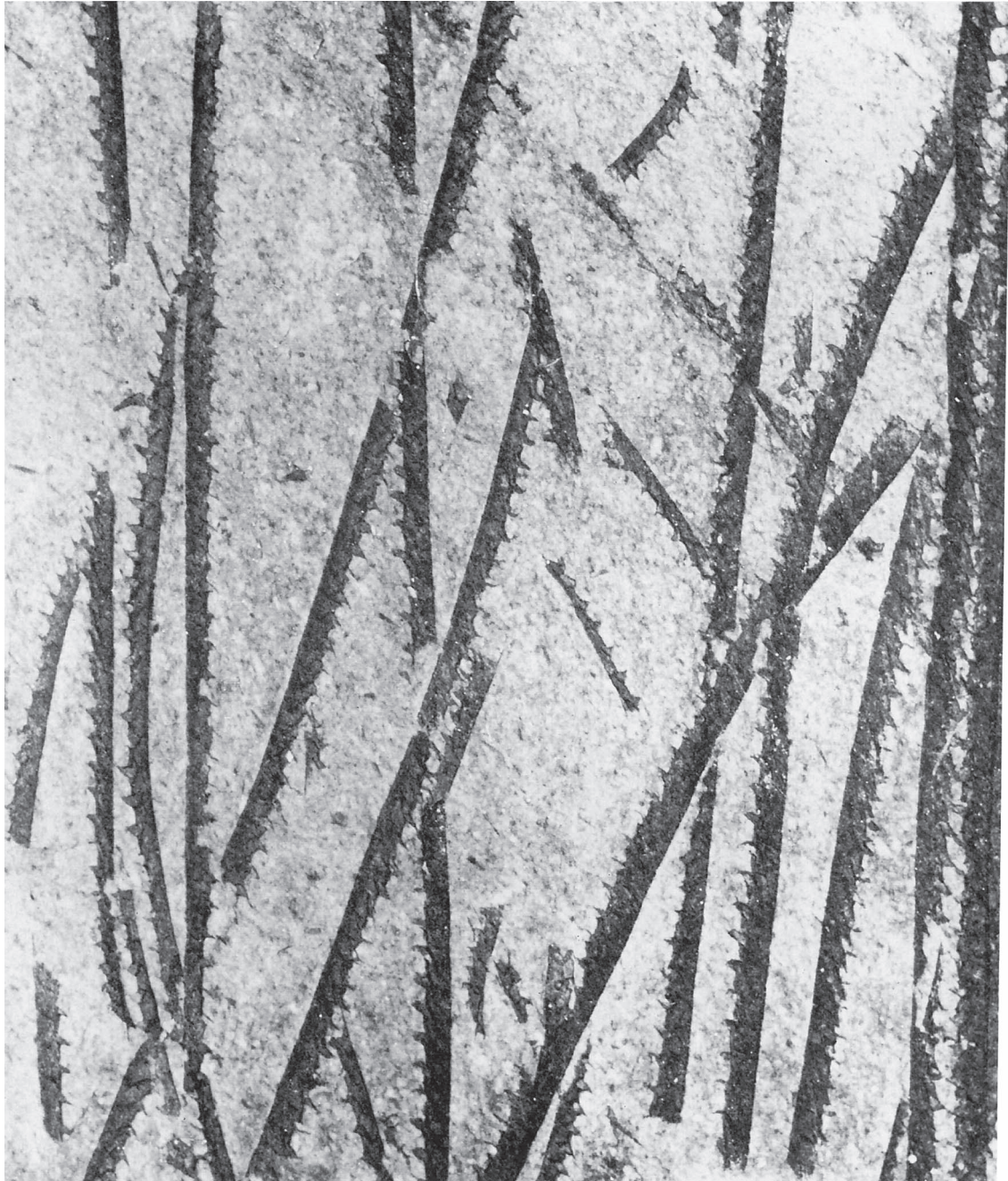


3

TAPHONOMY



Current aligned specimens of the Silurian graptolite *Monograptus riccartonensis*, x 6. (Photograph courtesy of R.B. Rickards.)

3.1 Decay Processes

P. A. ALLISON

Introduction

Decay processes are responsible for substantial preservational bias in the fossil record. The most obvious effect of this bias is the rarity with which organic soft parts are preserved. Such a bias has considerable importance for the palaeontologist since soft-bodied organisms may represent up to 60% of the individuals in a marine community (Jones 1969).

Where organic soft parts are encountered in the fossil record, they are indicative of exceptional sedimentological and diagenetic conditions. It is important to note, however, that the preservation of soft parts does not necessarily imply a minimal preservational bias. At some localities the conditions leading to soft part preservation have promoted the dissolution of biogenic hard parts. A good example is provided by the Iron Age 'Bog-people' of Northern Europe (Glob 1969). These human cadavers include cellular detail of skin, muscle, hair and clothes preserved from decay by tannic and fulvic acids in the peat. However, these conditions also promoted the dissolution of bone. In the extreme case cadavers occur as a body-shaped bag of skin devoid of hard parts.

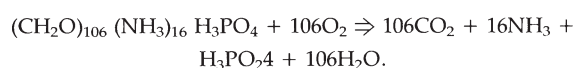
Under normal conditions decay processes are initiated by death and continue until a carcass is either completely destroyed or mineralized. If mineralization occurs after a period of prolonged decay then the overall level of preservation will be low; if, on the other hand, mineralization occurs prior to appreciable decay then the level of preservation will be high.

Process

Dead organisms are a valuable food source in any environment. If this food source is utilized by macro-organisms it is termed scavenging; if it is utilized by microbes, such as fungi and bacteria, it is termed decay. Rate of decay is controlled by three factors: (1) supply of oxygen and other electron donors; (2) environmental factors such as temperature, pH, and sedimentary geochemistry; and (3) the nature of organic carbon.

In an aerated environment, microbes break down

organic carbon using O_2 as the principal electron donor and produce CO_2 and water as by-products. Following the depletion of O_2 the microbes are forced to utilize a series of alternative electron acceptors (such as NO_3^- , MnO_2 , $Fe(OH)_3$, and SO_4^{2-}) for the respiration of organic carbon (see Section 3.8.2 for equations). The ordering of these reactions is controlled by the free-energy yield of the reaction. Thus, in the ideal case, these reactions would be layered — with those liberating the greatest free-energy nearest the sediment–water interface. Following the depletion of one of these oxidants, the sediment microbiota respire using the next most efficient reaction. When the oxidants have been fully depleted, degradation proceeds by fermentation during which organic matter is broken down by enzymes and CO_2 is reduced to methane. However, not all these oxidants are present in any given environment; typically sulphate reduction and methanogenesis dominate in a marine system, while methanogenesis alone dominates in freshwater. There are therefore three common decay regimes in aquatic sediments: (1) aerobic (in marine and freshwater systems); (2) marine anaerobic (sulphate reduction and methanogenesis); and (3) freshwater anaerobic (principally methanogenic although nitrate reduction and iron reduction may be important in some systems). Aerobic decay processes are commonly considered the most rapid and effective means of biodegradation. Thus euxinic conditions are generally accepted as a prerequisite for the preservation of lightly skeletonized and soft-bodied organisms. However, the oxygen requirement for aerobic decomposition is high. For instance, the decomposition of one mole of organic matter requires 106 moles of oxygen:



Thus, according to Avogadro's Principle, 1 mole (3.53 kg) of organic carbon requires 106 moles (2374.4 l) of oxygen. Decay rate is commonly expressed as a half-life. Since aerobic decay of 1 g of organic carbon requires 671 cm^3 of oxygen, the oxygen demand for aerobic decomposition can be expressed

as 335 cm³/g of carbon/half-life. With such a high oxygen requirement, demand can easily exceed supply, with anoxia as the result. In the case of most mud-grade sediments anoxia usually occurs when the volume of dispersed organic carbon exceeds 5%. Where organic carbon occurs as localized concentrations (such as macro-organisms), however, the increased mass–surface area ratio inhibits the transfer of oxygen and other electron donors from pore-water solutions. This results in a localized attenuation of bacterial reduction zones, with a reduction ‘sink’ centred upon the carcass. Thus an anaerobic microenvironment can even be formed in aerated waters if a carcass is big enough. The overall effect of anoxia is to reduce decay rate. This is because anaerobic decomposition of some compounds can only occur after a molecule has been degraded by respiratory processes with higher free-energy yields (Jørgensen 1982, 1983). For example, the methanogenic decay of lignified cellulose may require a period of aerobic decay followed by a period of nitrate reduction, then manganese reduction, etc. (see Fig. 2, p. 252). Thus in euxinic environments, where these bacterial reduction zones are severely attenuated (or even absent), the bacterial ‘chain’ of decomposition is broken and decay rate impaired.

Environmental factors such as temperature and pH probably exert most control on decay rate, but they are potentially the most difficult parameters to isolate in the rock record. Increased sediment temperature promotes higher decay rates and an attenuation of the bacterial reduction zones in sediment. The pH in most sediments is approximately neutral and therefore a suitable environment for microbial respiration. This is not the case in peat swamps, where tannic and fulvic acids liberated by the decomposition of plant material produce an acid environment which halts decay. Soft tissues entombed in such environments become tanned (like leather) and decay resistant. Examples of this type of preservation include the Iron Age ‘Bog People’ of Northern Europe (Glob 1969), and the Middle Eocene Geiseltal brown coal from around Halle in East Germany (Allison 1988a). Details preserved include muscle fibres and epithelial cell structure of frogs.

Organic carbon in sediment occurs as a variety of complex molecules in association with oxygen, nitrogen, hydrogen, and phosphorous. Particular varieties of molecules decay at different rates according to molecular configuration and chemical formulae. Those forms which are most amenable to

decay are known as volatiles, and those which exhibit a degree of decay resistance (and therefore have longer half-lives) are known as refractories. The soft parts of most animals are volatiles and are rapidly decomposed whereas some plant tissues (such as cellulose) are more decay resistant. The decay rate of cellulose, however, is variable and controlled by the presence or absence of other compounds. For example, both lignin (Stout *et al.* 1981) and certain phenolic compounds (Williams 1963) have been shown to increase the half-life of cellulose if present in decomposing tissue.

Effects of decay

Decay is one of the principal sources of information loss in the fossil record. The only way of halting this information loss is by mineralization (Allison 1988a) and a range of preservational characters can be described which reflect diagenetic timing relative to decay (Fig. 1). The highest level of preservation is that of permineralized, volatile, soft tissues such as muscle (for example, mantle muscle of squid from the Jurassic Oxford Clay of Wiltshire, U.K.; Fig. 2B). In some circumstances mineral formation occurs after the decomposition of soft tissues but prior to sediment compaction. In this case only the thin, flattened impressions of volatile soft parts are preserved (such as in the preservation of soft tissues in siderite nodules from the Carboniferous Mazon Creek fauna of Illinois, U.S.A (Section 3.11.5); Fig. 2B). If decay further outpaces mineralization, such imprints are destroyed and only refractory tissues such as chitin (from arthropod cuticle) and lignin or cellulose are preserved. These tissues may be preserved as permineralizations, altered organic residues or, with prolonged decay, as impressions. When even these refractories are destroyed, only biogenic hard parts such as bone and shell remain.

Decay has considerable impact upon the hydrodynamic properties of an organism and this is a further source of preservational bias. A high degree of completeness of soft bodied and lightly skeletonized taxa has been used to infer minimal transport prior to burial. Such a conclusion is important because it relates the life habitat of an organism to the sediments in which it was buried. However, a series of tumbling barrel experiments using carcasses of the polychaete worm *Nereis*, and the eumalacostracan crustaceans *Nephrops* and *Palaeomon* have shown that this relationship does not hold (Allison 1986). The barrel was allowed to rotate at 125 rpm for 5 h, equivalent to turbulent transport

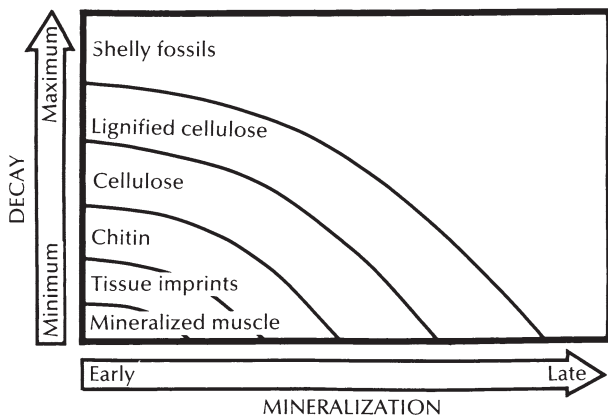


Fig. 1 The relationship between decay and mineralization in the preservation of soft-bodied and lightly skeletonized organisms. Reduced decay and early diagenetic mineralization are required for preservation of volatile tissues such as muscle. The preservational field of each tissue type extends from the bottom left-hand corner of the box to the boundary fence of the next most refractory type. (After Allison 1988.)

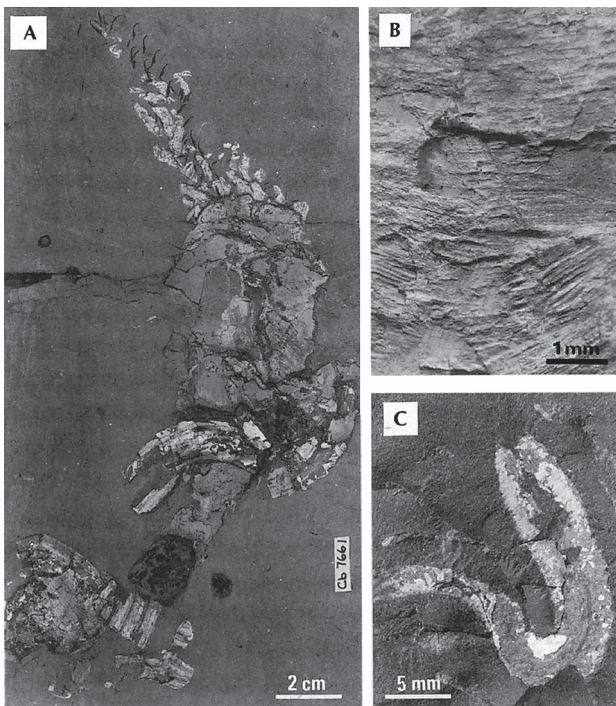


Fig. 2 A, Three-dimensional preservation of mantle and appendage musculature in squid from the Jurassic Oxford Clay of Wiltshire, U.K.; Bristol City Museum, Cb7661. B, Close-up of muscle fibres in A. C, Flattened polychaete worm from the Upper Carboniferous Mazon Creek biota of Illinois, U.S.A. (A, B from Allison 1988b; reproduced with permission from the *Lethaia* Foundation.)

for over 11 km. Freshly killed organisms subjected to tumbling were hardly damaged (Fig. 3A), while car-

asses which had been allowed to decompose for several weeks were disarticulated and fragmented (Fig. 3B). A sealed glass jar filled with seawater and carcasses of *Palaemon* was used as a control. The carcasses became buoyed up to the surface with decomposition gases and gradually disarticulated to produce a carpet of skeletal fragments upon the floor of the jar. Thus freshly-killed organisms could tolerate turbulent transport without fragmenting, while at the opposite extreme, carcasses were disarticulated when buoyed up by decay gases, even in the absence of currents. It is therefore primarily decay and not transport which determines the degree of fragmentation and disarticulation in soft bodied and lightly skeletonized taxa. Completeness or preservation is therefore no indicator of duration or nature of transport.

This interaction between decay and hydrodynamic processes has produced some difficult taxonomic problems. The most common instance of this form of distortion is provided by fossil plants. A living plant will produce a number of different preservable structures such as pollen, seeds, fruit, and leaves. Upon death, the stem of the plant is commonly fragmented and separated from its root system. Thus, plant fossils are rarely encountered as whole entities. As a result of this bias the remains of most fossil plants are given form names (Section 5.1.3). Animal remains too may be subject to this bias. An unusual example is provided by the large Middle Cambrian predator *Anomalocaris*, from the celebrated Burgess Shale of British Columbia (Section 3.11.2) (Whittington and Briggs 1985). This animal was one of the largest predators of its time, although for many years it was only known from disarticulated elements. The limbs were originally identified as arthropod bodies and named *Anomalocaris canadensis*, while the mouth parts were thought to be a medusoid coelenterate (*Peytoia nathorsti*). An incomplete body of the animal was named *Laganania cambria* and classified as a holothurian. These 'animals' are in fact all part of the same organism. When *Anomalocaris* died and began to decompose, the mouth parts, body, and appendages were separated and deposited according to the hydrodynamic properties of each particular element. The recognition of this decay-induced distortion of fossil taxonomy was only achieved by the discovery of a number of rare complete individuals. The preservation of complete animals required deposition prior to decay-induced fragmentation. Conversely, the occurrence of disarticulated skeletal elements indicates a period of decay prior to final burial.

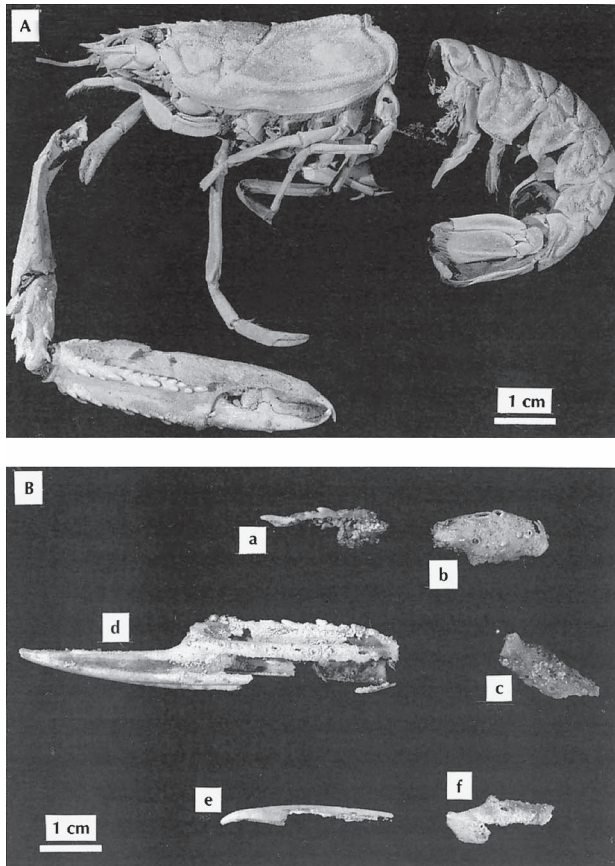


Fig. 3 Carcasses of *Nephrops*. A, Freshly-killed individual after tumbling in rotating barrel. Note that although carcass is decapitated, delicate structures such as the appendages have survived. B, Individual tumbled after 26 weeks of decay: a, rostrum; b, c, segments of chelae nearest to coxae; d, pincer; e, mandible; and f, segment of chela attached to pincer.

Characterization of decay

Decay in the fossil record can be characterized on three levels: (1) the identification of information loss and decomposition structures in particular fossil organisms; (2) the recognition of particular minerals and geochemical markers associated with particular decay regimes; and (3) the preservation of fossil microbes involved in the decomposition process.

The most basic characterization of decay, that of level of preservation in macro-organisms (e.g. permineralized muscle, tissue impressions), merely documents extent of decay prior to mineralization (Figs 1, 2).

A more detailed characterization relates specific geochemical markers to particular decay pathways (i.e. aerobic decay, nitrate reduction, manganese

reduction, iron reduction, sulphate reduction, or methanogenesis) used by microbes in the decomposition process. Sedimentary pyrite, for example, is produced as a by-product of bacterial sulphate reduction (Section 3.8.3), and manganese carbonates may be produced during manganese reduction (Section 3.8.2). Similarly, the fractionation of carbon isotopes during bacterial decay and their incorporation into the lattice of carbonate minerals is diagnostic of specific decay reactions (Coleman 1985)

The rarest and most spectacular characterization of decay processes is the preservation of fungi and bacteria in fossil organisms (Allison 1988a). When bacteria die they undergo autolysis, whereby enzymes and other cell contents begin to corrode and eventually destroy the cell wall. Such a process takes hours or days. Thus the mineralization of microbes implies extremely rapid diagenetic growth. Further work on these microbe–carcase associations is required in order to fully understand their significance.

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3.2 The Record of Organic Components and the Nature of Source Rocks

P. FARRIMOND & G. EGLINTON

Preservation and diagenesis

Organic molecules are abundant constituents of many sediments and sedimentary rocks. These components have been referred to as 'chemical fossils' in recognition of their biological origin, but the terms 'biological marker' or simply 'biomarker' are more commonly used. Macro- and microfossils are readily apparent in rocks, but the identification of chemical fossils requires sophisticated techniques of sample work-up and analysis; nevertheless, they too preserve a remarkably detailed record of past biological activity. 'Biological markers' are defined as organic compounds present in sediments (or petroleum) which possess chemical structures unambiguously related to present day biologically-occurring organic molecules (Fig. 1). Obviously, the possible sources of biomarkers in geological samples are almost limitless, comprising all organisms in the palaeoenvironment of deposition — aquatic, land, and air. Consequently, the molecular record is invariably complex. Furthermore, numerous chemical reactions, both biologically and non-biologically mediated, proceed within the water column and then during sedimentation and burial of the organic debris; these serve to modify and diversify the record of organic components still further.

Only a relatively small proportion of the organic matter produced within, or supplied to, ocean surface waters ever reaches the underlying sediments; the vast proportion of this material is recycled (much of it 'remineralized' to carbon dioxide) within the water column, particularly in the euphotic zone. Many processes act to modify the organic flux, including photo-oxidation, microbial activity, and predation by grazing organisms. Of the very small fraction of the original marine organic material which arrives at the sediment, a large proportion is generally transported in the form of faecal pellets released by zooplankton or organisms higher in the food chain. Such faecal pellet transfer is relatively rapid, allowing marine organic matter produced in the euphotic zone largely to escape photo-oxidative degradation. However, the molecular composition

of the algal material is changed during passage through the gut of the grazing organism; various organic components are preferentially assimilated and modified during digestion, and other lipids may be contributed from tissues of the grazer. An example of this 'editing' process is the observed increase in certain sterols, such as cholesterol (Fig. 1), in faecal pellets of zooplankton fed on phytoplankton (Harvey *et al.* 1987). Microbial activity, proceeding both in the gut of the feeder and, later, within the faecal pellets, also plays a role in modifying the molecular composition of the organic matter in its descent to the sea floor.

Upon arrival at the sediment, organic matter is further modified by a variety of processes acting during early burial. It is during this early diagenesis that biological compounds and debris are incorporated into insoluble sedimentary organic matter. In addition to the free lipids, the organic matter entering the sedimentary regime comprises biopolymers such as carbohydrates, proteins, cutins, and lignins, all of which are available for consumption and modification by benthic macro- and micro-organisms. There is evidence that a variable fraction of carbohydrates and proteins is initially converted to individual sugars and amino acids by enzymatic microbial attack prior to the use of the resulting monomers by microbes as a source of energy and to form new cell material. The remainder, not utilized in this way, can undergo polycondensation to form geopolymers; these complex, high molecular weight materials may incorporate fulvic and humic acids. This heteropolymeric debris has been termed 'protokerogen' — the precursor of kerogen. With further sediment burial, increasing condensation and insolubilization accompanies the slow diagenetic conversion to kerogen, which constitutes the bulk of the organic matter in ancient sediments.

Biolipids may be incorporated into kerogen in a similar way, or may be preserved in the sediment with only minor modification. Diagenetic reactions at various stages of burial appear to convert some lipids to hydrocarbons (Fig. 1) through the loss of functional groups via dehydration, hydrogenation,

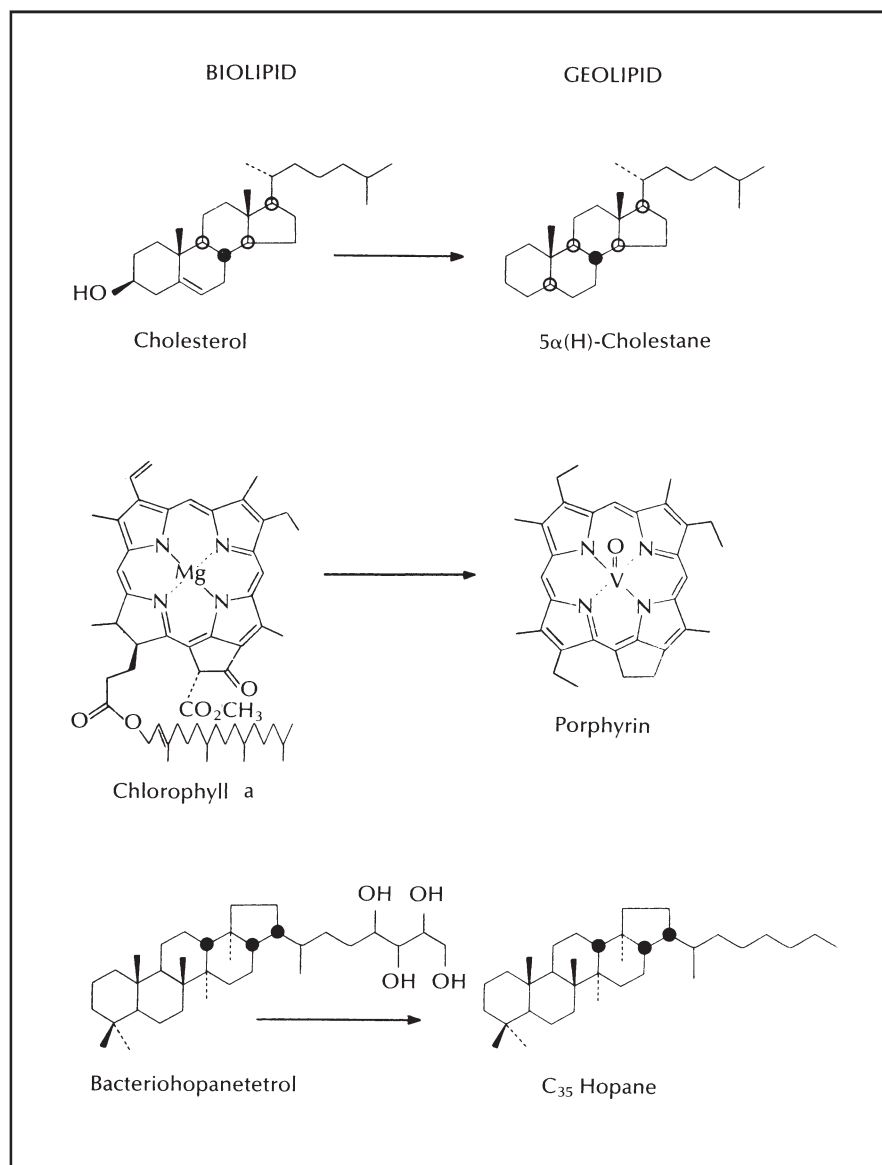


Fig. 1 Three biologically widespread molecules and their geologically occurring products after diagenesis. Note that, in each case, structural specificity is maintained — the geolipids are thus ‘chemical fossils’, having an unambiguous link with their precursor biolipids.

and decarboxylation. Such hydrocarbons cannot be readily incorporated into geopolymers by polycondensation reactions. However, a proportion may become trapped in the kerogen structure. The remaining free hydrocarbons and other related compounds comprise only a small proportion of the organic matter in a sediment (typically less than 5%), although they have a high information content. These ‘chemical fossils’ have been introduced into the sediment from their source organisms with only relatively minor changes to their molecular structure.

It is only through knowledge of the reactions proceeding during sedimentation of organic matter through the water column, and during its subsequent burial in the sedimentary record, that

geologically-occurring lipids may be used as a source of information. Certain lipid classes, notably the steroids (Mackenzie *et al.* 1982), are becoming well understood in this respect, although other classes await study. A knowledge of precursor-product relationships allows the use of sedimentary organic components as indicators of biological sources of organic matter, depositional environment or conditions, climatic variations, and organic matter maturity.

Biological marker compounds and their uses

Biological marker compounds have a wide variety of structures, all specifically indicative of a biological origin. The degree of specificity in the structure

may enable inferences to be made as to the precursor molecules, and hence the ultimate origin in a particular family, class, or even genus of organism (see also Section 2.1). Of course, detailed chemotaxonomic information for modern organisms is the essential basis for successful correlation with such biological sources. Furthermore, when applying biomarkers as source indicators in ancient sediments it is necessary to make the major assumption that ancestor organisms possessed similar molecular compositions to their modern descendants. However, there are often good biosynthetic grounds for such assumptions. Obviously, it is desirable for links to be established between specific fossils (macro and micro) and the molecular record. For example, what does the brown or black material comprising a leaf fossil really consist of? Is there a molecular record of the original lignin, cutin, or wax? Similar questions apply to other macrofossils (e.g. fish remains) and microfossils. Unfortunately such work is only in the early stages. Nevertheless, despite these constraints, a considerable number of indicative compounds, and, indeed, classes of compound, are generally accepted as reflecting certain biological inputs, as discussed below. These and other biological markers are reviewed by Brassell *et al.* (1978) and Philp (1985).

Straight-chain alkanes (*n*-alkanes) and their functionalized equivalents (*n*-alcohols (alkanols), *n*-fatty acids (alkanoic acids), and *n*-alkanones) are common constituents of the majority of organisms (e.g. leaf waxes of higher plants, membrane lipids of algae, etc.). In addition, the distributions of carbon chain lengths of these compounds are informative as to the origin of organic matter in a sediment. In general, short- (C_{15} – C_{19}) and medium-chain (C_{20} – C_{24}) compounds reflect algal and/or bacterial sources, whilst long-chain compounds (C_{27} – C_{33}) typify a higher plant contribution.

A class of organic compounds known as hopanoids are ubiquitous constituents of sediments. Several biological precursors of the geological hopanoids have been identified — almost all are bacterial in origin (Fig. 1). More specific biological marker compounds have also been proposed. For example, certain long-chain acyclic isoprenoids are common constituents of archaeobacteria; furthermore, some compounds appear to be restricted to methanogens (Brassell *et al.* 1981). Other widely accepted biological marker compounds include $18\alpha(H)$ -oleanane (higher plants), 4-methylsteroids (especially dinosterol; dinoflagellates), long-chain alkenones (prymnesiophyte algae), and botryococ-

cocane or botryococenes (only observed in the fresh- or brackish-water alga *Botryococcus braunii*).

An appraisal of the biological sources of the sedimentary organic matter, and the relative importance of specific contributions, aids the reconstruction of the environment of deposition of the sediment. For example, freshwater and marine sediments may usually be distinguished by their molecular signatures, owing to the contribution of organic matter from different organisms in the two environments. Furthermore, in the marine realm, the abundance of terrestrial organic matter is related to proximity to land and the importance of fluvial and/or aeolian transport of land-plant debris. In petroleum, the molecular composition is the best (if not the only) source of information regarding the environmental setting of its source rock.

In addition to providing clues to the broad depositional setting of a sediment, the molecular record is instructive with regard to the environmental conditions prevailing at the time of deposition. Of prime concern here is the oxicity of the water column. Didyk *et al.* (1978), in an extension of the work by Powell & McKirdy (1973), proposed the ratio of two related organic compounds, pristane and phytane, as an indicator of oxygen levels at the site of deposition. Whilst the basic rationale behind this indicator is sound — namely two different reaction pathways from the same precursor (the phytol side chain of chlorophyll; Fig. 1), the one followed being dependent upon the oxygen level of the environment — the effects of differences in organic matter sources and maturity complicate its use. However, when used in conjunction with other evidence, such as porphyrin content, this ratio can be a useful indicator of the degree of oxygenation.

Sediments deposited in hypersaline environments are frequently characterized by distinctive distributions of biomarkers (ten Haven *et al.* 1988). These unusual molecular signatures presumably reflect a contribution of organic matter from salinity-tolerant organisms, coupled with the presence of highly reducing conditions of deposition.

During sediment burial and organic matter maturation, biological marker distributions are modified through chemical reactions. Whilst early diagenesis is characterized mainly by reactions involving the loss of functional groups, during late diagenesis and catagenesis the biomarker reactions are dominated by isomerization and degradation processes (Mackenzie *et al.* 1980). Each reaction proceeds over a specific range of maturity, dependent upon time, temperature, and to a lesser extent, pressure (Tissot

& Welte 1984). Consequently, determination of the extent of such reactions in a sediment (typically by molecular product–precursor ratios) allows the assessment of maturation stage — critical in oil generation studies.

A further application of the molecular components of sedimentary organic matter lies in the reconstruction of palaeoclimatic fluctuations. Recent progress in this area includes the recognition of a molecular ‘palaeothermometer’ in a group of organic compounds called alkenones (Brassell *et al.* 1986). A simple molecular parameter is now available which can be used to illustrate past fluctuations in sea-surface temperatures, as prymnesiophyte algae modify their molecular composition in response to long-term temperature changes. This approach is currently being employed to record glacial or interglacial cycles in deep-sea sediment cores, and compares well with classical oxygen isotope measurements on foraminifera. Biological marker compounds may also record marine productivity changes, and variations in aeolian transport of terrestrial organic debris.

The nature of source rocks

Exactly what constitutes a hydrocarbon source rock has long been a matter of debate, although advances in petroleum geology and geochemistry have resulted in the general acceptance of a broad definition. Brooks *et al.* (1987) define a source rock as ‘a volume of rock that has generated or is generating and expelling hydrocarbons in sufficient quantities to form commercial oil and gas accumulations’. A *potential* source rock is a volume of rock which has the capacity to generate commercial hydrocarbon accumulations, but is of insufficient maturity. Most source rocks are fine-grained, typically dark-coloured shales or marls. However, the organic matter within a sediment must meet minimum requirements for organic richness and quality or type in order for the rock to be considered a source bed. Most potential source rocks contain between 0.8 and 2% organic carbon; an approximate limit of 0.4% is commonly accepted as the lowest organic carbon content for hydrocarbon generation and expulsion to occur. Of course, there is no general upper limit of organic richness, and many of the best source beds contain upwards of 5–10% organic carbon.

The kerogen in a source rock may contain particulate organic matter from a variety of sources — in fact, the nature of the hydrocarbons generated is

strongly dependent upon the kerogen composition. Most kerogens are mixtures of two types of organic matter: terrigenous higher plant debris and aquatic (marine or lacustrine) lower plant material. Microscopic analysis of source rocks reveals that most of the sedimentary organic matter is amorphous, with only a minor part comprising recognizable biological debris. Sediments containing large quantities of yellow-brown amorphous organic matter of algal and/or bacterial origin (i.e. types I or II; Tissot & Welte 1984) will produce petroleum given sufficient maturation. In contrast, sediments containing type III kerogens, comprising abundant particulate land plant debris, will liberate mainly gas.

There are two main prerequisites for the accumulation of significant quantities of organic matter in sediments: production of organic matter, and its subsequent preservation. Both are controlled by many variable factors (Fig. 2).

Production of organic matter. Source rocks may be deposited in marine or lacustrine environments. Owing to their greater importance, only marine source rocks will be discussed here, although many of the factors controlling organic matter accumulation apply in both environments.

Marine primary productivity typically supplies the bulk of organic matter to marine source rocks, although processes within the water column utilize much of the organic debris before it can reach the sediment. Surface productivity is largely controlled by water temperature, light intensity, and the availability of nutrients. The latter may be influenced by sea-level (with the flooding of coastal areas during periods of high sea-level introducing terrigenous nutrients), water column overturn (resulting from storm activity or improved deep circulation), and upwelling of nutrient-rich water. Upwelling is, in turn, controlled by the action of prevailing winds and the Earth’s Coriolis forces, and by the distribution of land masses. Present-day upwelling areas overlie many of the most organic-rich sediments in the oceans. Terrigenous higher plant debris, which may also be a significant constituent of hydrocarbon source rocks, may be introduced into the marine environment by flooding of coastal areas during transgression, or by aeolian or fluvial transport.

Preservation of organic matter. The accumulation of organic debris in sediments depends to a large extent upon the inhibition of chemical oxidation and biochemical degradation processes during transport, deposition, and early burial. These pro-

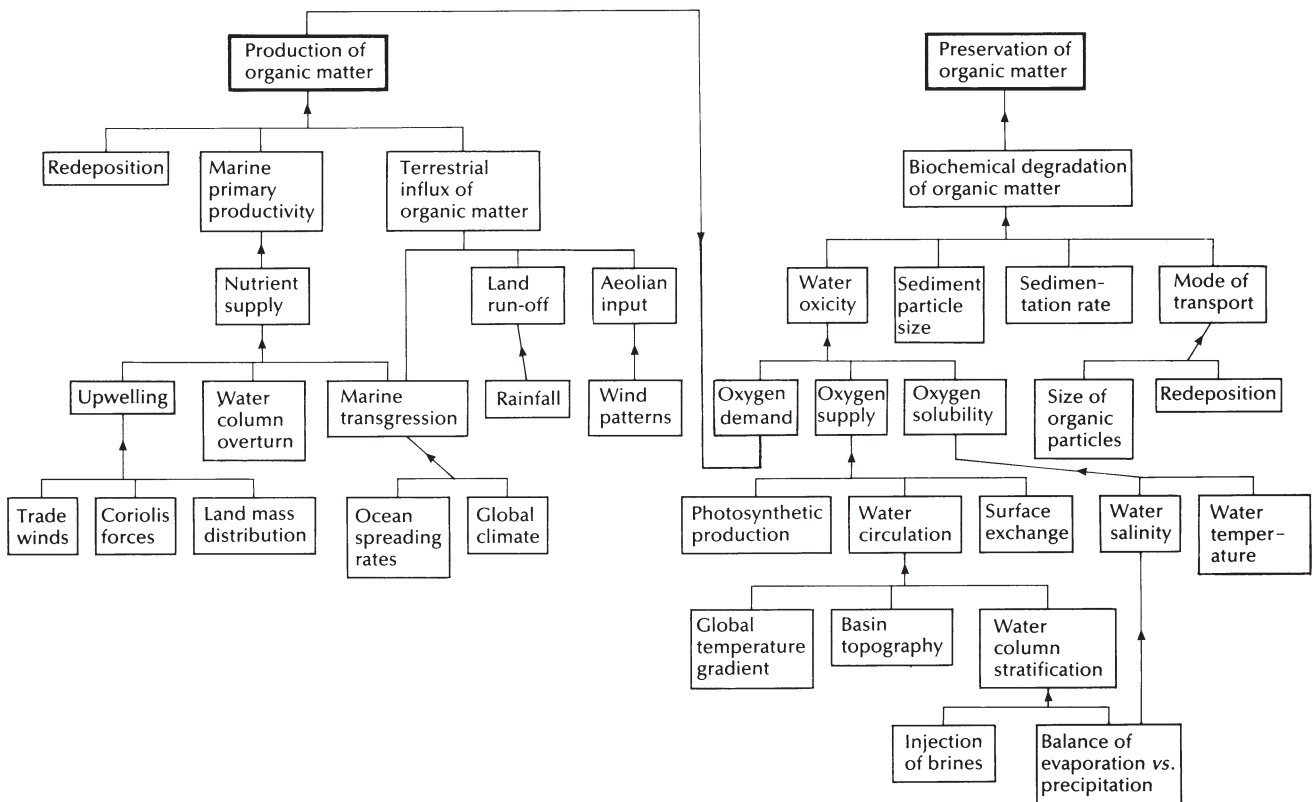


Fig. 2 Flow diagram showing various interrelated factors which influence the production of organic matter in the biosphere, and its subsequent preservation in the geosphere. These factors may all exert some control upon the accumulation of organic matter in marine sediments.

cesses, in turn, depend upon sediment particle size, sedimentation rate, mode of transport of organic matter to the sediment, and water column oxicity. Thus, organic-rich sediments are typically fine-grained, and are favoured by relatively high sedimentation rates, resulting in rapid burial. Rapid transit of organic debris through the water column, either through faecal pellet transport or sediment redeposition (turbidity currents, etc.), also favours organic matter preservation. However, the oxicity of the water column, particularly at the sediment surface where residence time of organic matter is generally high, has long been recognized as the major control on the preservation of organic carbon in sediments. Under oxygen-depleted conditions, aerobic bacterial activity is absent, and degradation of organic matter is limited to the action of the less efficient anaerobic bacteria (see also Section 3.1). Furthermore, the grazing of macro-organisms on the sediment surface ceases in low-oxygen conditions; consequently, there is no bioturbation to promote the access of oxygen and aerobic bacterial degradation within the upper sediments. The resulting sediments are usually finely laminated,

and typically contain relatively large amounts of organic matter.

The oxygen content at any point in the water column is controlled by oxygen demand (which is controlled by organic matter degradation), oxygen supply, and oxygen solubility (which is greatly reduced in warmer or more saline water). Oxygen supply in the marine environment is largely a function of deep-water circulation, although oxygen is supplied to surface waters by exchange with the atmosphere and photosynthetic production. Demaison and Moore (1980) discussed several models for the deposition of oil source beds — all involving highly oxygen-depleted conditions.

One such model is that of a restricted and/or stratified basin. Oxygen-deficient conditions may develop in sedimentary basins where physical barriers tend to inhibit water circulation, particularly in basins with a positive water balance (i.e. river inflow exceeding evaporation). The present-day Black Sea is a much-cited example of an anoxic silled basin with organic-rich sediments. Deposition of potential source beds is also favoured in permanently stratified lakes (e.g. Lake Tanganyika).

Density stratification in basins may be induced by the influx of dense, oxygen-poor, saline water (formed in shelf areas where evaporation is high), or by the influx of low density freshwater (in areas of high precipitation). Such stratification in the water column inhibits circulation, and hence oxygen replenishment is poor.

The second type of oxygen-deficient environment where organic-rich sediments are characteristic is that of an expanded mid-water oxygen-minimum layer. The best developed of these form in response to coastal upwelling of nutrient-rich waters in areas where oxygen supply cannot match demand as organic matter degrades in the water column (e.g. Peru Upwelling). Alternatively, oxygen-minimum layers may develop in areas where productivity is normal, but oxygen supply is poor due to isolation from a source of well oxygenated water. In either case, organic-rich sediments may be deposited where the oxygen-minimum layer impinges upon a continental slope or shelf. Open ocean oxygen minima, covering wide areas of the oceans, may have been important during specific times in the past — the so-called 'oceanic anoxic events'. These relatively short periods of geological time were characterized by widespread accumulation of organic-rich sediments. The best known examples occur in the Cretaceous (Aptian–Albian, Cenomanian–Turonian, and Coniacian–Santonian), although another well defined oceanic anoxic event occurs in the Toarcian (Jurassic). Organic-rich sediments from these intervals comprise a large proportion of the world's potential and actual source rocks.

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3.3 Destructive Taphonomic Processes and Skeletal Durability

C. E. BRETT

Destructive processes

Durability refers to the relative resistance of skeletons to breakdown and destruction by physical, chemical, and biotic agents. The processes of skeletal destruction can be subdivided into five categories which follow one another, more or less sequentially, as remains of organisms are exposed in different environments (Seilacher 1973; Müller 1979; Brett & Baird 1986): (1) disarticulation; (2) fragmentation; (3) abrasion; (4) bioerosion; and (5) corrosion and dissolution. Depending on the physical characteristics of the sedimentary environment, one or more of these processes may be more active.

1 *Disarticulation* is the disintegration of multiple-element skeletons along pre-existing joints or articulations. There is a paucity of hard data on disarticulation rates, although this has been partly alleviated by several observational and experimental studies (Schäfer 1972; Allison 1986, 1988; Meyer & Meyer 1986; Plotnick 1986). Disarticulation may occur even prior to death in the case of moulting, which yields recognizable exuviae in many arthropods. In most cases, disarticulation proceeds very rapidly after the death of an organism, and may involve biochemical breakdown of tissues by enzymes present in the body of the organism itself. Bacterial decay (see also Section 3.1) of ligaments and connective tissues proceeds at a variable rate depending upon the nature of the tissues, as well as the local environment of decay. Aerobic decay of tissues proceeds rapidly in most cases; e.g., the ligaments binding echinoderm ossicles are broken down within a matter of hours to a few days after death. Hinge ligaments composed of conchiolin in bivalves are evidently more resistant, and can remain intact for periods of months, despite fragmentation of the shells. Anoxia obviously inhibits bacterial decay. None the less, recent experiments indicate that anaerobic bacteria destroy ligaments and connective tissues within a matter of a few weeks to months.

Biotic agents, including scavengers and infaunal burrowers, may greatly accelerate disarticulation as

evidenced by decay experiments using controls in cages that exclude larger organisms. Scavenging and burrowing processes are precluded in anaerobic environments, thus favouring articulated preservation.

Physical agents, such as current and wave turbulence, also produce disarticulation in skeletons which have undergone some decay. It is frequently assumed that the transport of carcasses over any distance will result in their disarticulation. However, if organisms are transported just prior to death, or immediately thereafter, this may not be the case (Allison 1986; Section 3.1). Conversely, once connective tissues have decayed, even very minor currents (less than 5 cm/s) may be effective in producing complete disarticulation.

Interlocking structures of skeletons inhibit disarticulation. For example, the interlocking hinge-teeth of certain brachiopods (such as terebratulids) may prevent disarticulation of the valves for extended periods of time. The tightly crenulated sutures of some pelmatozoans and echinoids appear to be similarly resistant.

Thus, most multielement skeletons can only be preserved as articulated remains if they are buried extraordinarily rapidly (hours to a few days). Anoxic environments promote articulated preservation, as does an absence of turbulence. However, these factors are not sufficient in themselves to explain this mode of preservation. Tightly sutured skeletons (e.g. the tests of echinoids, and crinoid stems), on the other hand, may withstand much longer periods of exposure in marine environments.

2 *Fragmentation* of skeletons results both from physical impact of objects and from biotic agents such as predators and scavengers. Some fragmentation may occur prior to death, such as that produced by attempted predation (see also Section 4.13). Distinct fragments or patterns of breakage may be recognizable in certain instances, e.g. the curved fractures produced by peeling of gastropod apertures by crabs. However, more commonly, pre-

ation damage is indistinguishable from physical breakage.

Shells tend to cleave along pre-existing lines of weakness such as growth lines, or ornamentation such as ribbing, and yield consistent types of fragments (Fig. 1). Resistance to fragmentation relates to several aspects of skeletal morphology and composition, including thickness and curvature of shells, microarchitecture, and percentage of organic matrix. In general, nacreous (pearly) skeletal fabric in mollusc shells are most resistant to breakage by impact, whereas foliated shells are more fragile. Bacterial decomposition of organic matrix greatly weakens shells, and makes them much more susceptible to fragmentation by other agencies; hence, for example, the high organic content of the shells of certain nuculid bivalves has probably resulted in their under-representation in the fossil record. Surficial exposure time is also critical; microborings of endolithic algae and fungi greatly weaken shell structure and facilitate breakage. Delicate skeletons of corals, bryozoans, graptolites, and other fossils are particularly prone to fragmentation, even in slightly agitated waters. Hence, they form key taphonomic indicators of changes in current energy among facies. A high degree of fragmentation suggests persistent breakage and reworking, perhaps within normal wave base. Extraordinary events, such as storms, may also generate currents or waves that impinge on otherwise quiet environments and cause intermittent fragmentation.

3 Abrasion, or physical grinding and polishing, results in the rounding of skeletal elements and loss of surficial details (Fig. 1B). The extent of abrasion in any given type of skeleton is related to environmental energy, exposure time, and particle size of the abrasive agent. In general, the rate of abrasion increases with increasing grain size: clay-sized grains do not significantly abrade skeletons; sand- and gravel-sized material is probably the most effective agent. Semiquantitative measurements of abrasion rates have been obtained by tumbling shells artificially (Fig. 2; Chave 1964). Two factors strongly influence the relative resistance of skeletons: size relative to the grain size of the sediment, and microarchitecture. Not surprisingly, small bivalve shells are fragmented and abraded much more readily than large ones. Furthermore, dense skeletal microstructures, such as crossed-lamellar structure in molluscs, are relatively hard and resistant to abrasion. Gastropods with dense shells may survive over one thousand hours of continuous tumbling.

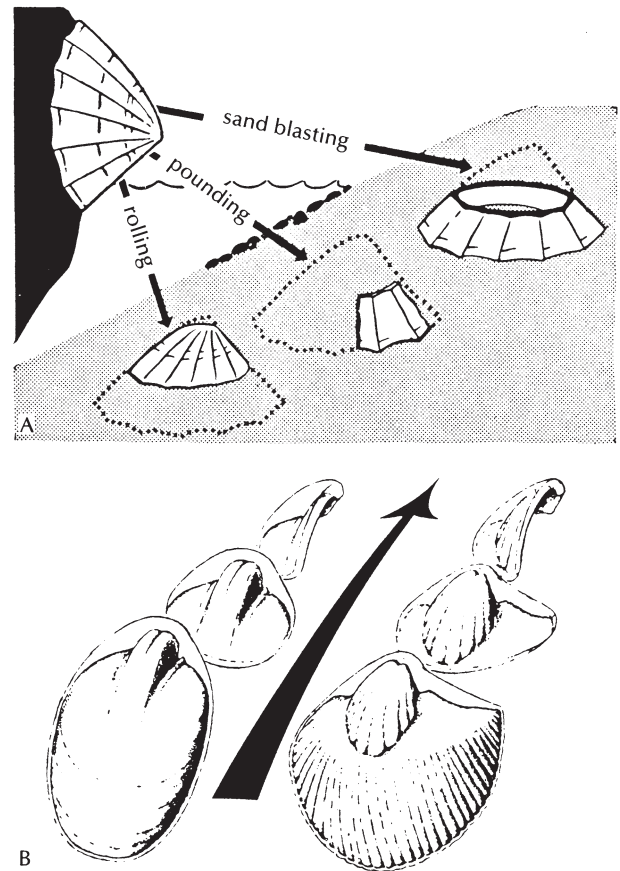
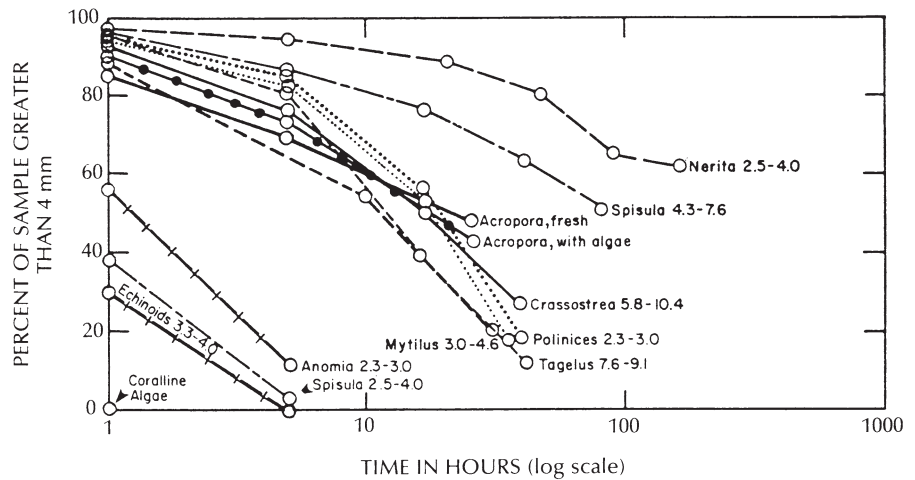


Fig. 1 A, Abrasion and breakage may produce fragments diagnostic of different depositional environments. Stably anchored shells are abraded from the top down (anchor faceting). Pounding of shells by surf produces fractures that follow medial and concentric lines of weakness in the shell. Rolling and gliding of the shell will abrade the outer edge (glide faceting). B, Roll fragments are produced by shells tumbling in an abrasive medium which preferentially destroys thinner parts of the shell, leaving thickened umbonal parts intact: spiriferid brachiopods from the Lower Devonian Oriskany Sandstone of Maryland. (After Seilacher 1973.)

Moderately porous and/or organic-rich shells display intermediate durabilities, while very porous skeletons, such as those of bryozoans and algae, abrade very rapidly and will be selectively removed from the fossil record of high energy environments. However, porous particles such as echinoderm ossicles may be cushioned against abrasion by their low density. Thus, it is commonly assumed that echinoderm ossicles can be strongly abraded only if they have undergone some early diagenetic permineralization.

4 Bioerosion, commonly associated with recognizable trace fossils such as the borings of clionid sponges and various endolithic algae, proceeds at

Fig. 2 Durability of invertebrate skeletal material in a tumbling barrel filled with chert pebbles. Numbers following each skeleton name give the initial size range in centimetres. (After Chave 1964; reproduced with the permission of John Wiley & Sons, Inc.)



very high rates in most shallow-marine environments. Rates from 16% to over 20% weight loss per year, as a result of algal and sponge boring, have been observed for modern marine mollusc shells. It is not clear whether such rates pertained in the Palaeozoic when clionid sponges were much less abundant. As with abrasion, shell thickness, organic content, and perhaps density may influence the relative resistance of skeletal material to destruction by bioerosion.

5 *Corrosion and dissolution* of skeletons result from chemical instability of skeletal minerals in seawater or in sediment pore-waters. Dissolution may begin at the sediment–water interface and continue to considerable depths within the sediment. Bioturbation of sediments commonly promotes dissolution by the inmixing of fresh seawater and by oxidation of sulphides to produce weak acids within sediment pore-waters.

A general ordering of the stability of minerals is as follows: phosphate > silica > echinoderm calcite > other skeletal calcite > aragonite. In addition, skeletal materials containing a high proportion of organic matter, such as nacreous shell, are relatively more resistant to dissolution than those with pure carbonate mineralogies, a trend which runs counter to destruction by abrasion or fragmentation. This differential stability results in biases in the records of different groups: e.g., calcitic brachiopod shells may be extremely well preserved where aragonitic molluscs occur as highly compacted internal–external moulds.

In practice, the effects of mechanical abrasion, most bioerosion, and corrosion are difficult to distinguish in fossils. Hence, Brett and Baird (1986) suggested the use of the term *corrasion* to indicate the general state of wear in shells resulting from any

combination of these processes. Corrasion provides a general index of exposure time to various agencies of wear on the sea floor.

Skeletal durability

Destructive processes of disarticulation, fragmentation, and corrasion are readily evident in the fossil record. These processes affected different skeletal types in different ways. Most marine skeletonized organisms can be assigned to one of five skeletal architectural categories: massive, arborescent, univalved, bivalved, or multielement. Table 1 provides a summary of biostratinomic processes, such as fragmentation and disarticulation, with respect to their influence upon each of the five skeletal types. In general, massive skeletons are the least subject to breakage and are most resistant to mechanical destruction. However, because they remain on the sea floor for prolonged spans of time, such massive skeletons often display the effects of corrasion to a greater extent than other skeletons. Arborescent skeletons are probably the most sensitive indicators of fragmentation; an absence of breakage in such skeletons is an excellent indicator of minimal disturbance of the sedimentary environment. Most bivalved skeletons become disarticulated relatively rapidly after death, although those with tough conchiolin ligaments may remain articulated for extensive periods. Finally, multielement skeletons provide the best indicators of rapid burial, as they disarticulate extremely rapidly in the absence of sediment cover. Taken together, various skeletal types and their varied sensitivities to destructive agents may provide excellent indicators of sedimentary processes, and can be used to define taphonomic facies (Section 3.9).

Table 1 Potential utility of various invertebrate skeletal types as qualitative indicators of physical environmental parameters. In each case the types of evidence useful for inferring a given condition (e.g. high energy) are listed as symbols, defined at the bottom of the table. (From Brett & Baird 1986.)

Skeletal type	Current/wave transport of skeletons		Environmental energy		Burial rate	
	Azimuthal (compass-bearing) orientation	Convex up/down	Low	High	Slow, reworked	Very rapid
<i>Single unit</i>						
Massive	—	—	—	++ (do)	++ (cor)	—
Encrusting	—	—	—	—	++ (cor)	—
Ramose, robust	+ (la)	—	+ (fr)	+ (fr)	++ (cor)	—
Ramose, fragile	++ (la)	—	+ (fr)	—	—	+ (fr)
Univalved shell	++ (la, d)	+ (do)			+ (cor)	+ (fr)
<i>Multiple unit</i>						
Bivalved shell, thick	+ (la)	+ (do)	+ (fr)	+ (fr)	+ (fr, cor)	+ (da)
Bivalved shell, thin	+ (la)	++ (do)	++ (da, fr)	—	—	+ (fr)
Multielement, tightly sutured	+ (la)	—	+ (da)	+ (da, fr)	+ (da, cor)	+ (da)
Multielement, loosely articulated	+ (la)	—	++ (da)	—	—	++ (da)

Utility as indicator of given condition: — not generally usable; + usable indicator; ++ very important indicator.

Type of indicator: cor = degree of corrosion; do = disorientation (overturning); fr = fragmentation (or lack of); da = disarticulation/articulation; la = long axis lineation; d = direction of apex.

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3.4 Transport — Hydrodynamics

3.4.1 Shells

J. R. L. ALLEN

Introduction

A consideration of the following as sedimentary particles exemplifies the range of behaviour of shelly hard parts: the shells of brachiopods, bivalve, gastropod and cephalopod molluscs (including those with internal hard parts), ostracodes, and articulated crinoid columnals. All but the crinoids typically have hard, calcareous coverings marked by a low mass per unit surface area. The brachiopods are protected by two normally unequal but bilaterally symmetrical opposed valves, which may separate after death on the decay of muscle tissue. Equal but asymmetrical (about the umbone) valves typify the bivalve molluscs; separation depends on the decay of the ligament. In the brachiopods, and particularly in the bivalve molluscs, there may be teeth and other processes projecting from the hinge. Typically, gastropods have spiral shells with a wide range of apical angle and external ornament, which approximate to axial symmetry. External shells in the cephalopods are chambered and vary from straight (axially symmetrical) to more or less tightly coiled (bilaterally symmetrical). The internal shell of the coleoid cephalopods varies from straight and axially symmetrical (e.g. belemnite guards) to flattened with bilateral symmetry (cuttlefish). Ostracode valves are equal, but not symmetrical normal to the hinge. Articulated crinoid columnals are axially symmetrical and virtually cylindrical.

Little is understood of the hydrodynamic behaviour of these hard parts, so abundant and ecologically important in modern shallow-water environments and the fossil record. Field studies are few (Nagle 1967; Salazar-Jiménez *et al.* 1982) and what laboratory experimental work exists (Kelling & Williams 1967; Brenchley & Newall 1970; Futterer 1978; Allen 1984) seldom faithfully reflects natural conditions. There is a particular paucity of data on the behaviour of shells *en masse*.

The hydrodynamic behaviour of shells is complex

and unpredictable, chiefly because of the huge diversity of forms involved. The shell properties of greatest influence are: (1) the kind and degree of symmetry; (2) the degree of elongation; (3) the degree of shell curvature (brachiopods, bivalve molluscs, ostracodes) or the apical angle (gastropods); (4) the character and distribution of ornament and the presence of teeth or processes along the hinge (brachiopods, bivalve molluscs); (5) the mean mass per unit shell area; and (6) the distribution of mass. Aside from fluid properties, the other factors controlling behaviour are: (7) the agent transporting the shell (river, tidal stream, waves, turbidity current); (8) the force exerted by the agent; (9) the nature of the bed on which the shell alights or over which it moves; and (10) the character and distribution of any other particles, either already deposited or moving with the shell. The ultimate response of the shell is to assume a characteristic *attitude* and *orientation* on the sedimentary surface; these properties, when summed over a sample of shells, constitute a *biofabric* (Kidwell *et al.* 1986; Section 3.5), which may be diagnostic of current direction and/or agency. Attitude, whether concave-up or convex-up, is especially important in the analysis of transported brachiopod, bivalve mollusc, and ostracode valves. Introducing the pointing direction afforded by an apex or umbone, shell orientation may be measured with respect to either the axis of symmetry of the shell (gastropods, orthocones, belemnite guards, crinoid columnals) or some convenient feature such as the line of elongation, the hinge, or a straight edge (brachiopods, bivalve molluscs, ostracodes).

Settling

Shells will eventually settle to the bed after having been either carried from shallow- to deep-water by turbidity currents or swept up into the water column by storm waves on a shelf. Laboratory experiments give some insight into the settling of bivalve mollusc valves.

A terminal settling velocity is reached when the upward drag acting on the sinking shell equals the downward-acting immersed weight. Valves of all studied species eventually fall concave-up (Fig. 1A).

The centre of mass of the shell then lies below the centre of fluid force, there being no turning couple. Released convex-up, a turning couple at once appears because, in this attitude, the centre of action of the prevailing fluid forces underlies the centre of particle mass (Fig. 1B). Valves with a length similar to the height sink steadily on a helical path, the shell spinning once about a vertical axis for each turn of the trajectory (Fig. 1C). The sense of the trajectory, either clockwise or anti-clockwise, varies with the species and whether the valve is on the left or the right. Valves with a length more than about 1.6 times the height settle unsteadily, the shell displaying a regular oscillation (pitching), amongst other motions, while settling either spirally or irregularly (Fig. 1D).

The drag coefficient of sinking mollusc valves is invariably substantially larger than for dynamically equivalent smooth spheres (i.e. those with the same

balance of inertial and viscous forces). Valves that settle unsteadily differ most from spherical particles, affording drag coefficients up to three times greater. Thus the 'quartz equivalents' (the size of a quartz grain or pebble with the same terminal settling velocity) of mollusc valves are much smaller than the valves themselves.

Transport in one-way currents (rivers, tidal streams)

Some understanding of the complex process of transport in one-way currents has come from field observations and laboratory experiments, but much remains unknown, particularly concerning shells in bulk.

In the case of dispersed bivalve molluscs, entrainment depends on the orientation and particularly the attitude of the shell, and on the roughness of the

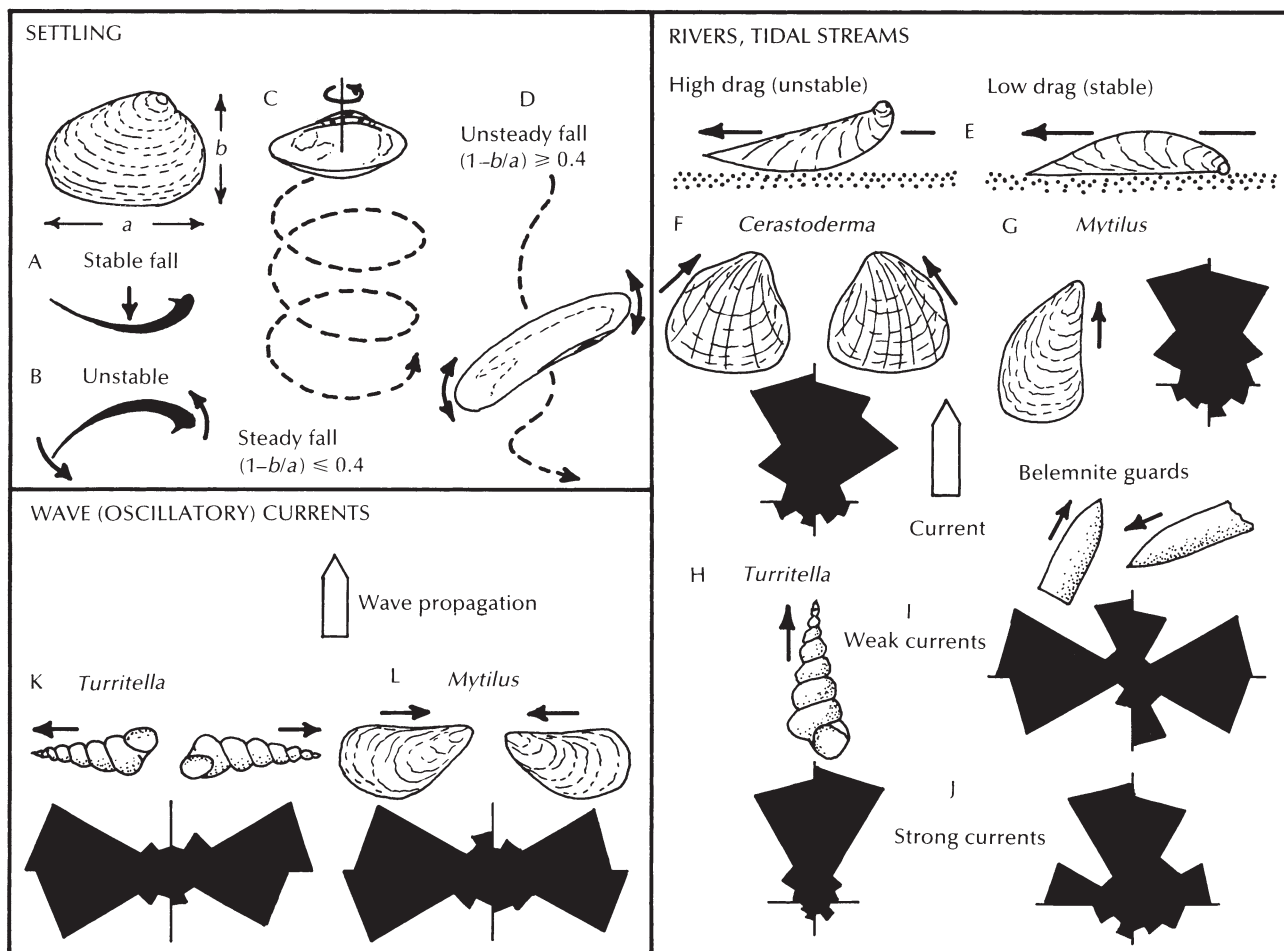


Fig. 1 Schematic summary of the behaviour and idealized biofabrics of representative shells (bivalve molluscs (*Cerastoderma*, *Mytilus*); gastropods (*Turritella*); belemnite guards) when settling in water, and when transported and deposited from one-way and oscillatory currents.

bed relative to the scale of the valves. For planar beds of particles much smaller than the valves, convex-up shells require a larger fluid force for entrainment than concave-up ones, the force for convex-up entrainment varying from a few to many times greater, depending on shell shape and mass per unit area. Hence the drag coefficient of a convex-up valve is smaller than for the same valve when concave-up; consequently a given valve is most streamlined when convex-up (Fig. 1E). Once entrained, convex-up valves take a variety of orientations depending on shell shape and the prominence and distribution of teeth and other processes along the hinge, which can act like a storm anchor (Fig. 1F, G). Convex-up valves tend, without change of attitude, to glide over relatively immobile planar beds, but on mobile, sandy ones they may speedily become partly buried and thus halted. Concave-up valves entrained on relatively fine-grained planar beds also maintain their attitude while gliding over the bed but become tilted downcurrent. Overturning into the more resistant and stable convex-up position occurs only where the moving valve encounters a substantial obstacle on the bed. An exception is the stout-shelled *Mytilus edulis*, valves of which at once turn over when entrained from the concave-up attitude. As natural beds abound in obstacles, and concave-up valves are the least resistant to entrainment, it is not surprising that the convex-up attitude is the norm for shells on river beds and beneath tidal currents.

Bivalve mollusc shells appear to undergo frequent changes in attitude as they travel over ripples and dunes, which are bedforms much larger than themselves. A valve that is transported convex-up over the upstream side of the bedform is liable to overturn on being propelled into the sluggish wake to leeward, with the result that the shell could slide concave-up into and be buried in the trough.

Because of their narrow conical form, high-spined gastropods become oriented with the apex upcurrent (Fig. 1H). Low-spined and coarsely ornamented forms assume a more random orientation. Cylindrical shells (tentaculitids, orthocones, belemnite guards, articulated crinoid columnals) develop a variety of orientations beneath a current, depending on flow and bed conditions (Fig. 1I, J). Particles of this form tend to roll over the bed, and so develop a flow-transverse biofabric. The fabric changes increasingly towards a flow-parallel one as the shells become rotated into the current direction on meeting obstacles, and as the amount of rotation increases with growing current strength.



Fig. 2 Mainly vertically packed and tightly nested shells of *Macoma balthica* forming a beach deposit in a laboratory wave tank.

Transport in oscillatory (wave) currents

Dispersed shells on smooth beds affected by wave swash and backwash behave much as in one-way flows. Wave action on concentrated bivalve shells forming beaches commonly results in a distinctive biofabric, the valves packing mainly vertically in nests and rosettes (Fig. 2). In wave-affected shallows, however, where genuinely oscillatory currents exist, field and laboratory experiments point to a different mode of behaviour. The shells either glide (convex-up if brachiopod or bivalve) or roll over the bed and become orientated so that the long dimension is in most cases parallel with the wave crests (Fig. 1K, L). The combination of oscillatory with steady (e.g. tidal) currents creates more complicated patterns which are as yet little understood.

Biofabrics due to organic activity

Some instances of a concave-up attitude assumed by disarticulated bivalve and brachiopod shells found in shallow-marine deposits are with little doubt a consequence of the reworking of the shelly sediment by scavenging organisms, but it is not known how exactly the biofabric arises. Shells disturbed by organisms should possess a random orientation, in contrast to concave-up shells that have settled on the bed in the presence of a current strong enough to swing the particles.

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3.4.2 Plant Material

R. A. SPICER

Introduction

Allochthonous plant fossil assemblages usually represent variously degraded fragmented parts of different individuals and species that lived at varying distances from their ultimate site of deposition and burial. Individual plants are composed of, and produce, an indeterminate number of organs. Whole plants are almost never found in the fossil record, so palaeobotanical systematics has to handle isolated organs (Spicer & Thomas 1986; Section 5.1.3) that have greatly differing potentials for transport, deposition, and preservation.

The interaction of a detached plant organ (or organ fragment) with a fluid medium is governed by its density in relation to that of the fluid medium, together with its shape, size, and surface characteristics. The transportability of a plant part is largely a function of its terminal fall velocity. Many plant parts are flexible planar objects containing air spaces (e.g. leaves) and their hydrodynamic properties are difficult to model theoretically. Empirical approaches have proved more successful. Leaves have received most taphonomic attention because of their abundance and utility in biostratigraphy and

palaeoclimatology (e.g. Spicer 1981, 1989; Ferguson 1985; Spicer & Greer 1986; Spicer & Wolfe 1987). Attention here is focused on potential megafossils of terrestrial plants.

Organ dispersal by wind

Aerial transport determines what organ sample a river or lake, for example, receives and therefore 'sees' of the surrounding vegetation. Factors affecting fall velocity in still air include:

Leaf weight. Weight per unit area at abscission is the most critical intrinsic property of a leaf that affects 'flight' and ground dispersal (Spicer 1981; Ferguson 1985). Evergreen taxa typically are heavier and have higher settling velocities.

Leaf shape. Leaf shape has an effect on fall velocity but shapes with major axes of markedly different length (long and narrow) tend to rotate about the longer axis; such behaviour slightly increases fall time and therefore the chance of greater dispersion from the source (Ferguson 1985).

Leaf size. Although not obviously correlated with fall rate, leaf size affects movement through the branch and trunk space within a forest. Large leaves tend to encounter static obstacles more frequently than small leaves, and any such event either traps the leaf directly, or affects its fall rate. Ferguson (1985) noted a weak positive correlation between leaf size and weight per unit area. Such a correlation would tend to favour the transport of smaller leaves. However, while this may be true for a tree crown as a whole, 'sun' leaves at the top of a tree tend to be smaller but have a higher weight per unit area. Long-distance dispersal of these leaves (and resulting preservational bias) is a function of their exposure to high wind energies and their initial height from the ground (Spicer 1981).

Petiole effects. The petiole rarely exceeds 20% of total leaf weight, and even large petioles have negligible effect on fall rate.

Dispersion resulting from air fall. Aerial dispersal of leaves away from a source follows a negative exponential model (Rau 1976; Spicer 1981). Rau, in a study of litter deposition in an open lake, used the following equation:

$$Z_x = Z_r \exp(-k[r-x]),$$