Lagerstätten, literally fossil "bedding sites" or fossil-enriched "ore deposits", have come to be defined as unusual skeletal concentrations in remarkable settings. Some taphonomists include here the more common carbonate shell and phosphatic bone beds of normal marine environments (Seilacher, 1970; Seilacher *et al.*, 1985). Seilacher has chosen to exclude reefs as fossil Lagerstätten (though in most senses of the word reefs are, indeed, Lagerstätten). Such unusual concentrations of fossils give us special insights into biotope conditions, the fate of soft parts as well as skeletons, sedimentary processes, and early diagenesis. Kidwell *et al.* (1986) preferred the term "fossil concentration" for normal accumulations of shelly fossils, and distinguished this from a "fossil assemblage", which is simply

any suite of fossils found on a bedding plane surface, not necessarily a concentration. Seilacher identified several types of "Lagerstatt" categories, sorting them into concentration and conservation beds with a broad facies distribution related to shorelines (Fig. 3). These can be directly applied to carbonate substrates. *Concentration beds* include: those featuring *slow or intermittent rates of sedimentation*, favouring accumulation of skeletons or soft parts (evident on carbonate hardgrounds); *placers*, where winnowing removed the fines and transport concentrated the coarser fragments (e.g., on reef flats); and *traps*, such as grooves, pockets, fissure or shell fillings that concentrated skeletons. *Conservation beds* encompass: *stagnation deposits*, taking place in sapropelic or anaerobic conditions which prevent attack by scavengers, predators or disturbance by bioturbators (e.g., reef lagoons); *obruption deposits*, with local biotas smothered by rapid sediment burial (tempestites, inundites, turbidites, tidalites, etc., for example, in carbonate slope areas or lagoons); and *conservation traps*, such as petroleum seeps, seagrass and mangrove habitats.

In analysis of fossil Lagerstätten, the functional morphology of organisms is of great significance in their preservation. Fossil bivalves have a preservation potential differing from most articulate brachiopods under the same sedimentological conditions. Bivalves favour an aragonitic shell, which rapidly recrystallizes and often dissolves after death, a weak hinge mechanism, which consists of shallow ridges and grooves, and a tough ligament, which tends to pull the shell open. Thus, bivalves usually disarticulate in short order when the soft parts decay. Articulate brachiopods, on the other hand, especially those with an interlocking ball and socket hinge mechanism, have two valves which remain closed and hold together firmly after death; disarticulation, therefore, requires greater mechanical energy. Thus, disarticulated bivalves and brachiopods should be differently interpreted. Substrates with a significant or dominant skeletal component are often named after the producing organism. Coquinites, or shell beds, are the result of the accumulation of shelly organisms, such as bivalves (mostly Mesozoic-Cenozoic, e.g., oyster or mussel beds), brachiopods (Paleozoic, less commonly Mesozoic), gastropods, nautiloids (Paleozoic), ammonoids (Devonian-Cretaceous), tentaculitids (Ordovician-Devonian), ostracodes (Ordovician-Holocene), hyolithids (Cambrian), pteropods (Holocene), etc. Encrinurites are made up of crinozoan or pelmatozoan ossicles, nearly always the stems or columnals. Foraminifera (foram sands) or foram oozes may consist of 100% foram tests (e.g., fusulinids in the Late Paleozoic, nummulitids in the Cenozoic). "Coralline" organisms may also form biostromal skeletal accumulations:

green algal *Halimeda* "granola" beds, platy phylloid algal layers, "finger" beds of cylindrical to branching bryozoans, phaceloid-dendroid corals (Holocene *Porites* beds, Devonian *Thamnopora* coral beds, and *Stachyodes* or *Amphipora* stromatoporoid sponge beds), sheet-like bryozoans, stromatoporoids or tabulates, and the meadows of solitary rugosans (see later discussion and Figs. 8-9).

The small-scale geometry of such concentrations may be as stringers, beds or biostromes  $\leq 1-2$  m thick, patches, nests or pods, channels or grooves, lenses, and wedges (figures in Kidwell *et al.*, 1986). Currents, waves, sorting in channels, or gravity on slopes may align elongate shells as unidirectional (if apices point the same way) or bidirectional (either way) or in telescoped fashion. Shells in life position show orientations related to their attachment or sedentary, current stable position. After death, these may be oriented parallel, normal or oblique to the substrate or bedding plane. Disarticulated shells may be further stacked in edgewise position (if concentrations are dense), stacked convex upward or, less commonly, convex downward (indicating sinking to depth), or in current-sorted clusters. All of these convey taphonomic information, particularly in terms of energy regimes.

#### TROPICAL CARBONATE ENVIRONMENTS

The equator bisects the tropical carbonate belts which today, in a global oscillating icehouse setting, terminate at approximately 30° north and south (Fig. 4). The polar regions are essentially devoid of carbonates, instead featuring clays and biosiliceous oozes. Tropical ocean gyres spill warm water over the eastern seaboard, leaving the western shelves relatively cool and barren. These equatorial settings have the thickest, most rapidly produced and geographically broadest carbonate successions on the continental shelves, and the most prominent coral reef development (Heckel and Witzke, 1979). Some carbonate sediment types are limited to tropical and subtropical belts, e.g., chloralgal muds, ooids, grapestones and indurated pellets. Most tropical carbonate habitat settings feature relatively stenothermic skeletal invertebrates; many of the shelly and coralline taxa of modern and ancient equatorial oceans are exclusively tropical in their distribution. However, it is not the average seasonal temperatures which determine their distribution, but the seasonal frost line. For example, around Miami, Florida, seasonal average temperatures would indicate that corals can thrive (reefs are absent), but the area just south of Miami still is affected by occasional seasonal frosts, which have a dramatic effect on the reef flat at low tides. A similar situation exists on the east coast of Australia, where the Great Barrier Reef ends south of Brisbane. Reefs did not develop on



the eastern shelf during the cold Oligocene, but, as Australia moved northward, reefs again began to develop in the north in the Miocene, and continue their development today (Feary *et al.*, 1991). It is not that difficult to draw up lists of groups which prefer the tropics, and even within those groups there are tropical "specialists".

There are broad diagnostic features of tropical carbonate substrate organisms:

- 1) Ability to build larger and more rapidly growing, thick calcium carbonate shells (*e.g.*, giant tridacnid bivalves in the Cenozoic, megalomid bivalves in the mid-Paleozoic), large forams (*e.g.*, fusulinids, nummulitids); presence of ooids, with bacterial films,
- 2) Construction of giant coralline colonies that are metres across, *e.g.*, corals, sponges,
- 3) Specialization in dense, massive colony construction and specific, complex modular growth forms (Rosen, 1986), *e.g.*, cerioid, thamnastreoid, aphroid, cateniform and "brain" (labyrinthiform) corals,
- 4) Increased numbers of symbiotic relationships, *e.g.*, zooxanthellae in hermatypic,

scleractinians, tabulate-stromatoporoid intergrowths in the Paleozoic ("caunopores"), coral and sponge wall-inhabiting polychaetes,

- 5) Capacity to build reefs with a prominent, often frame-building skeletal component, and
- 6) Substantially greater diversity of taxa in single communities.

Groups typical of tropical carbonate habitats encompass the following:

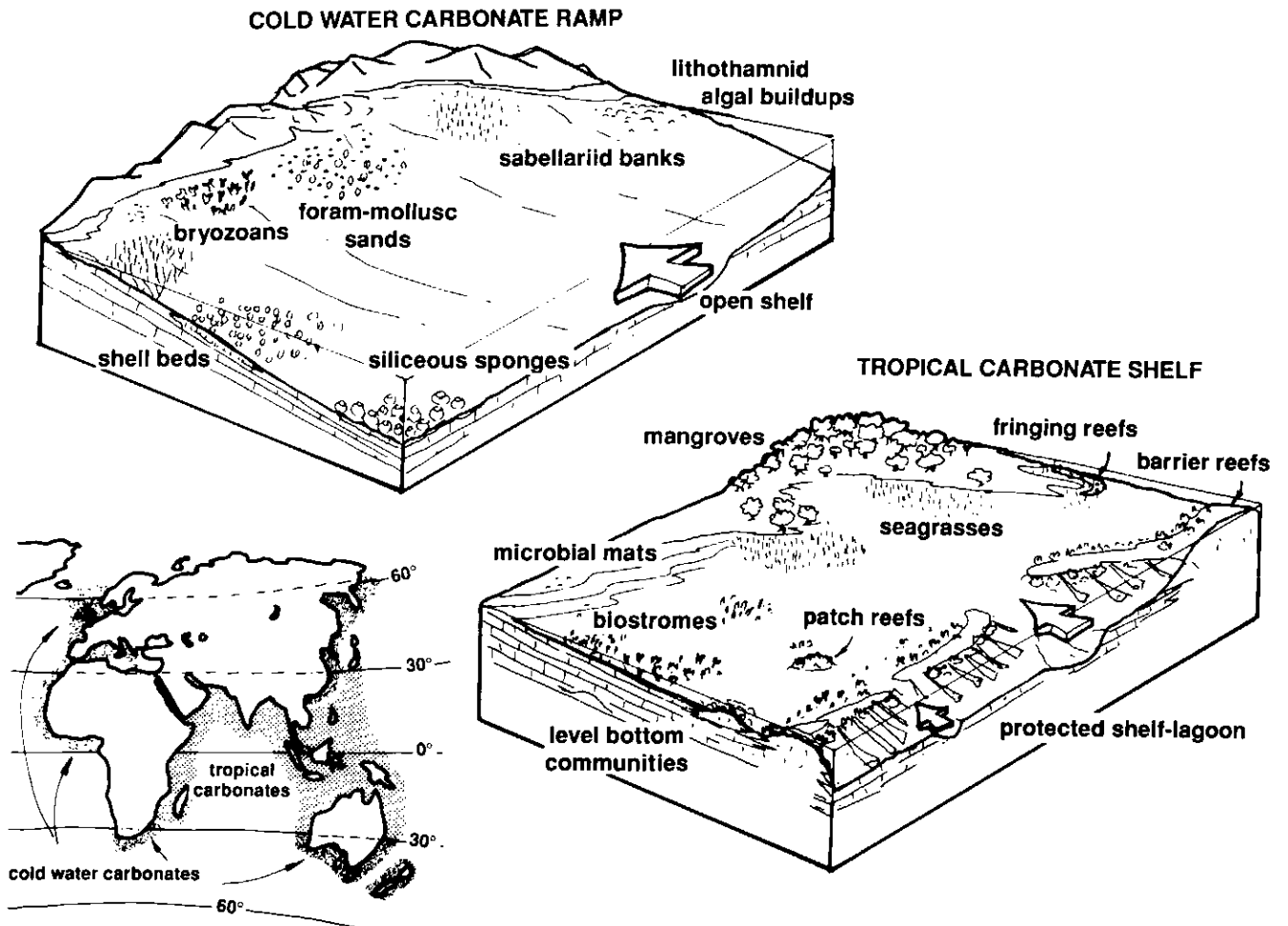
- 1) Mangrove angiosperms and their biota (Late Cretaceous: Retalack and Dilcher, 1981; Davis, 1940; Scoffin, 1970), seagrasses (monocots: Late Eocene-?),
- 2) Reef-building red algae (*Goniolithon*, selenoporids, *etc.*), calcareous green algae or chlorozoans (*Halimeda*, cyclocrinittids, receptaculitids, dasyclads, *etc.*), coccoliths, non-skeletal stromatolites, skeletal porostromatolites,
- 3) Reef-associated forams with larger, thicker-walled, more ornamented skeletons (*e.g.*, fusulinids in the late Paleozoic, orbitolinids, alveolinids, peneroplids in the Meso-Cenozoic), cementing forams,
- 4) Calcareous sponges, stromatoporoids,

5) Larger and complex skeletal hydrozoans, most tabulates, most colonial rugosans, large solitary rugosans,

- 6) Larger and more diverse brachiopods in the Paleozoic, *e.g.*, atrypids, pentamerids, strophomenids, lingulids. Interstitial and cementing brachiopods in the Meso-Cenozoic,
- 7) Specialist bivalves (tridacnids, megalomids, pteriods, rudistids, *etc.*),
- 8) Most nautiloids (*e.g.*, *Nautilus* today, most complex orthocones in the Paleozoic),
- 9) Most ammonoids,
- 10) Specialist gastropods, *e.g.*, conids, cerithiids, spider conchs, large shelled forms,
- 11) Specialist crustaceans, *e.g.*, hermit crabs, fiddlers,
- 12) Ornamented ostracodes, specialist trilobites, many mound-building shrimps, and
- 13) Many crinozoans, some regular and irregular echinoids.

**TEMPERATE OR COOL-WATER CARBONATES**

Increasing interest in cool (*i.e.*, temperate or high-latitude) water carbonates in the 1970s



**Figure 4** Idealized features of Holocene cold and tropical carbonate ecosystems. The map shows the confinement of the Holocene cold-water carbonate ramp regime to western continental shelves and high latitudes above 30° (after Nelson, 1988). Reef-rimmed shelves are typical of the tropical latitudes.

(Lees and Buller, 1972; Lees, 1975) has led to a search for environmental and biologic signatures for such carbonate precipitation processes. Although  $\text{CaCO}_3$  production is more difficult in cooler shelf or deeper ocean waters because of the solubility of aragonite, the process is still quite widespread in higher latitudes from 30° to 50° (Fig. 4). Calcite is favoured in cooler seas today, but, by analogy, there are apparently contradictory data from the past; warm Paleozoic seas are usually calcite-dominated. In the higher latitudes, the annual temperature range of sea water is steeper, and can range from near freezing to 20°. Thus, temperature effects should be stronger than in the tropics. Lees (1975) coined the term *foramols*, or foram-molluscan associations, for such shelf sediments. Shell banks and shelly sands are very widespread, probably to a greater degree than in tropical carbonate habitats. Leonard *et al.* (1981) and Nelson (1988) have identified general keys to non-tropical carbonates, which are summarized below. Since reefs are absent, shelves tend to be open oceanic systems, unless the shelf is flanked by carbonate sand banks. Carbonate muds tend to be produced by physical or chemical reduction of grain size, rather than by direct *in situ* precipitation from green algae, such as *Hallimeda*. Glauconites and phosphorites are more common components of the carbonates. Oolites are absent. Such cold-water carbonate models have been applied, for example, to the Permian of Tasmania (Rao, 1981) and Middle Ordovician (Black River-Trenton) carbonates of Ontario and New York (Brookfield, 1988).

Biotic groups typical of cooler water carbonates include the following:

- 1) Red algae, such as *Lithothamnion*, *Corallina*, but few skeletal chlorophytes. Stromatolites are usually rare (Shark Bay lies at 25° south, but on the cooler west coast). Spongiostromes and "stromatolites" may be common. Seaweeds (brown algae) are common to abundant; seagrasses are less common, disappearing at ~40° north and south.
- 2) Specific families of benthic forams, mostly smaller taxa, with less diversity.
- 3) Spiculate demosponges and siliceous sponges.
- 4) Smaller solitary corals and fasciculate ahermatypic corals (soft-bodied anthozoans in shallow shelf habitats).
- 5) Abundant bryozoans.
- 6) Common to abundant regular and irregular echinoids.
- 7) Barnacles, few burrowing shrimps.
- 8) Vermetid gastropods and tube-building worms (sabellariid banks: Carey, 1987).
- 9) Abundant and diverse, small to large burrowing and epibenthic bivalves (oyster, mussel banks), abundant cuttlefish tests.
- 10) Abundant large articulate brachiopods: terebratulids, rhynchonellids.

### ORGANISM-CARBONATE SUBSTRATE INTERACTIONS

The biotic effect on the mass properties of carbonate substrates which sustain large benthic populations is considerable (Vernberg and Vernberg, 1981; McCall and Tevesz, 1982). Organisms contribute in four direct ways to substrates: through bioturbation, and by providing their skeletons, their soft organic tissues, and their excretory by-products. The level of sediment modification is related to the sizes and activity rates and densities of organisms, which decrease with increasing water depth. Organisms have the capacity to alter: 1) grain size, shape and sorting, usually by digestive activity; 2) the texture and fabric of the sediment, by mechanical displacement of substrate; 3) sedimentary structures such as bedding, lamination and surface topography; 4) water content and fluid movement in pore spaces, by respiration and excretion; 5) compaction; 6) shear stress and stability, e.g., softness or hardness of the substrate; 7) grain composition, such as selectivity *via* feeding and harvesting processes; and 8) sediment chemistry, through the addition or deletion of soluble or biodegradable elements or materials (Levinton, 1982).

Organisms require substrates as a food resource (the organic matter in the sediment), for anchoring, fixation and stable platform, as larval settlement sites, and as shelter or protection. Schäfer (1962) coined the terms *vital* and *lethal* substrates to mark the presence or absence of organisms, and *liposubstrates* and *pan-substrates* to characterize substrates with omission surfaces and areas of continuous sedimentation. He thereby recognized both biological and sedimentological input. The absence of organisms on or in Phanerozoic substrates does not necessarily mean that the substrate was hostile to organisms. The sea bottom is not universally packed with shelly, coralline skeletal or soft-bodied elements; settlement processes were often a matter of chance, rates of sedimentation may have been relatively rapid, or seasonal temperatures excessive.

In turn, the substrate may be a strong (often the dominant) determining factor in the kinds of organisms that come to rest upon it. Suspension-feeding organisms selectively favour a firm, hard or rocky ground or coarse-grained substrates; deposit feeders prefer the silty-muddy fractions (Gray, 1981). The benthic biota have learned to cope with soft, muddy substrates by adaptively evolving mechanisms to raise themselves off the sea floor or to prevent sinking into unstable substrates. Some organisms (the generalist pioneers) have the capacity to move quickly into areas of fresh sediment influx, especially after storms. Others (the climax specialists) require a substantial lag time and will only move in when the substrate is stabilized or when suitable attachment sites are available. Rates of

sediment accumulation are also important. Areas of rapid sedimentation favour deposit feeders and burrowers which have escape mechanisms to prevent "drowning" in sediment. Areas of slow, intermittent or non-deposition favour suspension-feeding organisms. Ultimately, the substrate is also the burial medium that captures not only the benthic fauna and flora, but also the planktic and nektonic biota that occupy the water mass above it, and provides us with the fossil record. Analysis of fossilization mechanisms has led to a special subdiscipline called *taphonomy*, defined as the study of the burial and preservation processes of organisms (Briggs and Crowther, 1990; Brett, 1991; Allison and Briggs, 1991).

Several remarkable biological revolutions in substrate modification have occurred through geologic time. The first of these was the evolution of the Ediacaran soft-bodied benthic animal community, the oldest of which appears to have preceded the Late Precambrian glaciation event, ~630-580 Ma. Ediacaran trace fossils indicate that the first mobile invertebrates moved around on the substrate and were capable of shallow burrowing parallel to the sediment-water interface. The second development was the skeletalization of the Cambrian biota (Fig. 1). Skeletons and hard parts (rigid exoskeletons, or internal food gathering mechanisms like radulae or teeth) provided an enormous advantage in plowing through sediment, removing nutrients, or grazing-browsing on microbial mats. The possession of a skeleton became a deterrent to predation. Live or abandoned skeletons also provided the sites for attachment of larvae and adults of fixo- and libero sessile animals, enabling these to produce shelly or coralline pavements. Prior to that time, the only available rigid, stable attachment sites were sedimentary clasts, such as sand grains, pebbles, and boulders or hard and rocky grounds. Thus, the earliest organisms had fewer opportunities for larval settlement.

The earliest shelly fauna (the Tommotian fauna) were largely of meiofaunal (fitting into the 0.1-0.5 mm size range) to small macrofaunal sizes (0.5- <2 mm), and perhaps interstitial, fitting into the sand size range of sediments. The reason for this is obscure; size may simply have been a biological limitation in earliest skeletal forms. The Tommotian fauna preceded the introduction of the larger trilobite and shelly brachiopod-molluscan fauna of the Atdabanian (Early Cambrian). Predation of shelly benthos began in the mid-Paleozoic, accelerating in the Late Paleozoic (Signor and Brett, 1984). However, the large-scale introduction or widespread proliferation of new marine predators expanded greatly in the Mesozoic-Cenozoic, including molluscans (carnivorous snails), starfishes, marine reptiles, skates and rays, birds and placental mammals (Vermeij,



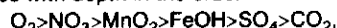
(1987). This resulted in the evolution of the fused siphon, enabling bivalves to become burrowers; deep-burrowing shrimp; and the deep burrowing of the irregular echinoids, among others. It also appears to have encouraged much more thorough exploitation of the substrate, aerating sediment, accelerating local resuspension of fines, and increasing substrate mobility and potential for erosion.

#### BIOCHEMISTRY OF CARBONATE SEDIMENTS

The macro- and microbenthos of substrates have a strong effect on their chemistry. This is especially critical in carbonates, where diagenesis plays a major role, even at early stages prior to lithification. Organisms accelerate the rate of exchange of dissolved elements and compounds across the sediment-water interface, produce and disturb the pH, oxidation and reduction haloes, advect reduced compounds from the lower layers to the water mass above, and cycle the major elements (S, P, N, C). Lithification of carbonates is often rapid and early; beach rock, for example, forms *in situ* while the sediment around it is still mobile. Feeding, burrowing, tube or skeleton construction and irrigation (solid fecal excretion, and lophophore, gill or other respiratory outpumping of fluids and gases) are the main biotic processes which affect solubility and oxidation-reduction reactions in carbonates. Most of these reactions are related to bacterial decomposition and cycling. The macrobenthos translocates sedimentary particles, influencing porosity and permeability. Burrowers, *via* bioturbation, cause advection of fluids and ventilation of gases through burrow linings. Deposit feeders rely largely on bacteria for food and produce significant amounts of fecal pellets (Gray, 1981). Fecal matter alters the microchemical environment by concentrating phosphates, nitrates and sulphates. Mucus linings, stringers, sheets and concentrations produced by benthic invertebrates can produce an enclosing blanket on the substrate, or films around sedimentary particles, thus reinforcing chemical reactions. Most important, diagenetic reactions are associated with concentrations of organic matter and bio-activity.

Substrates are chemically stratified from the surface downward (Meadows, 1986; Hesse, 1986). Chemical reactions appear to be generally more marked in carbonate than siliciclastic sediments, and more sharply defined in finer-grained sediments, especially muds or muddy silts. With increasing depth, the following reaction layers occur: a zone of aerobic respiration ( $O_2$  rich), followed downward by nitrate-fixation, manganese oxidizing, iron hydroxide formation, sulphate reduction and, at the base, methane and fermentation generation (Fig. 5). Sulfate reduction may also occur in the oxygenated layer (Canfield and Des Marais, 1991). The thickness of these layers depends on grain size

(oxidation zones are deeper in coarse-grained, bioturbated sediments) and organic matter content. Such chemical fluxing occurs as haloes around burrows, where bioturbation is common (Meadows, 1986). Some infaunal invertebrates have the capacity to produce specific chemicals which may inhibit microbial activity in sediments (Meadows, 1986). The first stages of oil and gas formation occur as a result of biological activity. Metabolic energy available to bacteria declines with depth in the order



with minimal energy available at depth. Bioturbation tends to increase the subduction of organic matter below the sediment-water interface. In addition, surface grazing and browsing maintain microbial activity at a high level. In hostile environments, the dense spacing of burrows or surface tubes is preferred in maintaining sediment irrigation (Rhoads, 1967). Thus, small size of tubes and dense packing not only stabilize the substrate, but may also be a signature of chemically hostile substrates, as organisms use specific strategies to counteract negative factors.

Trace fossils often have specific gradational associations with oxygen-depleted, reducing environments, as it is clear that infaunal benthic animals have even a more critical requirement for oxygen in their respiratory processes than do the epibenthos. Increasing oxygen concentration in the upper pore fluids of sediments has an impact on the life habits of deposit feeders. Indeed, oxygen content may be a more critical factor than depth control. Ekdale and Mason (1988) have pointed out that from barren, laminated substrates with reducing settings, to well-oxygenated substrates, there is a progression of trace fossils with specific life habits.

*Pascichnia* (surface trails for feeding) are favoured in interstitial water which is dys-aerobic, *fodinichnia* (ichnia systematically mining sediment for food) thrive in organic matter-rich anaerobic sediment with a sediment-water interface which is aerobic to dys-aerobic, and *domichnia* (vertical tube-dwellers) suit well-oxygenated substrates (Seilacher, 1964).

Ecologic succession is important in changing surface and subsurface chemistry. With time, relatively anaerobic sediment can be converted by pioneering elements that live at or near the surface and move relatively little sediment, to a higher-order community in which the oxidized zone expands, the infauna feeds at depth, and particle mixing becomes intensive (Rhoads, 1967). Alternatively, in biostromal to biohermal carbonate environments, rapid growth rates of expanding individuals and colonies may cause aggressive expansion of the cover of sediment, resulting in exclusion of the infauna. Competition for surficial substrate space by invertebrates, such as barnacles and clonal bryozoans and corals (e.g., Jackson, 1983) leads to rapid encrustation as each species stakes a claim (the "squatters principle").

#### MUDDY, SOFT BOTTOMS

There are four main types of marine muddy bottoms with a biological component: clays (clay minerals); calcareous muds (the result of direct biologic precipitation of fine particles by phytoplanktic or benthic bacteria and algae, or the size reduction of larger biogenic particles by biologic processing or chemical breakdown); organic muds (sapropels, pelletal muds); and siliceous muds (diatomaceous, radiolarian ooze), with the last three having a biogenic origin. Evaporitic (i.e., gypsiferous or halitic) muds are excluded here

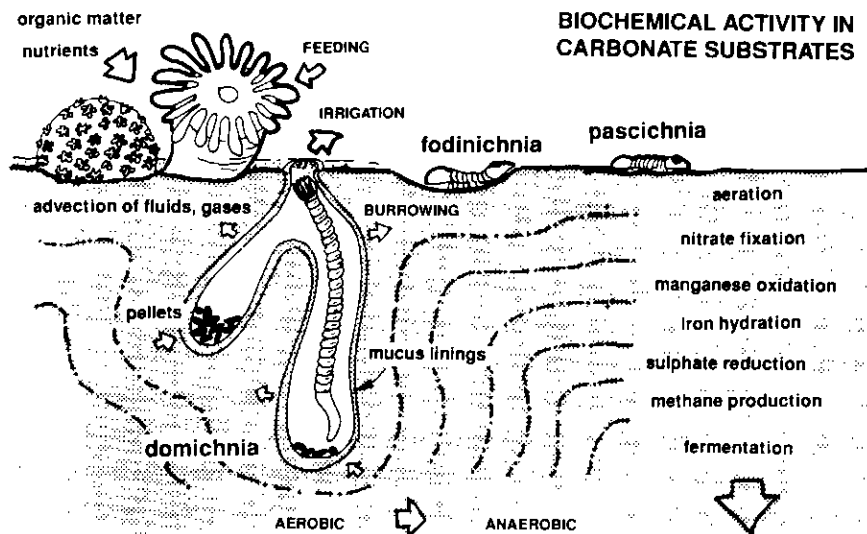


Figure 5 Chemistry of carbonate substrates is strongly influenced by bioturbation (left side) and bacterial production of nitrates, manganese oxides, iron hydroxides and sulphides, methane and carbon dioxide (fermentation; sketch after Meadows, 1986).

because of their minor skeletal or minimal organic content. Muds may contain up to 90% water and are, therefore, usually soft and mobile. Organisms have basically the same problems in coping with life on such soft bottoms: they must prevent sinking, and they have to find mechanisms to cope with the smothering effect these muds have on their feeding and respiratory habits. Both require adaptations. Fine sediments tend to stay in suspension under higher-energy conditions, and to be precipitated under quieter conditions, though carbonate mud may also readily precipitate interstitially even in high-energy habitats (Reid *et al.*, 1990). This restricts environments where such muds are found to quiet-water sheltered embayments, lagoons, or muddy tidal flats (where muds are left behind as tides recede), and deeper water environments, below the fair weather

and storm wave base. Some muds represent drowning events related to abnormal effects (e.g., obrution deposits). Others have a strong seasonal overprint related to annual storms or monsoons.

Soft muddy bottoms are usually level, due to gravity settling of fines, with few irregularities, except those created by the bottom-dwelling biota. Thus, bedding plane surfaces are remarkably even and can often be traced for long distances. Mudmounds are a variant of such level-bottom carbonate mud environments, and are not treated here. Modern mudmounds are generally a feature of waters deeper than 20 m, such as the *Halimeda* mounds of the Great Barrier Reef and Java Sea (Roberts *et al.*, 1987). Such mounds should not be confused with chloralgal (*Halimeda*, *Penicillus*, *Udotea*, etc.) meadows which produce sheets or banks of

muddy sediments. Another general feature of carbonate muds is fine lamination. Rhythmites are not uncommon, and may be due to twice-daily tidal flows in tidal flats or lagoons, or to seasonal factors (deposition in the quiet season), with thicker beds possibly related to Milankovic cycles. Coccolith or organic mud production may be due to seasonal planktic blooms. Some varvites may be non-cyclically produced, e.g., the production of sediment from whittings (Shinn *et al.*, 1989).

Feeding mechanisms of organisms have a broad relationship to sedimentary grain size. Suspension feeders generally decrease in abundance as the mud fraction increases (Sanders, 1958) (Fig. 6). Thus, suspension feeders favour coarser sands, silts, pavements or hardgrounds. Deposit feeders, on the other hand, increase in density with increasing mud content, probably largely because the organic content of muds is greater than that of coarse sediments.

The activity of deposit feeders tends to stir up muds, which excludes suspension feeders. The organic content of sediments is broadly reflected in marine sediment colour: dark gray to black shales hold substantially greater amounts of organic detritus, with the black colour largely derived from carbon breakdown or finely disseminated sulphides. The bacterial content of sediment also increases with mud content, since bacterial sizes are in the 2-10 micron range, close to that of mud particles, and bacteria utilize electron charges to fix to such grains. There are some limitations to the increase in deposit feeders in muds. These limitations relate to the increased cohesiveness, compaction capacity and shear strength of muds, which make it more difficult for deposit feeders to plow through, unless a certain silt, sand or "humus" loosening factor is introduced. A second limitation is the amount of organic matter present. The number of deposit feeders tends to peak at 3% organic matter and drop off markedly when it increases to more than 5% (Fig. 6). At higher organic levels, anaerobic bacterial activity increases and animal respiration becomes difficult. This is seen in "black shale" environments. Seasonal surface plankton blooms may produce increased bottom organic content, which causes a decline in benthic deposit feeding inhabitants (Pedersen and Calvert, 1990).

Adaptations by epibenthic suspension feeders to soft muddy bottoms are diverse (Copper, 1967; Bassett, 1984; Brett, 1991), but mainly involve finding ways to prevent sinking (Fig. 7). One strategy for this includes increasing surface area by development of frills, ears, flanges, wings, rapid lateral growth, or flat shells (the "snowshoe effect"). Another strategy is to develop linear extensions of the shell, such as along the hinge of mud-adapted spiriferid brachiopods (the "ski effect"). A third strategy is to grow lateral spines or pontoons ("outriggers"), or to de-

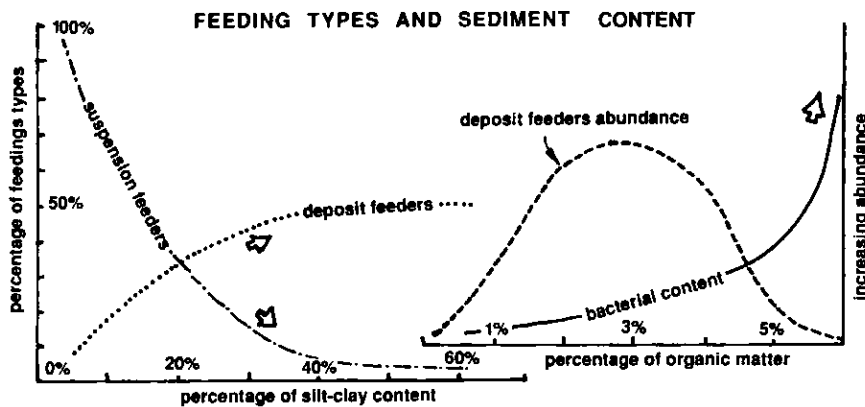


Figure 6 The presence of finer (silt-clay sized) fractions and organic matter in sediments influences the arrival and departure of suspension and deposit feeders (after Sanders, 1958). Deposit feeders decline in abundance if organic detritus content in carbonates exceeds 3%, due to bacterial interference (McCall and Tevesz, 1982).

ADAPTATIONS FOR SOFT MUDDY SUBSTRATES

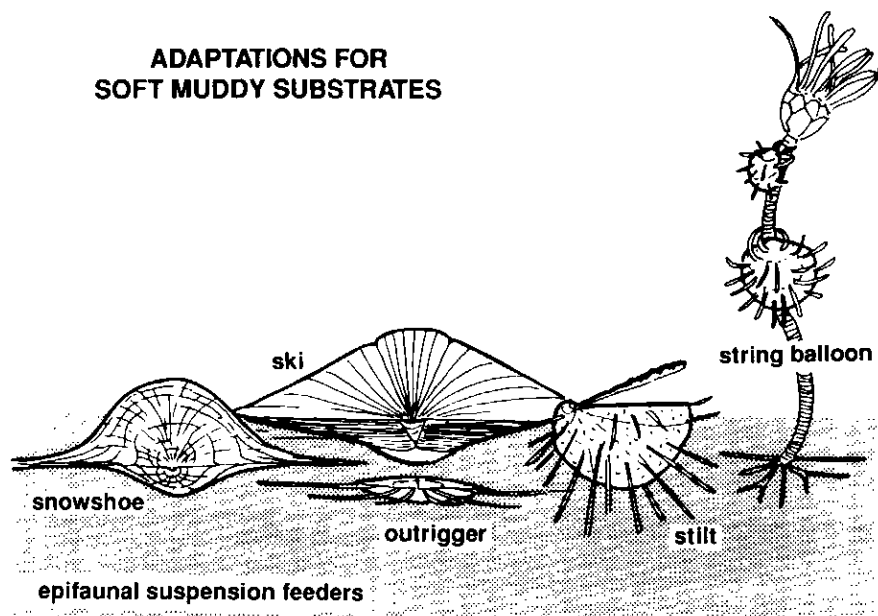


Figure 7 Paleozoic brachiopod adaptations to soft muddy carbonate substrates. Demonstrated in cartoon fashion are snowshoe atrypids (Copper, 1967), ski spiriferids, outrigger chonetids (Racheboeuf, 1981), still and balloon-suspended productids (Grant, 1963, 1966).

velop spines, "prop roots" or poles to raise the organism sufficiently above the sea bottom (as seen in the growth of spines in productid or atrypid brachiopods: the "stilt effect"). A fourth strategy is to use an anchor for attachment and a long stem to rise above the substrate (the "string balloon effect"), or to become epibenthic by attaching to other organisms which have tried the above strategies. Thus, many smaller organisms (bryozoans, forams and larvae of other invertebrates) attach themselves to objects which already occur on the sea bottom.

Muddy bottoms sometimes retard growth, or stunt organisms which may be of "normal" size under optimal conditions elsewhere. Such environmental stunting may be related to difficulties with feeding or respiration in muddy environments, or to the chemical, reducing activity of bacteria in muds. Thus, a prevalence of stunted species, or reduced species diversity, may indicate marginal living conditions in habitats where mud is frequently in suspension or where microbial activity alters substrate chemistry.

Muds are commonly the beginning of new successional cycles (McCall and Tevesz, 1982). The aftermath of turbulence or catastrophic events, such as storms (tempestites), floods (inundites), or submarine avalanches (turbidites) is usually a sheet of muds, the result of the fines coming out of suspension (Seilacher, 1982). These "drown" previous communities and provide a vacant substrate niche. Black shale or sapropel horizons may follow a successional pattern, if oxidation takes place. Soft-bottom successions are initially populated by pioneering organisms with high reproductive rates, greater tolerance for extremes, smaller sizes, and strategies for coping with life on muddy bottoms.

#### MANGROVE-SEAGRASS CARBONATES

Mangroves, in the mangal swamp ecosystem, exist in an intertidal-supratidal tropical halfworld between land and sea, trapping sediment derived from both land and sea, protecting the shore from erosion, and acting as accretionary prisms for sediment away from the shoreline. Mangroves only survive in areas where seasonal temperatures do not drop below 20°C. They occur in low-energy environments primarily affected by tidal currents, which are channelled through them. The proproot and cableroot systems and respiratory pneumatophores baffle currents and provide a range of attachment sites for calcareous epibionts, and nurseries for marine invertebrates. Effectively, the mangal and seagrass community acts as a biological conservation Lagerstatt. Most mangals are mud-based and may establish equally well in clays or lime muds (many flank rainforests). Mangroves produce large amounts of leaf litter, which is a food resource for a host of detritivores, and a potential source of hydrocarbons. Sedimentation rates in and around

mangroves are high, up to 1 cm/a (Risk and Rhodes, 1985), thus this organic matter may be readily conserved. The mangal ecosystem dates back to the Late Cretaceous, the first instance of the invasion of marine habitats by angiosperms (Retallack and Dillcher, 1981; Little, 1990). It is possible that some of the bushy, somewhat mangrove-like Late Paleozoic glossopterid gymnosperms of the Gondwana region were inhabitants of the intertidal zone, but this is generally discounted, and no glossopterids are known from carbonates. Raymond and Phillips (1983) have suggested that some cordaitid gymnosperms of the Late Carboniferous formed "mangrove" communities, since they are typically associated with marine transgressions. Little (1990) has proposed that Late Silurian rhyniophytes may have lived in a saltmarsh environment, but these are not associated with carbonates. The relatively new mangal ecosystem of the last 75 m.y. may have added a special dimension to carbonate sedimentation.

The next invasion of the carbonate habitat by vascular plants was the Late Eocene evolution of salt-tolerant angiosperm grasses, e.g., *Thalassia testudinum* or turtle grass, and other species. Seagrasses not only baffle currents, but provide a wide range of attachment sites for carbonate-secreting algae, forams, bryozoans, gastropods and bivalves, which settle as sediment when the grasses die. The sediment then acts as a protective cover for corals and mobile molluscs. Seagrasses help to bind and stabilize carbonate grains, either as level bottoms or mounds (Scoffin, 1970). The total area covered by seagrasses and mangroves has not been calculated, but may well be globally comparable to the area covered by coral reefs. Since seagrasses leave virtually no geological evidence, their functional equivalent is unknown. Jux and Strauch (1974) figured brown algal phyto-benthos in the sheltered lime mud communities of the Devonian of Germany, housing a community of brachiopods like *Uncites* and *Stringocephalus*. Such Paleozoic "seagrass" communities may have been more widespread in carbonates than is evident in the fossil record.

#### COQUINITES (SHELL BEDS)

Coquinites (coquinas, shell beds, shell gravels, shell pavements, etc.), which are beds produced by the exoskeletons of a host of shelly organisms, have received particular attention in papers related to event stratigraphy and taphonomy, with emphasis on physical rates of sedimentation (e.g., papers in Einsele and Seilacher, 1982; Aigner, 1977, 1979; Kidwell, 1986a, 1986b). The spectrum of the interaction of live organisms and abandoned skeletons has been termed "taphonomic feedback" (Kidwell and Jablonski, 1983; Kidwell, 1986b), and possibly plays a leading role in forcing ecologic successions. In ecologic successions, pioneering organisms pre-

pare the substrate for later occupation by a climax community (taphonomic feedback may thus be confined to the pioneers and have no long-term role in forcing successional change).

Concentrations of shells may be entirely the result of biologic processes of larval settlement, neanic and adult growth patterns, and the feeding or sorting behaviour of ancient or living organisms. An initial nest or clump of shells may expand laterally and vertically in a prevalently uniform sedimentary setting. Rapid early growth and expansion of the modern Great Lakes pest, the zebra mussel, may take place in a few months or years, as soon as the first spat are introduced. Marine mussels and oysters create sea-floor roughness, which, in turn, creates microturbulence that helps to circulate nutrients within the community. Biogenic shell concentrations may also be produced by predators which dump discarded shells around their burrows or nests in the substrate, and by middens produced by marine, shell-eating fossil crustaceans, cephalopods, birds, reptiles or mammals. Graded bedding, with coarser bioclast fractions grading upward into fines, can be produced biogenically by sea cucumbers and polychaete worms (Rhoads and Stanley, 1965). Some organisms use the shells of others to line their burrows or build shelters (e.g., hermit crabs may discard a number of shells in their lifetime, and, in sufficient numbers, may concentrate whole shell beds). Some marine polychaetes selectively backfill their burrows with the coarser comminuted debris (i.e., fecal pellets) or fossil shells. Kidwell *et al.* (1986) called the shell-bed end product of these various behavioural methods "extrinsic biogenic concentrations". Rates of modern shell production rarely exceed 0.5 kg·m<sup>-2</sup>/a. Preservation of shell beds in cold climate regimes normally requires quick burial because of rapid chemical dissolution of shells below the sediment-water interface (Davies *et al.*, 1989), but in tropical latitudes, shell beds can form at rates exceeding background sedimentation.

Sedimentologic concentrations represent the physical or hydraulic end of the spectrum. Shells may be viewed as sedimentary particles or bioclasts to be sorted, winnowed, transported and/or deposited by agents such as currents, waves, downslope gravity, and mass transport (slumping, turbidites, etc.). Such deposits may contain an admixture of imported skeletons and skeletons reworked *in situ*, with the exported material, whether coarse or fine skeletal debris, transferred elsewhere. Long distance transport for more than a few tens of metres does not seem to be significant in the formation of most shell beds, i.e., most shell beds form more or less in place (Boucot, 1953, 1981; Craig and Hallam, 1963). Examples of physical concentrations include beds concentrated from storm events, groove, fis-

sure, ripple mark, and channel fills, and the graded shell-beds formed in turbidites. Kidwell *et al.* (1986) also identified diagenetic concentrations, e.g., compaction and pressure-solution features, but these are not treated here. Selective dissolution, e.g., of more soluble aragonitic bivalves and gastropods over less soluble calcitic brachiopods and trilobites, can bias the fossil record, leading to erroneous conclusions regarding the original biota.

The production of specific types of shell beds is affected by three important factors: 1) the environmental range, diversity and functional morphology of the biota (e.g., few brachiopods tolerate the intertidal zone, but cerithid gastropods love tidal flats), 2) the evolution of the group (there are no oysters in the Cambrian), and 3) the sedimentary setting (onshore-offshore, shallow-deep, etc.). The last of these, and energy factors, have usually been given prime consideration. In terms of marine environments, there is a gradient from the intertidal-supratidal zone to proximal shelf environments, which include beach, sand bar-shoal, estuarine, enclosed embayment to lagoons, mid- to distal shelf deposits (affected by fair weather to storm waves), and slope to basinal environments (which include talus and turbidite deposits). In most tropical carbonate environments, the shelf edge is typified by shoaling or reef development, and may include features seen more commonly in nearshore situations (Fig. 3).

**CARBONATE SAND TO GRAVEL BOTTOMS**

Calcarene substrates (including those composed of comminuted shell fragments) are strongly physically controlled by hydro-

lic energy, with biological factors tending to play a secondary role, except as a source of sedimentary particles. Usually, there is less nutrient and organic matter available than in muddy sediments. Relatively few small organisms are capable of coping with these substrates, although some specializations include interstitial live faunas. Many organisms settling on these substrates tend to be much larger: larger bivalves, and especially the settlement of coralline elements, such as the encrusting sponges, bryozoans and corals. Suspension feeders often dominate because of the absence of fine muds which can clog up their filtering mechanisms. Substrates also tend to be irregular: megaripples, sand bars, and scour and groove channels disturb bottom topography.

Current and wave sorting, winnowing of the fines, and at least localized transport and redistribution of sediments are common. The sediment is mobile, and the substrates tend to be unstable and to shift periodically. Such highly mobile substrates are often favoured by burrowers which can dig out rapidly from sedimentary events; thus, deposit feeders are very common, especially if there is ~3% organic detritus in the sediment (Fig. 6). Vagile epibenthic life is abundant. Many calcarenites are light coloured, showing a removal of nutrients, loss of bacteria, and decreased organic content.

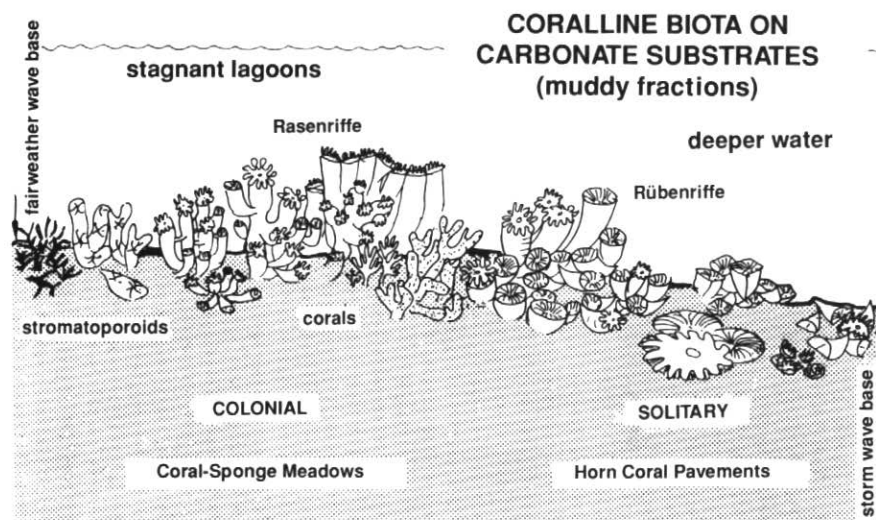
Types of carbonate sands depend primarily on the nature of the organism composing the particles and the amount of physical or biological reworking. Ooid sands are invariably surrounded by bacterial films: since they are formed in shallow, open waters with high rates of evaporation and agitation, they represent unstable bottoms to which organisms have difficulty adapting.

Bivalves, gastropods and forams are the most common shelly components in ooid banks. Foraminiferal shelf sands originated in Late Devonian time, beginning with the first development of multi-chambered tests and the evolution of calcite walls, expressed in Late Paleozoic examples, such as fusulinid limestones, and continuing with Mesozoic forams accumulations rich enough to form thick rock units. The first aragonite-walled and the first deep-sea benthic and pelagic forams appeared in the Jurassic; this revolutionized the productivity of the oceans in terms of forams (the diatoms and calcareous nanoplankton notably appeared about the same time). Although deep-water carbonate currently makes up only ~7-8% of the total carbonate mass, 60-80% of CaCO<sub>3</sub> is said to be deposited in the deep oceans. It is thus possible that an evolutionary shift in carbonate production to plankton has resulted in a change from shallow shelf to deep sea accumulation, as noted by Caldeira (1991), although carbonate precipitation per unit area in the deep sea is extremely slow, and pelagic carbonate is cycled very rapidly, eight times more quickly than shelf carbonates.

**CORAL-SPONGE-BRYOZOAN-ALGAE-DOMINATED SUBSTRATES (BIOSTROMES)**

"Coralline" organisms, those producing basal skeletons on top of which, or in the upper-most galleries or spaces of which, rest the soft-bodied organisms, have a basically different strategy of substrate adaptation. Such organisms may produce algal-dominated substrates (e.g., algal rims of reefs, or stromatolites), or sponge-, coral- or bryozoan-dominated substrates. Nearly all of these organisms, barring calcareous algae and cyanobacteria and possibly sponges, are clonal. The initial larval settlement and first production of the basal skeleton proceed from a single individual, which expands asexually by budding or fission. All other individuals developed are clones of the first (Jackson, 1983). The exception is the lime-secreting sponges, which grow by skeletal cell expansion. Many of these sponges have a remarkable capacity to vary skeletal composition (Wood, 1990). The chief factor seems to be lateral expansion by aggressive competition for space on the substrate. This lateral expansion can be achieved in two principal ways: horizontal encrustation through sheets, shoots or mounds; and vertical, upright or erect colonies, which may be dendroid, phaceloid, cylindrical, palisade (cateniform), fenestrate, conical, or fan shaped (Fig. 8).

Cup or horn corals have the capacity to form biostromal accumulations which have been called "Rübenriffe" ("beet" biostromes, after fields of sugar beets; see Birenheide, 1962). They may be abundant enough to form extensive coral cobble pavements stretching



**Figure 8** Paleozoic branching and fasciculate corals (*tabulates* and *rugosans*) and stromatoporoids (*stachyodids*, *amphiporids*) favoured muddy carbonate substrates in quieter waters (left): erect structures enabled ready shedding of sediment between the coralla or coenostea (middle). These thickets and meadows (*Rasenriffe*) baffled sediment. Horn coral pavements (*Rübenriffe*) (right) common to the Siluro-Devonian (after Wedekind and Trip, 1930; Birenheide, 1962), formed in deeper waters below fair-weather wave base. Such cup coral pavements today occur only in waters >150m deep.



for hundreds of metres along strike, as in the well-known Mid-Silurian *Dokophyllum* or "*Omphyma*" beds of Gotland, or the Mid-Devonian *Heliophyllum* biostromes of Ontario, thus providing ideal attachment for later benthic fauna (Fig. 8). Their orientation, rates of growth, and growth shapes, as well as epibenthic attaching or boring organisms, provide clues to the substrate (Poty, 1980; Elias, 1982, 1984; Elias *et al.*, 1988). Such conical, cylindrical to horn-shaped basal skeletons normally settled on softer substrates by having a pointed end facing downward, by developing prop-roots or flanges, by having a flattened underside and/or upper surface, or by growing laterally or curving upward to cope with the substrate (Neumann, 1988). The Wenlock slipper coral *Holophragma* had an Eifelian counterpart, operculate *Calceola*, with a flat underside. The Llandovery button coral *Palaeocyclus* has its Devonian *Microcyclus*, Carboniferous *Gymnophyllum*, and Recent *Fungicyathus* mimics. The dinner-plate Llandovery "mushroom" corals *Craterophyllum* and *Cystiphorolites*, adapted to calcarenites, have their modern counterpart in the genus *Fungia*. Specific coral strategies have, therefore, evolved repetitively to cope with life on soft, muddy, or mobile calcarenitic substrates. Modern substrates dominated by scleractinian "cup" corals generally tend to occur in deeper waters, like *Caryophyllia*, which forms pavements at depths of 150 m off the coast of Australia. Whether their Paleozoic equivalents lived at such depths is uncertain.

Colonial fasciculate, cateniform and ramose corals, and digitate bryozoans and stromatoporoids have the ability to form underwater thickets, meadows, coppices or biostromes, first termed "Rasenriffe" or coral meadows (Wedekind and Tripp, 1930). Such thickets baffle currents and initiate the precipitation out of suspension of silt to mud-sized carbonate fractions from the water mass in zones above the fair-weather wave base (Fig. 8). Thickets like this behave sedimentologically somewhat like shallow, near-shore sea or turtle grass communities today. Modern coral thickets in the Caribbean are generated by dense growths of branching taxa like *Porites porites*, *Oculina diffusa*, and *Cladocora arbuscula*. In the Paleozoic, Rasenriffe were constructed by ramose tabulate coral forms like *Thamnopora*, *Coenites* and *Syringopora*, and fasciculate rugosans like *Paleophyllum* and *Diplophyllum*. Some Devonian lagoonal environments featured stromatoporoids with similar ramose configurations, e.g., the digitate forms *Stachyodes* (in slightly better aerated habitats) and matchstick-like *Amphipora*, under more stagnant conditions. One particular group of stromatoporoids, the cylindrical tree-trunk-size Late Ordovician aulacerids, were so large that they nearly always toppled over after death, either from becoming unstable

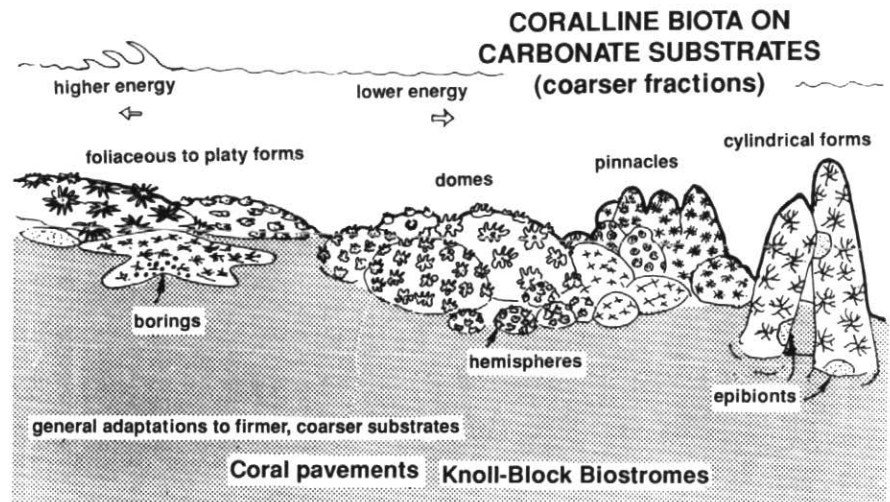
or from storm activity (Copper and Grawbarger, 1976). Digitate bryozoans played an identical role to the corals and stromatoporoids: they similarly may be thick and bed forming (Cuffey, 1973). A specific, descriptive carbonate rock terminology has developed around the growth habits of such coralline organisms: bafflestone, branchstone, globstone, lettucestone, etc. (Tsien, 1981; Cuffey, 1985).

Substrates dominated by foliaceous, platy, tabular, encrusting to domal coralline organisms play a double role. The first of these is the role of settling, spreading and establishing themselves on the substrate, and the second role is to become significant hardground for subsequent epibenthos, or a hiding place for cryptic organisms (Fig. 9). Their chief characteristic is a relatively planar underside, which may rest directly on or be slightly raised above the substrate (Segars and Liddell, 1988). The ability to spread laterally over the substrate may have been the result of a number of factors, some of which may not have been related to the nature of the substrate itself. Firstly, a flat underside is current stable, so is commonly favoured under higher-energy conditions where it reduces the chance of overturning and smothering. Additionally, in the sponges, a flat upperside allows currents to sweep over the surface, removing wastes from exhalant, astrorhizal canal systems (high-energy forms of stromatoporoids appear to have fewer raised mamelons or chimneys for the astrorhizal canals than those which live in quiet waters). Thirdly, flat undersides have a snowshoe effect, i.e., a method of preventing specimens from sinking into soft substrates. Fourthly, rapidly spreading clonal organisms have a competitive advantage in conquering sea-floor space. And lastly, coralline skeletons of photosynthetic algae and cyanobac-

teria, or clonal invertebrates with algal symbionts, maximize solar uptake, particularly in deeper waters or "clouded" watermass, by spreading laterally. Internally, the massive clonal corals, bryozoans and coralline sponges have often taken on special modular forms to accommodate to colonial life on the substrate. Rosen (1986) has used hierarchical first and second levels of modular organization to characterize some of these CaCO<sub>3</sub> skeletons (with plocoid, cerioid and thamnasterioid fitting in the first, and verrucose, meandroid and hydnochoroid in the higher levels).

#### HARD SUBSTRATES

Hard substrates are here defined to include any immobile substrate that is firm enough or hard enough to take encrusting and boring organisms, represents a non-depositional omission surface, and is resistant to erosion. This definition includes firm grounds, classic "hardgrounds", and conglomeratic to skeletal and rocky grounds. Brett (1988, 1991) has pointed out that hardgrounds, because they preserve a surface coated by encrusting epibenthos and penetrated by endoliths, form a good model for *in situ* communities (there is no transport). Hardgrounds give us information about rates of sedimentation: they must be extremely slow or intermittent. Carbonate substrates are especially well endowed in terms of hardgrounds specifically because early cementation and diagenesis, often while the sediment is being deposited, lead to syndepositional hardening. Reef surfaces, for example, have had abundant hard substrata for attachment by invertebrates, especially in open-pore and cavity spaces, since the Cambrian (Kobluk and James, 1979; Kobluk, 1988) and continue to do so today (Kobluk and van Soest, 1989). Hard substrata are also favoured by clonal inver-



**Figure 9** Coarser-grained carbonates and firmgrounds favour the establishment of basally stable and encrusting corals and sponges, which in turn act as a rocky hardground for borers and epibionts (example from Siluro-Devonian, in part following Birenheide, 1962). Foliaceous to platy forms are replaced locally by domal-hemispherical and cylindrical forms (as seen in Kershaw, 1990, for stromatoporoids).

tebrates, which have complex life cycles (Jackson and Hughes, 1985).

*Firmgrounds* represent sedimentary substrates in which sediment has begun to consolidate penecontemporaneously through early compaction from the overlying water-mass, from physical cohesiveness of fine particles, from biological agglutinants (mucus, slime, biological films, mats, etc.), or from very early stages of cementation before the sediment turns to a hardground or rock. Such firmgrounds are solid enough to prevent organisms from sinking through or depressing the substrate, and firm enough to require some mechanical effort to penetrate or remove. Exceptional storms or physical damage may rip up some firmgrounds and produce shale clasts or intraformational pebbles. Such subtidal limestone or intraformational flat pebbles are common in Cambrian through Silurian carbonate sequences, involving episodic deposition of lime muds, rapid firming, and subsequent rip-up clast re-deposition (Sepkoski, 1982). Sepkoski (1982) argued that such flat-pebble conglomerates vanished with expansion of the mid-Paleozoic benthic marine fauna, but they are still commonly represented in Silurian and Devonian carbonate shelf successions.

*Hardgrounds* mark the next step, defined by lithification of the omission surface to produce a rock-hard, concrete-like surface which requires substantial mechanical effort to break down. Storms are insufficient to rip up the surface, and only boring or chemical solution processes are feasible. Hardgrounds, like firmgrounds, are usually composed of fine-grained carbonates: the carbonate acts as an early cement. Many examples are known from the terrestrial onshore and estuarine zone (tropical lateritic hardpans), through intertidal ("beachrock"), to subtidal (Palmer and Fürsich, 1974; James *et al.*, 1976; Fürsich, 1979, *etc.*), and deeper shelf regions (Neumann *et al.*, 1977).

Sedimentologic criteria which are useful for hardgrounds include sharp omission discontinuities, often with an irregular surface that includes overhangs, cavities or recesses (Koch and Strimple, 1968; Brett, 1988). Many firm and hardground surfaces are identified by darker, pyritic, manganese, phosphoric or ferrous (pyritic) crusts, indicating temporary reducing or stagnation conditions. Evidence for episodic sedimentation, stagnation and omission surfaces or erosion is typical. Many micritic hardgrounds are capped by calcarenites which infill cavities, borings or undercut recesses; sharp grain-size differences are common as the omission surface is buried by new sediment. If the time gap is considerable, e.g., a Cretaceous rocky ground covered by Eocene marine sediments, this may be used as evidence. Early lithification of burrow linings may, in itself, produce a hardground. When the burrow host dies, or leaves, such syndimentary linings may be preserved as

hardgrounds (for chalks, see Rasmussen, 1971).

#### ROCKY GROUNDS OR ROCK-DOMINATED SUBSTRATES

Rocky grounds here include boulders, large fossil skeletons (e.g., coral and stromatopora colonies) (Fig. 9), and bedrock surfaces, including carbonate rock. Rocky grounds usually represent substantial unconformity surfaces in the order of thousands to millions of years. Recognition of substantial time breaks requires paleontologic definition. Most are indicative of shoreline environments, such as rocky headlands, rocky shelves, and boulder surfaces, where strong erosional and high energy current, wind and wave processes are at work (Sousa, 1985). Marine organisms require considerable survival skills to exist on rocky grounds or shores. They need to adapt to very strong scour and wave disturbance, and tolerate desiccation and daily and seasonal temperature variation. Boucot (1981) noted that the evidence for a fossil biota on rocky shores is rare, and many may have been overlooked. He suggested that this habitat may have been occupied rather late in the geologic record, or may have been different in the past. Efforts have been made to document the fossil record of ancient rocky shorelines, not just carbonates, and these go back to the Cambrian (Johnson, 1988; Johnson *et al.*, 1988). Carbonate rocky shores may be easier to exploit by borers because of the relative ease of carbonate solution. Common encrusting inhabitants today include the barnacles (Late Cretaceous-), limpets (?Jurassic-), oysters and mussels (Triassic-), calcareous red algae, and a range of soft-bodied forms, particularly the brown and green algae. In the Paleozoic, there appear to have been few encrusters comparable to these adapted to exposed rocky shorelines, although subtidal hardground inhabitants are common, including nearly every invertebrate phylum.

Biologic features which characterize most subtidal carbonate hard substrates (firmgrounds, hardgrounds and boulder-rocky surfaces) in the Phanerozoic include three important elements.

##### **Encrustation.**

Encrusting organisms include basal crusts of clonal organisms (sheet-like crusts of bryozoans, corals, calcareous algae), holdfasts (e.g., crinoid, bryozoan disks, rootlets, etc.), cementing valves (left valves of oysters, pedicle valves of articulate brachs, orbiculoid inarticulates, vermetid gastropods, basal discs of edrioasteroid echinoderms), remnant tests of barnacle crustaceans, and tubes of sabellarid and serpulid worms. Non-skeletal organisms are not recognizable as encrusting fossils.

##### **Bio-erosion.**

Boring organisms produce holes *via* mechanical scraping, drilling or frictional mech-

anisms, or *via* chemical solution by secreting acids. Organisms that leave recognizable boring trace fossils include nearly every phylum. Borings are at two scales: microscopic or micro-borings made by cyanobacteria, green or red algae and fungi; or macroborings made by higher invertebrates such as sponges, worms, gastropods (although usually for live prey), bivalves (into wood, hard peats, and rock), brachiopods and echinoids. Most such macro-borings can be identified by being relatively smooth sided, often with a calcite or aragonite lining, and by being relatively straight or short (cylindrical to vase to spheroidal in shape). The concentration and density of borings are good indications of the amount of time the hardground or surface object was exposed to bioerosion (Risk *et al.*, 1987). This is something like fission track dating: the longer the exposure to nonsedimentation, the greater the time available for bioerosion at the micro and macro level.

##### **Ecologic successions.**

The presence of typical ecologic successions for firm- and hardgrounds shows the developmental changes as the substrate hardens and accommodates a different biota (Baird and Fürsich, 1975).

#### CARBONATE DISTURBANCE OR EVENT HORIZONS

Biologic and sedimentary processes in tropical carbonate marine habitats are nearly always disrupted by depositional or erosional "events", a topic of increasing interest to marine earth science (e.g., Einsele and Seilacher, 1982; Aigner, 1985; Miller *et al.*, 1988). Carbonate substrates appear to be particularly affected, as the equatorial latitudes lie in the easterly typhoon or hurricane belts, where storms often have higher wind velocities and greater frequency than in the higher latitudes. Nearly every bedding plane marks an event of some type, and in carbonates, early diagenesis tends to emphasize such events by accentuating the horizons as resistant ledges. Some workers have separated regular, rhythmic, "cyclic" processes or events from "catastrophic" events. To what extent, for example, is a storm a regular seasonal or longer-term cyclical "event", or a random "catastrophe"? Hurricanes, typhoons or cyclones characteristic of carbonate and reef environments tend to come in 60-100 year cycles. The coral reef biota recovery time is shorter than this, and thus reef organisms have "learned" to cope with such natural disturbance. Physical event horizons can range from very small scale, at the lamina (thin section) level, with no distinct lateral continuity, to mass extinction events with a global impact. Some physical events may be reasonably *predictable* (e.g., tidal, lunar, seasonal, biennial, 7-8 year El Nino, 11-22 year solar, or longer-term 21,000-100,000 year orbital eccentricity cycles). Events may also be relatively stochastic: earthquakes (seis-



mites, mass flows, talus breccias, tsunami deposits, turbidites), volcanic eruptions (ash falls, submarine flows), and meteorite impacts (fallout layers, tektites). Events can also be biologically induced, e.g., the settling and metamorphosis of benthic larvae in shell beds or coral biostromes, migration events with the rapid introduction of invading new species, or elimination of existing species because of the opening or closing of a maritime "gate" (the closing of the Tethys ocean with the collision of the African plate into Eurasia, or the connection of the isthmus of Panama). Mass extinctions may also leave a sedimentological record (the absence of specific members of the food chain, changeover in plankton, or loss of major abundant benthic and nekto-planktic groups). For example, the elimination of the carbonate reef ecosystem at the Frasnian-Famennian and Permo-Triassic boundaries left a clear sedimentological signature.

Rhythmic sedimentary packages or rhythmites are a typical feature of many carbonate successions, and are proportionally scarcer in marine siliciclastic environments. The origin of limestone-marl periodites is still debated (Schwarzacher and Fischer, 1982). These tend to be more distinct in pelagic to hemipelagic quiet water, lagoonal or deeper-water micrite sequences. Here, carbonate layers are interrupted by thin clay (shale) partings deposited below wave base. Such "Milankovic" cycles may well be global in warm temperate to tropical latitudes, and precipitate in 21,000-, 41,000- or 100,000-year packages at rates of 0.5-3 cm per 1000 years (Einsele, 1982). Such sediments represent soft, muddy, calcareous bottom conditions. They may be influenced by temperature variations, ocean venting and changes in the carbonate compensation depth (CCD), redox variations, atmospheric fluctuations in CO<sub>2</sub>, sea level change, or phytoplankton and/or benthic cyanobacterial and algal productivity blooms. Deep-water periodites are rarely interrupted by storm layers, and if so, the effects are usually minor. Nor is there extensive bioturbation, except in sporadic horizons. Terrestrial processes (runoff, sediment supply) do not seem to play a major role. Early cementation favours preservation of carbonate periodites. In shallow-water environments, short-term periodites may include tidalites, as recorded in intertidal stromatolitic layers, which should produce a twice-daily rhythm, depending on local tidal regularity and relief. Such tidalites may be overprinted by the diurnal growth pattern of photosynthetic calcareous algae and cyanobacteria. Two-year marine cycles and 7-8 year El Niño cycles also have the possibility of leaving a carbonate biosedimentary record. El Niño events are known to kill reef and peri-reefal biotas locally, such as on the west coast of Panama in the last decade (e.g., "coral bleaching"; Glynn and D'Croz, 1991).

Tropical storms, as recorded in storm beds or *tempestites* (Aigner, 1982), have a more severe impact on nearshore habitats than the offshore; effects are thus tempered by water depth, and the location of the prevailing fair weather wave base and storm wave base (Aigner, 1985). In tropical carbonate belts, the primary seasonal effects are those created by monsoons, as the annual temperature range is insignificant. Since they are geologically instantaneous, storm beds represent good markers in sedimentary basins, and thus provide us with better stratigraphic resolution. Storm events disrupt the ecosystem and reset the local substrate community; a climax succession will be replaced by a pioneering one. Storms reorganize substrate conditions (muds may be replaced by shell beds on a scoured surface, or shell beds may be suffocated by muds). Many storm horizons appear to be followed by hardgrounds (Miller *et al.*, 1988). Overturned, toppled and storm-buried coral and sponge heads that have successfully regrown on the sea bottom are known from the Ordovician through Recent. Stochastic carbonate deposits include carbonate turbidites, debris flows, and reef megabreccias, which are common at the toe of slope or continental shelf edge margins. Nearly all the coarse clasts here are imported, but the local invertebrate or algal fauna that settles upon these re-establishes an equilibrium. Relatively few examples of ecologic recovery from such random debris-producing events are known. Since the organisms are moved into deeper waters and new habitats, or buried rapidly, death is more likely than recovery.

In nearshore intertidal to estuarine to very shallow water regimes, land-derived flood sediments or *inundites*, can accompany monsoon and hurricane seasons. Such *inundites*, where they interfinger with marine carbonates, should be featured by considerable amounts of terrestrial plant debris (in Devonian and younger sequences, following the arrival of vascular plant vegetation and soils), and fresh water invertebrates or pollen and spores mixed with marine forms.

## CONCLUSIONS

Carbonate substrates represent a major biochemical clue to the global atmosphere-ocean system, and are also environments exploited by some of the greatest diversity of species on Earth. Carbonate environments have been cyclical through time. At times of global warming and flooding of continental lowlands, carbonate environments, especially in the tropics to subtropics, were much more widespread. Carbonates are the most significant store of carbon on the planet, far exceeding production of the tropical rainforest and oceanic plankton. Understanding the rise and fall of carbonate ecosystems, especially those of reefs, at a global scale, should unlock secrets to climat-

ic change. Much remains to be discovered.

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## REFERENCES

- Aigner, T., 1977, Schalenpflaster im Unteren Hauptmuschelkalk bei Crailsheim: Neues Jahrbuch Geologie Paläontologie Abhandlungen, v. 153, p. 193-217.
- Aigner, T., 1979, Schill-Tempestite im Oberen Muschelkalk: Neues Jahrbuch Geologie Paläontologie Abhandlungen, v. 157, p. 326-343.
- Aigner, T., 1982, Calcareous tempestites: storm-dominated stratification in upper Muschelkalk limestones, Middle Trias (s.w. Germany), in Einsele G. and Seilacher, A., eds., *Cyclic and Event Stratification*, p. 180-198.
- Aigner, T., 1985, Storm depositional systems: dynamic stratigraphy in modern and ancient shallow-maritime sequences. *Lecture Notes in Earth Science*, v. 3, 174 p.
- Allison, P.A. and Briggs, D.E.G., 1991, *Taphonomy: Topics in Geobiology*, v. 9, 560 p.
- Baird, G.C. and Fürsich, F.T., 1975, Taphonomy and biologic progression associated with a submarine erosion surface from the German Lias: Neues Jahrbuch Geologie Paläontologie Monatshefte 6, p. 321-338.
- Bassett, M.G., 1984, Life strategies of Silurian brachiopods: *Special Papers in Palaeontology*, v. 32, p. 237-263.
- Berner, R.A., 1990, Atmospheric carbon-dioxide levels over Phanerozoic time: *Science*, v. 249, p. 1382-1386.
- Birenheide, R., 1962, Siedlungs- und Wuchsformen mitteldevonischer Korallen aus der Eifel: *Natur und Museum*, v. 92(1), p. 21-28.
- Bolin, B., 1970, The carbon cycle: *Scientific American*, January, p. 47-56.
- Boucot, A.J. 1953, Life and death assemblages among fossils: *American Journal of Science*, v. 251, 25-40.
- Boucot, B., 1981, Principles of benthic marine paleoecology: Academic Press, New York, 463 p.
- Brett, C.E., 1988, Paleoeecology and evolution of marine hard substrate communities: an overview: *Palaios*, v. 3, p. 374-378.
- Brett, C.E., 1991, Organism-sediment relationships in Silurian marine environments: *Special Papers in Palaeontology* 44, p. 301-344.
- Briggs, D.E.G. and Crowther, P.R., eds., 1990, *Palaeobiology — a synthesis*: Blackwell Scientific Publications, Oxford, 583 p.
- Brookfield, M.E., 1988, A mid-Ordovician temperate carbonate shelf — the Black River and Trenton Limestone groups of southern Ontario, Canada: *Sedimentary Geology*, v. 60, p. 137-153.
- Buick, R., 1991, Microfossil recognition in Archean rocks: an appraisal of spheruloids and filaments from a 3500 m.y. old chert-barite unit at North Pole, Western Australia: *Palaios*, v. 5, p. 441-459.

- Caldeira, K., 1991, Continental-pelagic carbonate partitioning and the global carbonate-silicate cycle: *Geology*, v. 19, p. 204-206.
- Calvert, S.E. and Pedersen, T.F., 1992, Organic carbon accumulation and preservation in marine sediments: how important is anoxia? in Whelan, J.K. ed., *Productivity: Accumulation and Preservation of Organic Matter in Recent and Ancient Sediments*: Columbia University Press, p. 231-263.
- Canfield, D.E. and Des Marais, D.J., 1991, Aerobic sulfate reduction in microbial mats: *Science*, v. 251, p. 1471-1473.
- Carey, D.A., 1987, Sedimentological effects and palaeoecological implications of the tube-building polychaete *Lanice conchilega* Pallas: *Sedimentology*, v. 34, p. 49-66.
- Chave, K.E., Smith, S.V. and Roy, K.J., 1972, Carbonate production by coral reefs: *Marine Geology*, v. 12, p. 123-140.
- Copper, P., 1967, Adaptations and life habits of Devonian atrypid brachiopods: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 3, p. 363-379.
- Copper, P. and Grawbarger, D., 1976, Paleoeological succession leading to a late Ordovician biostrome on Manitoulin Island, Ontario: *Canadian Journal of Earth Sciences*, v. 15, p. 1987-2005.
- Craig, G.Y. and Hallam, A., 1963, Size-frequency and growth-ring analysis of *Mytilus edulis* and *Cardium edule* and their palaeoecological significance: *Palaeontology*, v. 6, p. 731-750.
- Cuffey, R.J., 1973, Bryozoan distribution in the modern reefs of Eniwetok atoll and the Bermuda Platform: *Pacific Geology*, v. 6, p. 25-50.
- Cuffey, R.J., 1985, Expanded reef-rock textural classification and the geologic history of bryozoan reefs: *Geology*, v. 13, p. 307-310.
- Davies, D.J., Powell, E.N. and Stanton, R.J., 1989, Relative rates of shell dissolution and net sediment accumulation — a commentary: can shell beds form by the gradual accumulation of biogenic debris on the sea floor? *Lethaia*, v. 22, p. 207-212.
- Davis, J.H., 1940, The ecology and geologic role of mangroves in Florida: *Papers Tortugas Laboratory* 32, p. 302-412.
- Einsele, G., 1982, Limestone-marl cycles (periodites): diagnosis, significance, causes — a review, in Einsele, G. and Seilacher, A., eds., *Cyclic and Event Stratification*: Springer Verlag, Berlin, p. 8-53.
- Einsele, G. and Seilacher, A., eds., 1982, *Cyclic and event stratification*: Springer Verlag, Berlin, 536 p.
- Ekdale, A.A. and Mason, T.R., 1988, Characteristic trace-fossil associations in oxygen-poor sedimentary environments: *Geology*, v. 16, p. 720-723.
- Elias, R.J., 1982, Paleoecology and stratigraphy of solitary rugose corals of the Stony Mountain Formation (Upper Ordovician), Stony Mountain, Manitoba: *Canadian Journal of Earth Sciences*, v. 19, p. 1582-1598.
- Elias, R.J., 1984, Paleobiology of solitary rugose corals, Late Ordovician of North America: *Palaeontographica Americana*, v. 54, p. 533-537.
- Elias, R.J., Zeilstra, R.G. and Bayer, T.N., 1988, Paleoenvironmental reconstruction based on horn corals, with an example from the Late Ordovician of North America: *Palaios*, v. 3, p. 22-34.
- Feary, D.A., Davies, P.J., Pigram, C.J. and Symonds, P.A., 1991, Climatic evolution and control on carbonate deposition in northeast Australia: *Global and Planetary Change*, v. 89, p. 341-361.
- Fürsich, F.T., 1979, Genesis, environments and ecology of Jurassic hardgrounds: *Abhandlungen Neues Jahrbuch für Geologie und Paläontologie*, v. 158, p. 1-63.
- Gieskes, J.M., 1974, The alkalinity-total carbon dioxide system in sea water, in E.D. Goldberg, ed., *The Sea*: John Wiley and Sons, San Francisco, v. 5, p. 123-151.
- Ginsburg, R.N. and James, N.P., 1976, Submarine botryoidal aragonite in Holocene reef limestones, Belize: *Geology*, v. 4, p. 431-436.
- Glynn, P.W. and D'Croz, L., 1991, Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality: *Coral Reefs*, v. 8(4), p. 181-192.
- Grant, R.E., 1963, Unusual attachment of a Permian inoprodicid brachiopod: *Journal of Paleontology*, v. 37(1), p. 134-140.
- Grant, R.E., 1966, Spine arrangement and life habits of the productoid brachiopod *Waagenoconcha*: *Journal of Paleontology*, v. 40(5), p. 1063-1069.
- Gray, J.S., 1981, The ecology of marine sediments: *Cambridge Studies in Modern Biology*, v. 2, 185 p.
- Guillaume, M., 1990, Growth and calcium carbonate production of massive *Porites* (barrier reef flat of French Polynesia): *Comptes Rendus du Congrès 1990, International Society for Reef Studies (Noumea)*, p. 87-90.
- Hallock, P. and Schlager, W., 1986, Nutrient excess and the demise of coral reefs and platforms: *Palaios*, v. 1, p. 389-398.
- Heckel, P.H. and Witzke, B. J., 1979, Devonian world palaeogeography determined from distribution of carbonates and related lithic climatic indicators: *Special Papers in Palaeontology* 23, p. 99-123.
- Hesse, R., 1986, Early diagenetic pore water/sediment interaction: modern offshore basins: *Geoscience Canada*, v. 13, n. 3, p. 277-316.
- Holland, H.D., 1978, *The Chemistry of the Atmosphere and Oceans*: Wiley Interscience, New York, 351 p.
- Jackson, J.B.C., 1983, Biological determinants of present and past sessile animal distributions, in Tevesz, M.J.S. and McCall, P.L., eds., *Topics in Geobiology*, v. 3, p. 39-120.
- Jackson, J.B.C. and Hughes, T.P., 1985, Adaptive strategies of coral-reef invertebrates: *American Scientist*, v. 73, p. 265-274.
- James, N.P., Ginsburg, R.N., Marszałek, D.S. and Choquette, P.W., 1976, Facies and fabric specificity of early subsea cements in shallow Belize reefs: *Journal of Sedimentary Petrology*, v. 46, p. 523-544.
- Johnson, M.E., 1988, Why are ancient rocky shores so uncommon?: *Journal of Geology*, v. 96, p. 469-480.
- Johnson, M.E., Skinner, D.F. and Macleod, K.G., 1988, Ecological zonation during the carbonate transgression of a Late Ordovician rocky shore (northeastern Manitoba, Hudson Bay, Canada): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 65, p. 93-114.
- Jux, U. and Strauch, F., 1974, Die mitteldevonische Brachiopoden-Gattung *Uncites* Defrance 1825: *Palaeontographica*, v. 125A, p. 176-222.
- Kazmierczak, J. and Kempe, M. S., 1990, Modern cyanobacterial analogs of Paleozoic stromatoporoids: *Science*, v. 250, p. 1244-1248.
- Kempe, S. and Kazmierczak, J., 1990, Chemistry and stromatolites of the sealinked Satonda Crater Lake, Indonesia: a Recent model for the Precambrian sea?: *Chemical Geology*, v. 81, p. 299-310.
- Kershaw, S.D., 1990, Stromatoporoid paleobiology and taphonomy in a Silurian biostrome on Gotland, Sweden: *Palaeontology*, v. 33, n. 3, p. 681-705.
- Kidwell, S.M., 1986a, Models for fossil concentrations: paleobiologic implications: *Paleobiology*, v. 12, n. 1, p. 6-24.
- Kidwell, S.M., 1986b, Taphonomic feedback in Miocene assemblages: testing the role of dead hardparts in benthic communities: *Palaios*, v. 1, p. 239-255.
- 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.
- Kidwell, S.M. and Jablonski, D., 1983, Taphonomic feedback: ecological consequences of shell accumulation, in Tevesz, M.J.S. and McCall, P.L., eds., *Biotic Interactions in Recent and Fossil Benthic Communities*: Plenum Press, New York, p. 382-395.
- Kinsey, D.W. and Hopley, D., 1991, The significance of coral reefs as global carbon sinks — response to Greenhouse: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 89, p. 363-377.
- Kitano, Y., 1983, Calcification and atmospheric CO<sub>2</sub>, in Westbrook, P. and DeJong, E.W., eds., *Bio-mineralization and Biological Metal Accumulation*: Reidel Publishing, Dordrecht, p. 89-98.
- Kobluk, D.R., 1988, Cryptic faunas in reefs: ecology and geologic importance: *Palaios*, v. 3, p. 379-390.
- Kobluk, D.R. and Crawford, D.R., 1990, A modern hypersaline organic mud- and gypsum-dominated basin and associated microbialites: *Palaios*, v. 5, p. 134-148.
- Kobluk, D.R. and James, N.P., 1979, Cavity-dwelling organisms in Lower Cambrian patch reefs from southern Labrador: *Lethaia*, v. 12, p. 193-218.
- Kobluk, D.R. and van Soest, R.W.M., 1989, Cavity-dwelling sponges in a southern Caribbean coral reef and their paleontological implications: *Bulletin of Marine Science*, v. 44, n. 3, p. 1207-1235.
- Koch, D.L. and Strimple, H.L., 1968, A new Upper Devonian cystoid attached to a discontinuity surface: Iowa Geological Survey, Report of Investigations 5, p. 149.
- Lees, A., 1975, Possible influence of salinity and temperature on modern shelf carbonate sedimentation: *Marine Geology*, v. 19, p. 159-198.
- Lees, A. and Buller, A.T., 1972, Modern temperate-water and warm-water shelf carbonate sediments contrasted: *Marine Geology*, v. 13, p. M67-M73.
- Leonard, J.E., Cameron, B., Pilkey, O.H. and Friedman, G.M., 1981, Evaluation of cold water carbonates as a possible paleoclimatic indicator: *Sedimentary Geology*, v. 28, p. 1-28.
- Levinton, J.S., 1982, *Marine Ecology*: Prentice Hall, New Jersey, 526 p.
- Li, Y.H., Takahashi, T. and Broecker, W.S., 1969, Degree of saturation of CaCO<sub>3</sub> in the oceans, *Journal of Geophysical Research*, v. 74, p. 5507-5525.
- Little, C., 1990, *The Terrestrial Invasion*: Cambridge University Press, 304 p.

- Lovelock, J., 1988, *The Ages of Gaia*: W.W. Norton and Co., 252 p.
- Lowenstam, H.A., 1981, Minerals formed by organisms: *Science*, v. 211, p. 1126-1131.
- Margulis, L. and Stolz, J., 1983, Microbial systematics and a Gaian view of the sediments, in Westbrook, P. and DeJong E.W., eds., *Bio-mineralization and Biological Metal Accumulation*: Reidel Publishing, Dordrecht, p. 27-53.
- McCall, P.L. and Tevesz, M.J.S., 1982, Animal-sediment relations: *Topics in Geobiology*, v. 2, p. 1-336.
- Meadows, P.S., 1986, Biological activity and seabed sediment structure: *Nature*, v. 323, p. 207.
- 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: *Palaaios*, v. 3, p. 35-52.
- Nelson, C.S., 1988, An introductory perspective on non-tropical shelf carbonates: *Sedimentary Geology*, v. 60, p. 3-12.
- Neumann, A.C., Kofoed, J.W. and Keller, G.H., 1977, Lithoherms in the straits of Florida: *Geology*, v. 5, p. 4-10.
- Neumann, B.E., 1988, Some aspects of life strategies of Early Paleozoic rugose corals: *Lethia*, v. 21, p. 97-114.
- Palmer, T.J. and Fürsich, F.T., 1974, The ecology of a Middle Jurassic hardground and crevice fauna: *Palaeontology*, v. 17, p. 507-524.
- Palmer, T.J., Hudson, J.D. and Wilson, M.A., 1988, Paleoecological evidence for early aragonite dissolution in ancient calcite seas: *Nature*, v. 335, p. 809-810.
- Pedersen, T.F. and Calvert, S.E., 1990, Anoxia versus productivity: what controls the formation of organic carbon-rich sediments and sedimentary rocks? *American Association of Petroleum Geologists, Bulletin*, v. 74(4), p. 454-466.
- Pentecost, A. and Riding, R., 1985, Calcification in cyanobacteria: p. 73-90.
- Poldervaart, A., 1955, Chemistry of the earth's crust: *Geological Society of America, Special Paper* 62, p. 119-144.
- Poty, E., 1980, The stratigraphy and paleobiogeography of Belgian Visean corals: *Acta Palaeontologica Polonica*, v. 25, p. 587-595.
- Racheboeuf, P.R., 1981, Chonetacés (Brachiopodes) siluriens et devoniens du sud-ouest de l'Europe: *Mémoires Société Géologique Minéralogique Bretagne*, v. 27, 294 p.
- Rao, C.P., 1981, Criteria for recognition of cold-water carbonate sedimentation: Berriedale Limestone (Lower Permian), Tasmania, Australia: *Journal of Sedimentary Petrology*, v. 51, n. 2, p. 491-506.
- Rasmussen, H.W., 1971, Echinoid and crustacean burrows: *Lethaia*, v. 4, p. 191-216.
- Raymond, A. and Phillips, T.L., 1983, Evidence for an Upper Carboniferous mangrove community, in Teas, H.J., ed., *Biology and Ecology of Mangroves*: Junk Publishing House, The Hague, p. 19-30.
- Reid, R.P., MacIntyre, I.G. and James, N.P., 1990, Internal precipitation of microcrystalline carbonate: a fundamental problem for sedimentologists: *Sedimentary Geology*, v. 68, p. 163-170.
- Retallack, G. and Dilcher, A., 1981, A coastal hypothesis for the dispersal and rise to dominance of the flowering plants, in Niklas, K.J., ed., *Paleobotany, Paleoecology and Evolution*: Praeger Publishing, v. 2, p. 27-77.
- Rhoads, D.C., 1967, Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbor and Buzzard's Bay: *Journal of Geology*, v. 75, p. 461-474.
- Rhoads, D.C. and Stanley, D.J., 1965, Biogenic graded bedding: *Journal of Sedimentary Petrology*, v. 35, p. 956-963.
- Risk, M.J. and Rhodes, E.G., 1985, From mangroves to petroleum precursors: an example from tropical northeast Australia: *American Association of Petroleum Geologists, Bulletin*, v. 69(8), p. 1230-1240.
- Risk, M.J., Pagani, S.E. and Elias, R.J., 1987, Another internal clock: preliminary estimates of growth rates based on cycles of algal boring activity: *Palaaios*, v. 2, p. 323-331.
- Roberts, H.H., Phipps, C.V. and Effendi, L., 1987, *Halimeda* bioherms of the eastern Java Sea, Indonesia: *Geology*, v. 15, p. 371-374.
- Rosen, B.R., 1986, Modular growth and form of corals: a matter of metameres?: *Royal Society of London, Philosophical Transactions*, v. B313, p. 115-142.
- Sanders, H.L., 1958, Benthic studies in Buzzard's Bay. I. Animal-sediment relationships: *Limnology and Oceanography*, v. 3, p. 248-258.
- Schäfer, W., 1962, *Aktuo-Paläontologie*: Kramer Verlag, Frankfurt, 666p.
- Schwartzmann, D.W. and Volk, T., 1989, Biotic enhancement of weathering and the habitability of Earth: *Nature*, v. 340, p. 457-459.
- Schwarzacher, W. and Fischer, A.G., 1982, Limestone-shale bedding and perturbations of the earth's orbit, in Einsele, G. and Seilacher, A., eds., *Cyclic and Event Stratification*: Springer Verlag, Berlin, p. 72-95.
- Scoffin, T.P., 1970, The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas: *Journal of Sedimentary Petrology*, v. 40, p. 249-273.
- Segars, M.T. and Liddell, W.D., 1988, Microhabitat analysis of Silurian stromatoporoids as substrata for epibionts: *Palaaios*, v. 3, p. 391-403.
- Seilacher, A., 1964, Biogenic sedimentary structures, in Imbrie, J. and Newell, N.D., eds., *Approaches to Paleoecology*: Wiley Press, San Francisco, p. 296-316.
- Seilacher, A., 1970, Begriff und Bedeutung der Fossil-Lagerstätten: *Monatshefte Neues Jahrbuch für Geologie und Paläontologie*, p. 34-49.
- Seilacher, A., 1982, General remarks about event deposits, in Einsele, G. and Seilacher, A., eds., *Cyclic and Event Stratification*, p. 161-174.
- Seilacher, A., Reif, W.E. and Westphal, F., 1985, Sedimentological, ecological and temporal patterns of fossil Lagerstätten: *Royal Society of London, Philosophical Transactions*, v. B311, p. 3-23.
- Sepkoski, J., 1982, Flat-pebble conglomerates, storm deposits and the Cambrian bottom fauna, in Einsele, G. and Seilacher, A., eds., *Cyclic and Event Stratification*: Springer Verlag, p. 371-385.
- Shinn, E.A., Steinen, R.P., Lidz, B.H. and Swart, P.K., 1989, Whitings — a sedimentologic dilemma: *Journal of Sedimentary Petrology*, v. 59, n. 1, p. 147-161.
- Signor, P.W. and Brett, C.E., 1984, The mid-Paleozoic precursor to the Mesozoic marine revolution: *Paleobiology*, v. 10, p. 229-245.
- Sousa, W.P., 1985, Disturbance and patch dynamics on rocky intertidal shores, in Pickett, S.T.A. and White, P.S., eds., *The Ecology of Natural Disturbance and Patch Dynamics*: Academic Press, San Diego, p. 101-124.
- Strickland, J.D.H., 1965, Production of organic matter in the primary stages of the marine food chain, in Riley, J.P. and Skirrow, G., eds., *Chemical Oceanography*: Academic Press, London, 610 p.
- Tsien, H.H., 1981, Ancient reefs and carbonates: Fourth International Coral Reef Symposium, Manila, v. 1, p. 601-609.
- Vermeij, G.J., 1987, *Evolution and Escalation*: Princeton University Press, 527 p.
- Vernberg, F.J. and Vernberg W.B., 1981, *Functional Adaptations of Marine Organisms*: Academic Press, New York, 347 p.
- Wedekind, R. and Tripp, R., 1930, *Die Korallenriffe Gotlands*: *Zentralblatt für Mineralogie und Geologie*, v. 8, p. 295-304.
- Westbrook, P. and De Jong, E.W., eds., 1983, *Bio-mineralization and Biological Metal Accumulation*: Reidel Publishing, Dordrecht, 533 p.
- Wilkinson, B.H. and Walker J.G.C., 1989, Phanerozoic cycling of sedimentary carbonate: *American Journal of Science*, v. 289, p. 525-548.
- Wood, R.A., 1990, Reef-building sponges: *American Scientist*, v. 78, p. 224-235.

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