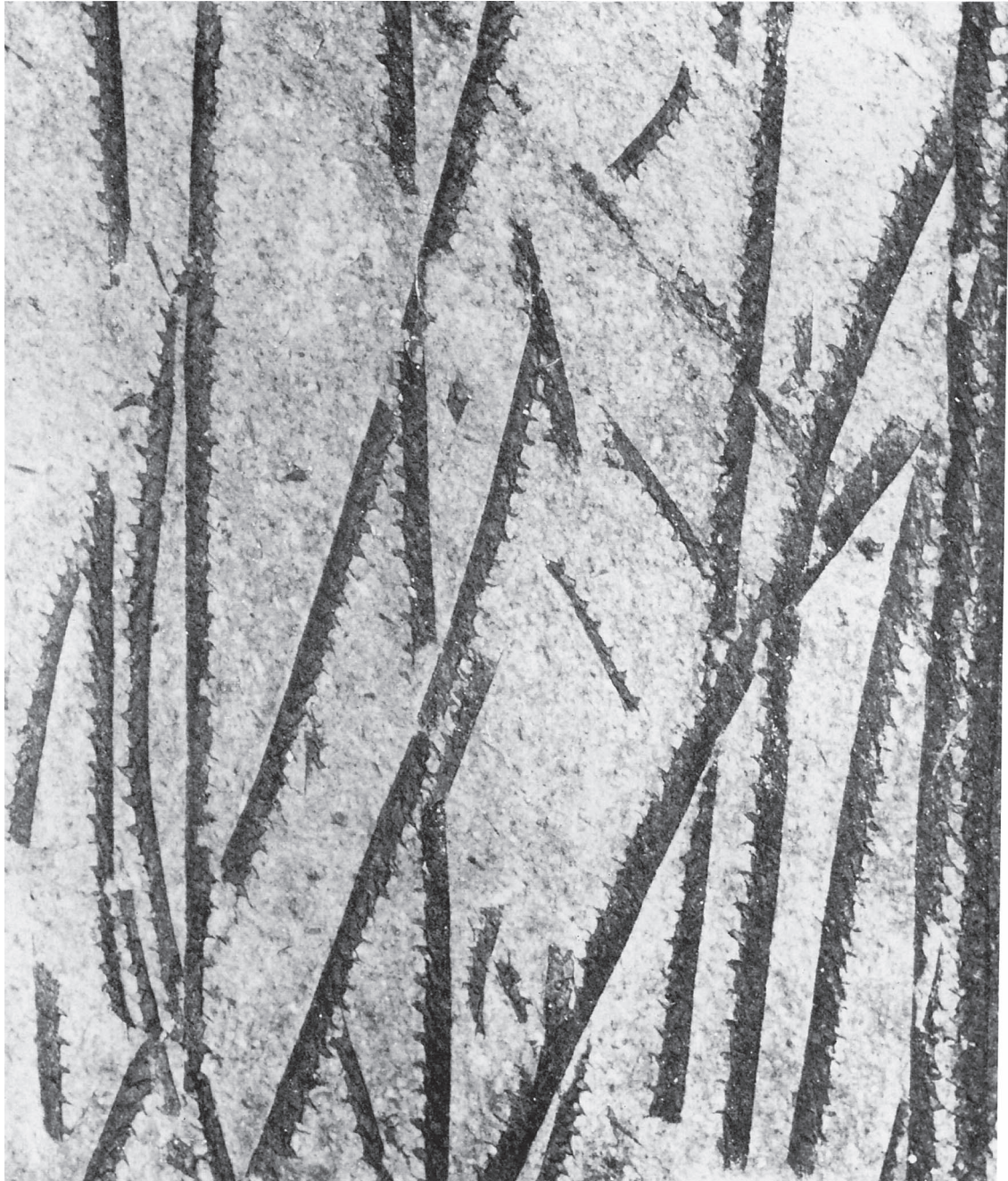# 3
TAPHONOMY

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 Northen 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:

$$(CH_2O)_{106} \, (NH_3)_{16} \, H_3PO_4 + 106O_2 \Rightarrow 106CO_2 + 16NH_3 + H_3PO_24 + 106H_2O.$$
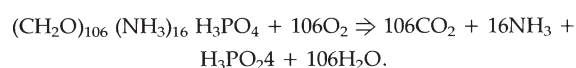
Thus, according to Avogadro's Principle, 1 mole (3.53 kg) of organic carbon requires 106 moles (2374.4 l) of oxygen. Decay rate is commonly expressed as a half-life. Since aerobic decay of 1 g of organic carbon requires 671 cm^3 of oxygen, the oxygen demand for aerobic decomposition can be expressed

as 335 cm^3/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 carcase. Thus an anaerobic microenvironment can even be formed in aerated waters if a carcase 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 (Jørgenson 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 Geiseltalles 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 *Palaemon* 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
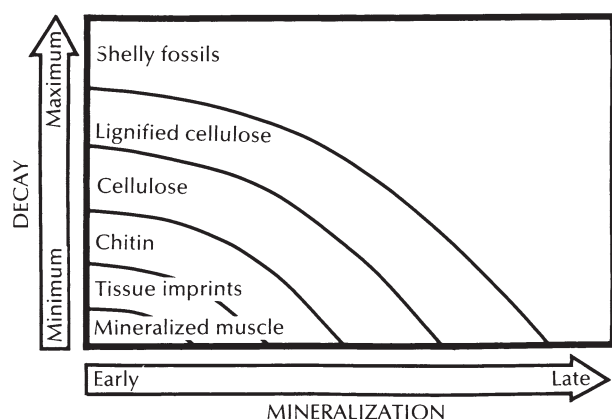
Fig. 1 The relationship between decay and mineralization in the preservation of soft-bodied and lightly skeletonized organisms. Reduced decay and early diagenetic mineralization are required for preservation of volatile tissues such as muscle. The preservational field of each tissue type extends from the bottom left-hand corner of the box to the boundary fence of the next most refractory type. (After Allison 1988.)
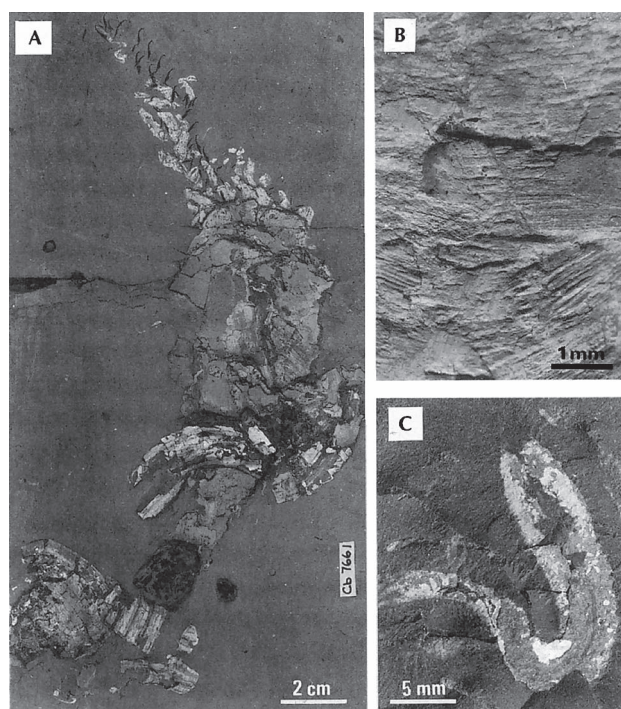

Fig. 2 A, Three-dimensional preservation of mantle and appendage musculature in squid from the Jurassic Oxford Clay of Wiltshire, U.K.; Bristol City Museum, Cb7661. B, Close-up of muscle fibres in A. C, Flattened polychaete worm from the Upper Carboniferous Mazon Creek biota of Illinois, U.S.A. (A, B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

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

casses 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 *Lagania 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.
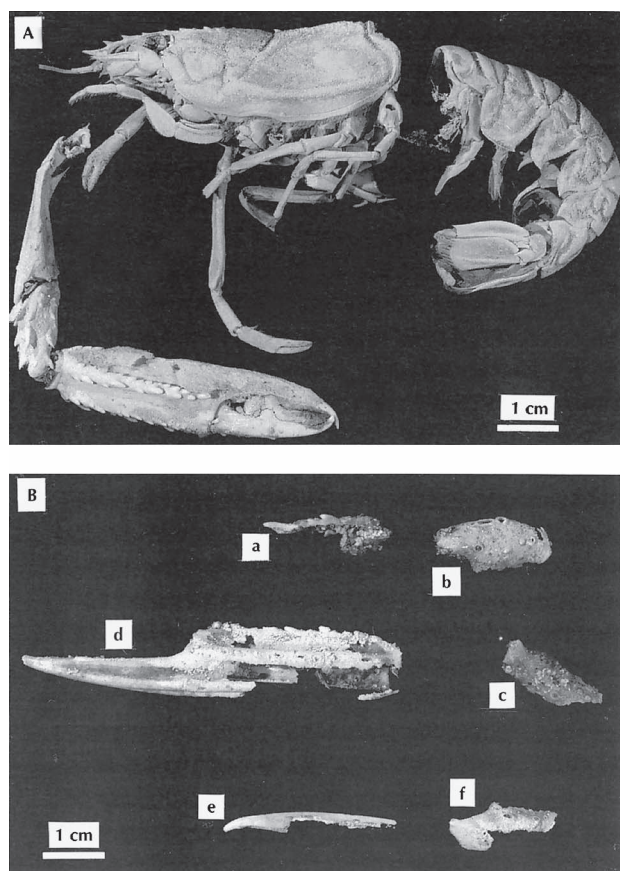
Fig. 3 Carcasses of *Nephrops*. A, Freshly-killed individual after tumbling in rotating barrel. Note that although carcase is decapitated, delicate structures such as the appendages have survived. B, Individual tumbled after 26 weeks of decay: a, rostrum; b, c, segments of chelae nearest to coxae; d, 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 petroleums) 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,
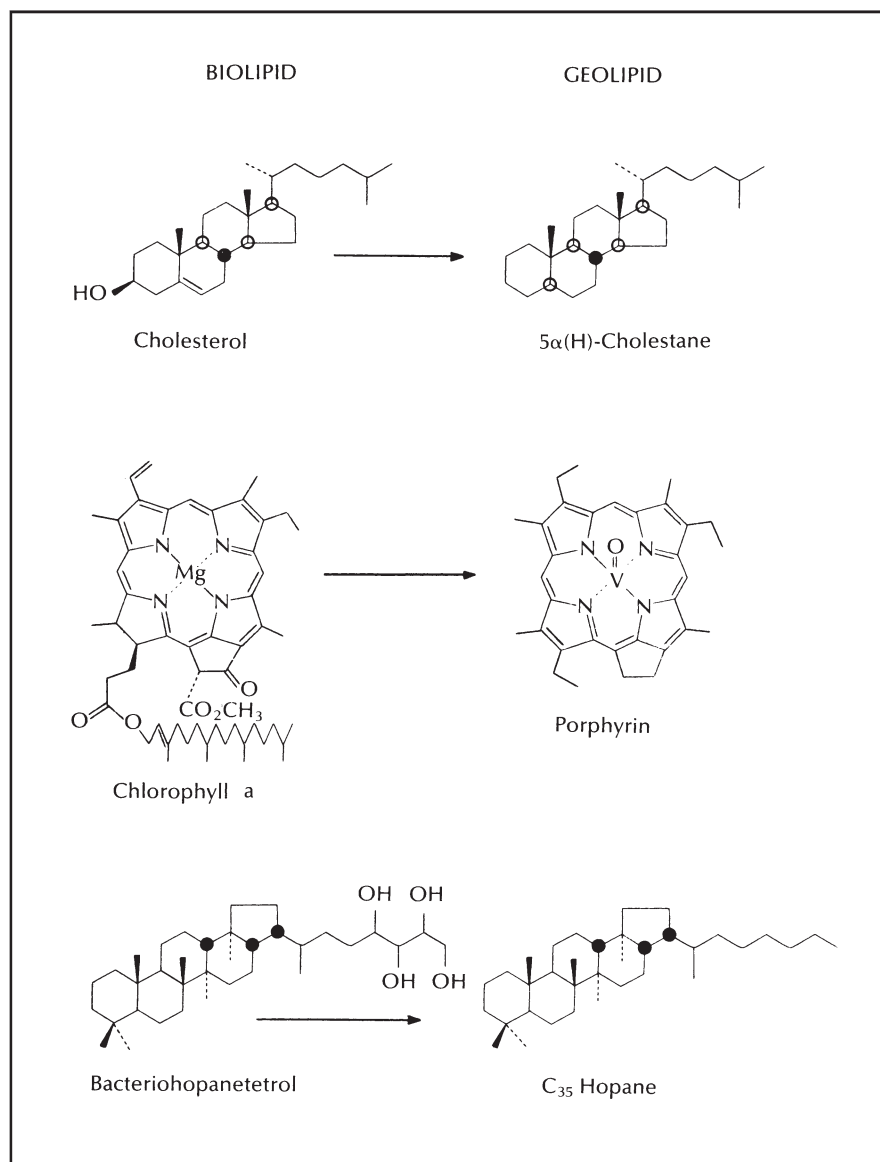
BIOLIPID   GEOLIPID

Cholesterol   5α(H)-Cholestane

Chlorophyll a   Porphyrin

Bacteriohopanetetrol   C₃₅ Hopane

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 poly-condensation 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 sub-sequent 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 archaebacteria; furthermore, some compounds appear to be restricted to methanogens (Brassell *et al*. 1981). Other widely accepted biological marker compounds include 18α(H)-oleanane (higher plants), 4-methylsteroids (especially dinosterol; dinoflagellates), long-chain alkenones (prymnesiophyte algae), and botryo-

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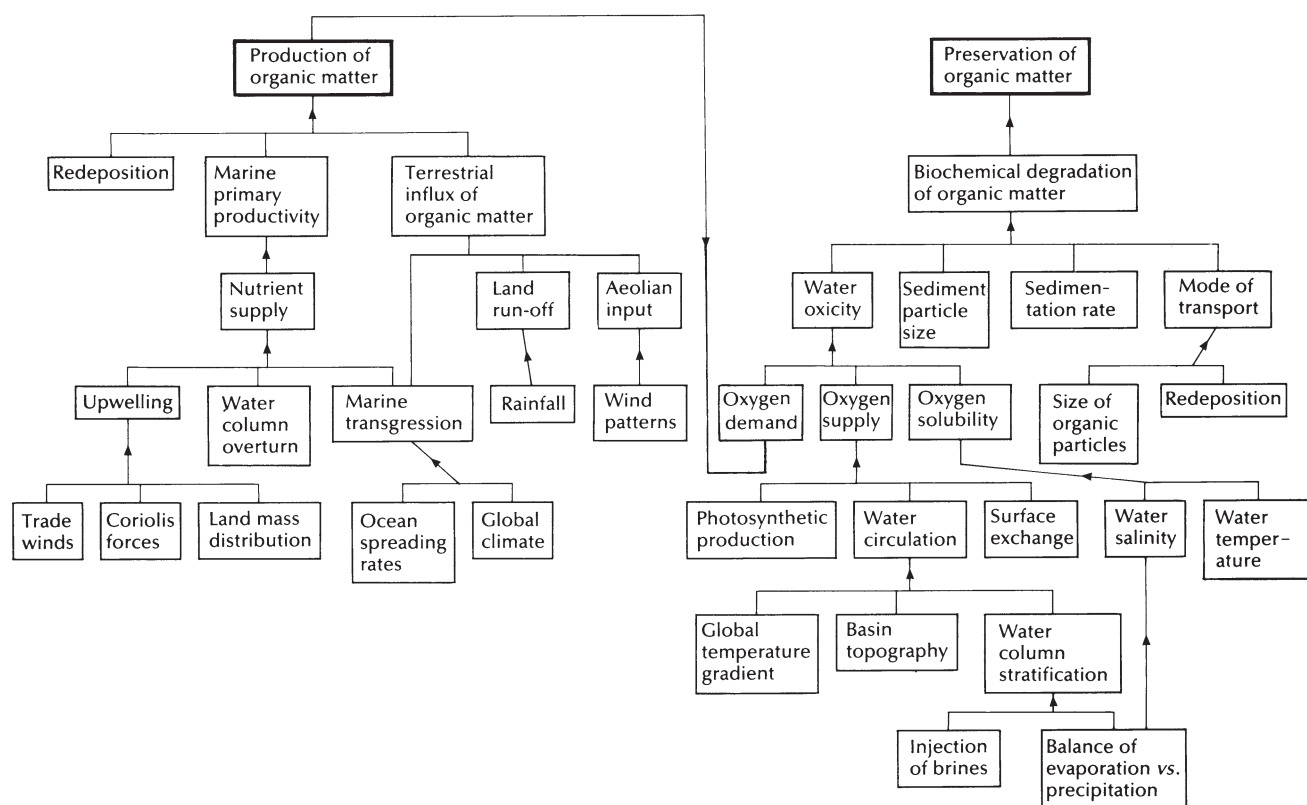
Fig. 2 Flow diagram showing various interrelated factors which influence the production of organic matter in the biosphere, and its subsequent preservation in the geosphere. These factors may all exert some control upon the accumulation of organic matter in marine sediments.

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-

dation 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.
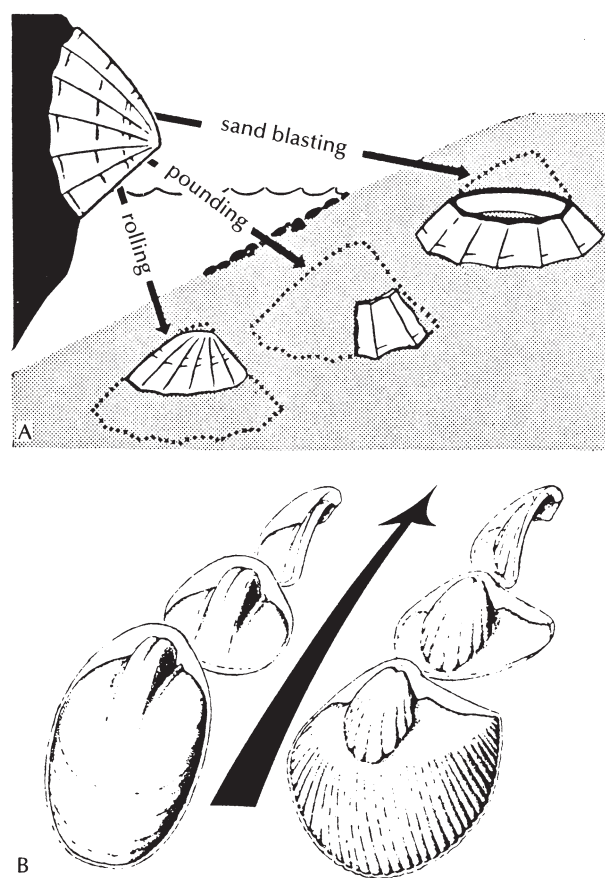

Fig. 1 A, Abrasion and breakage may produce fragments diagnostic of different depositional environments. Stably anchored shells are abraded from the top down (anchor faceting). Pounding of shells by surf produces fractures that follow medial and concentric lines of weakness in the shell. Rolling and 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.)
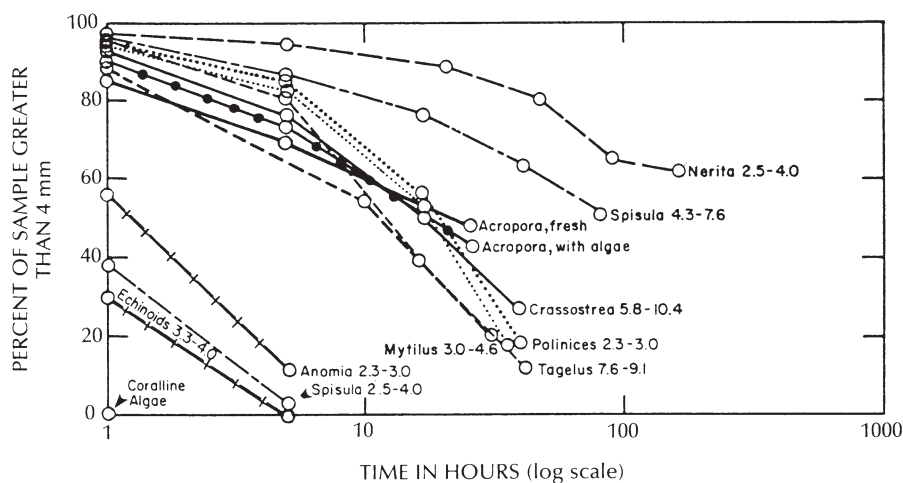
very high rates in most shallow-marine environments. Rates from 16% to over 20% weight loss per year, as a result of algal and sponge boring, have been observed for modern marine mollusc shells. It is not clear whether such rates pertained in the Palaeozoic when clionid sponges were much less abundant. 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
Single unit						
Massive	−	−	−	++ (do)	++ (cor)	−
Encrusting	−	−	−	−	++ (cor)	−
Ramose, robust	+ (la)	−	+ (fr)	+ (fr)	++ (cor)	−
Ramose, fragile	++ (la)	−	+ (fr)	−	−	+ (fr)
Univalved shell	++ (la, d)	+ (do)			+ (cor)	+ (fr)
Multiple unit						
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
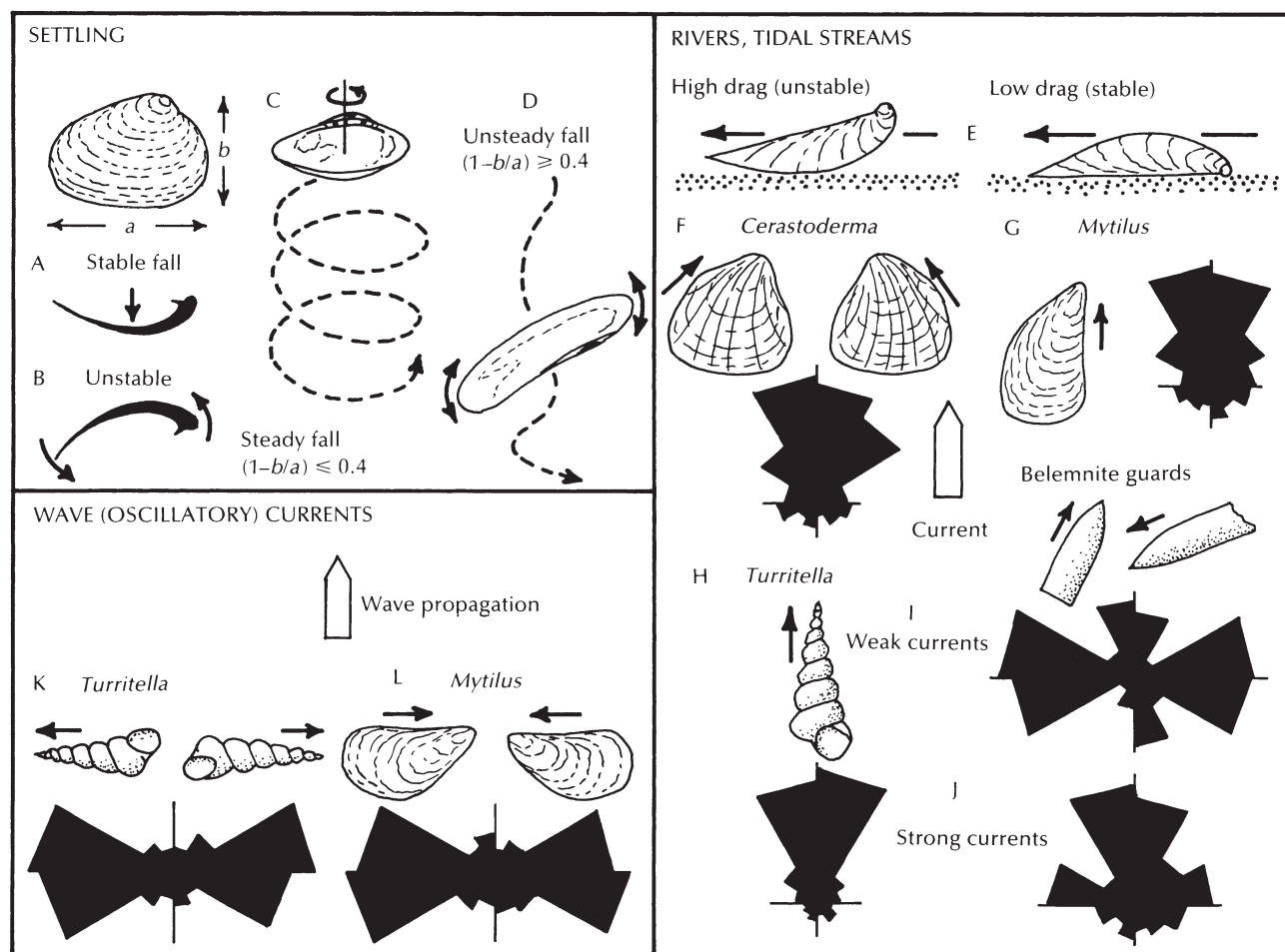

Fig. 1 Schematic summary of the behaviour and idealized biofabrics of representative shells (bivalve molluscs (*Cerastoderma*, *Mytilus*); gastropods (*Turritella*); belemnite guards) when settling in water, and when transported and deposited from one-way and oscillatory currents.

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-spired gastropods become oriented with the apex upcurrent (Fig. 1H). Low-spired 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 abscision 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:

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

where x = distance from the lake centre, Z_x = deposition occurring at distance x, r = distance from the lake centre to the shoreline, Z_r = deposition at the shoreline, and $k = -(r-x)^{-1} \ln(Z_x Z_r^{-1})$. Under some circumstances estimates of ancient litter productivity may be obtained from the fossil record.

Post-descent dispersion over the ground. Leaves blown along the ground are distributed laterally by a combination of saltation and rolling. In laboratory experiments the greatest dispersion was found with circular shapes that tended to roll (Spicer 1981). Dispersion is little affected by leaf size but, as with fall velocities, weight per unit area did prove important with light leaves travelling the furthest. Dry curled leaves are easily transported, but wet leaves tend to stick together and suffer minimal ground dispersion. Field experiments (Ferguson 1985) show that most woodland leaves are never disseminated very far from the parent trees (although dispersion is greater in open sites) and that, barring flooding or volcanic activity, even the tallest temperate trees must be growing within 50 m of a body of water to stand any chance of becoming fossilized.

Water transport

Floating. Immediately upon landing on water, plant material absorbs water and soluble substances begin to be leached out. Initially a dry leaf will float and may remain buoyed up by surface tension for several weeks, provided that only the bottom surface of the leaf is wetted and the water surface is calm (Spicer 1981). Plant material could be transported long distances this way, but such conditions are likely to pertain only in slow-flowing rivers protected from wind (i.e. subcanopy streams), situations in which long-distance transport is unlikely to occur.

Water absorption by leaves is governed by the thickness of cuticle and of epicuticular wax, abundance of stomata and/or hydathodes, lamina or petiole damage, water temperature and chemistry, and to a lesser extent by leaf anatomy (Spicer 1981; Ferguson 1985). Floating times range from several hours to several weeks (Fig. 1); thin chartaceous leaves tend to sink earlier than thick coriaceous leaves (Spicer 1981; Ferguson 1985). Intact compound leaves float longer than their individual leaflets.

Dispersed fruits and seeds (diaspores) exhibit a greater range of floating times than do leaves (e.g. Collinson 1983). Floating times do not appear to be directly related to diaspore size or to the habit of the parent plant (Collinson 1983).

Wood, and in particular logs, can remain afloat for several years and potentially therefore the only hindrance to log dispersal downstream from the growing site is water (channel) depth and instream obstacles.

Transport in the water column. Progressive plant tissue saturation follows an 's' shaped curve and does not cease until long after the object has sunk (Greer, unpublished data). Progressive post-sinking water absorption continues to affect the submerged density of the object, and therefore its behaviour during transport in the water column, until full saturation is reached. When and where the object eventually settles is determined mostly by submerged density and shape, two factors important in determining settling velocity and entrainment behaviour. In an aquatic environment plant debris is degraded by biological and mechanical agents, both of which affect the hydrodynamic properties but which produce characteristic degradation patterns seen in fossil material (Spicer 1981, 1989; Ferguson 1985).

Fig. 1 Floating times for freshly abscised leaves of coriaceous evergreen *Rhododendron*, chartaceous deciduous *Fagus sylvatica* (abscised dry and brown), and *Alnus glutinosa* (abscised moist and green). The leaves were placed in mildly agitated water at room temperature. (Data from Spicer 1981.)
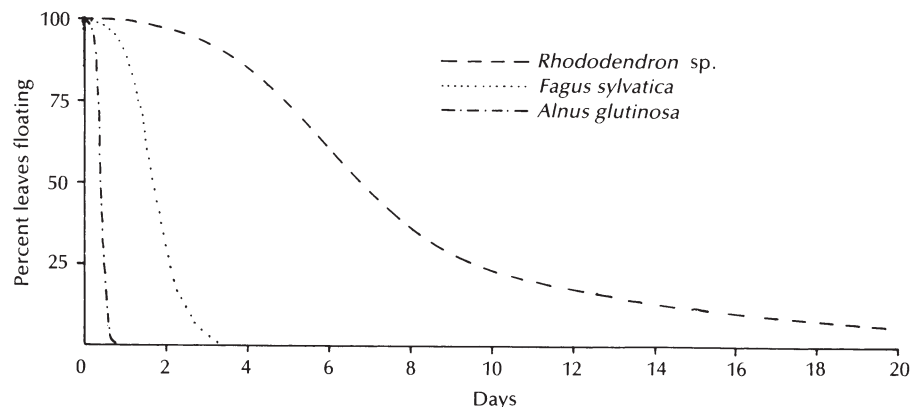
Settling (fall) velocity in water. In spite of their irregular two-dimensional shape, angiosperm leaves exhibit within-taxon uniformity of settling velocities, as do the more prismatic shapes of conifer needles (Spicer & Greer 1986). Even irregularly shaped fern pinnules and moss leafy shoots have settling velocities that fall within narrow, moderately well defined, limits. Statistically there is no significant difference between the settling velocities of different broad-leaved taxa (including *Ginkgo* and fern pinnules), but significant differences do exist between conifer needles and broad-leaved taxa, and between individual conifer taxa (Greer, unpublished data). In general, conifer needles have a higher settling velocity (e.g. 3.03 cm/s for *Picea pungens* at full saturation) than angiosperm leaves (e.g. 1.5 cm/s for *Fagus sylvatica* at full saturation). Individual leaves of other broad-lamina taxa such as *Ginkgo biloba*, however, exhibit fall velocities as high as 6.7 cm/s when petiole and lamina configuration produce a hydrodynamically efficient shape that results in a stable gliding fall. Hydraulic sorting, primarily related to settling velocities, has been observed in both low and high energy fluviolacustrine delta systems and modelled in relation to spatial and temporal pattern in the source vegetation (Spicer 1981; Spicer & Wolfe 1987).

Entrainment. For any given flow, particles concentrated near the stream bed are mostly those with the greatest settling velocity. The heaviest particles are transported as bedload and are only in suspension for brief periods of time. As current flow wanes, the lighter fractions progressively settle out. Conversely, increases in current flow progressively entrain material. Flow rate in natural streams and rivers is rarely constant and plant debris is likely to undergo several cycles of deposition and entrainment before permanent burial takes place.

Leaf aspect and orientation to fluid flow influence entrainment. Curved leaves, or planar particles inclined with their raised edge facing into the flow, are entrained at lower flow rates than those lying flat on the stream bed or inclined with their raised edge pointing downstream.

Bed roughness, including bedforms, affects plant particle entrainment (Spicer & Greer 1986). If bedforms (e.g. ripples) are large enough for the plant particles to settle between, the particles are protected from entrainment and often buried rapidly by bedform migration. Larger particles pass through the system. Thus, if ripples are noted in a fossil deposit, and only conifer needles are preserved, it cannot be

assumed that angiosperms were not present (even in large numbers) within the source vegetation: they may have been deposited elsewhere because they were too large to be trapped between the ripples.

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3.4.3 Bones

A. K. BEHRENSMEYER

Introduction

After death, vertebrate skeletons interact with biological, physical, and chemical processes at or near the Earth's surface. These processes determine whether the bones are destroyed (i.e. recycled) or fossilized. Transport is one of the important processes that can affect bones prior to fossilization. Both physical and biological mechanisms of transport may alter life associations of organisms by carrying bones away from the original environment and by mixing taxa from different habitats and time

periods. Such processes also cause abrasion and other types of damage, as well as sorting and differential preservation of body parts (see also Section 3.3).

Biological transport

Biological mechanisms of transport include predators and scavengers that derive some benefit from collecting bones. One notable modern bone collector is the African hyaena (*Crocuta crocuta*); other mammals such as canids, felids, humans, elephants, porcupines, and pack rats also transport bones or parts of carcasses (Shipman 1981). Predatory birds carry off carcasses and leave accumulations of bones of small vertebrates as regurgitated pellets or debris below a favoured perch. Various small mammalian carnivores leave concentrations of bones in their faeces. Harvester ants (*Messor barbarus*) also collect bones of small vertebrates and transport them underground (Shipman 1981). Trampling causes bones to move outward from disintegrating carcasses (Hill 1979).

Fossil accumulations in preserved burrows and cave deposits attest to the bone-transporting activities of ancient species. It is likely that the fossil record includes examples of biological bone-transporting processes for which there are no modern analogues. The Phanerozoic history of such processes and their effect on the vertebrate fossil record is not yet known.

Physical transport

Physical processes causing bone transport include water currents and wave action, wind, and gravity. Unfossilized bones are relatively light, with high surface area to volume ratios and irregular shapes, all of which make them readily transportable by moving water. Although bone mineral (hydroxy-apatite) has a density of about 3.2, bones themselves have densities varying from less than 1.0 (i.e. they float) to 1.7 (Behrensmeyer 1975). This is because pore spaces and organic components make up a significant percentage of a fresh bone. Pores may retain air or other gases and keep bones relatively buoyant for hours to days (Behrensmeyer 1975). Weathered bones that have lost their organic material and become cracked are less buoyant. Currents of 20−30 cm/s can move bones of small to medium-size vertebrates (e.g. rodent to sheep) but stronger currents are required for bones of larger animals (e.g. cow, elephant). Teeth have densities approaching 2.0 and almost always require stronger currents for transport than do bones, regardless of the size of the animal. Experiments in natural rivers with flood velocities of 1.0 m/s demonstrate that bones can be transported a kilometre or more in a single year.

The hydrodynamic behaviour of bones can be predicted to some extent by considering them as sedimentary particles and calculating their 'quartz-equivalents'. This is the size of a quartz grain with a settling velocity equal to that of the bone, and it can be calculated based on measurements of actual settling velocities of bones in water (Behrensmeyer 1975; Shipman 1981). Bones and teeth of approximately equal sizes can have very different quartz-equivalents (Fig. 1). Those with smaller equivalent quartz grains are generally more transportable, although shape and orientation to a current can cause exceptions to this rule. Scapulae are small and light relative to other bones in a skeleton, but their shape is also streamlined so that they are less easily moved than an equivalent quartz sphere.

In fossil deposits, the difference in grain size of matrix sediment and bone has been used to assess transport history (Shipman 1981). If bones are preserved with grains of near-equal quartz diameters, this is interpreted as an indication that the bones were transported and hydraulically sorted. In contrast, if bones are associated with sediment of much finer quartz-equivalents, then minimal transport is inferred. Since the relationship between transport and quartz-equivalents can be influenced by individual bone shapes, considerable caution is necessary in such interpretations. Moreover, the grain sizes that are available for transport, rather than hydraulic sorting, can control which quartz-equivalents are associated with bones at the time of burial.

Sorting. Differing hydrodynamic behaviour of bones in a single skeleton results in sorting (separation of body parts according to transport rates) and winnowing (removal of the lighter elements, leaving a 'lag' of the heavier, less transportable bones). Experiments in flumes and natural rivers have demonstrated that there are three distinct transport groups ('Voorhies Groups') for medium to large mammals (in order of decreasing mobility): Group I — vertebrae, ribs, sternum; Group II — limb parts; Group III — skulls, mandibles, teeth (Voorhies 1969; Behrensmeyer 1975; Shipman 1981). Bones from a single point source (i.e. a skeleton) show progressive sorting with continued current action. Distinct pat-
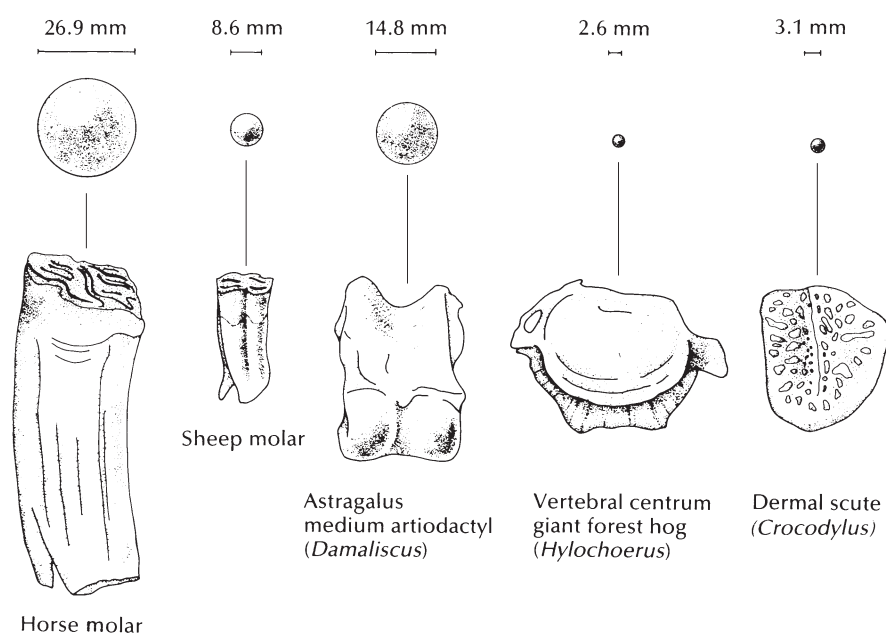
26.9 mm   8.6 mm   14.8 mm   2.6 mm   3.1 mm

Horse molar

Sheep molar

Astragalus
medium artiodactyl
(*Damaliscus*)

Vertebral centrum
giant forest hog
(*Hylochoerus*)

Dermal scute
(*Crocodylus*)

Fig. 1 The hydraulic equivalents of examples of Recent bones, as determined by their settling velocities and calculations of the diameter of a quartz sphere that would settle at the same velocity. Bones and quartz grains are drawn to the correct relative sizes. (After Behrensmeyer 1975; reproduced with permission from the Museum of Comparative Zoology, Harvard University.)

terns of sorting in a fossil deposit thus indicate the interaction of currents with a localized bone source. Input from multiple sources of bones along natural rivers or beaches obscures patterns of sorting for individual carcasses. If there are many point sources of bones, all body parts (from different individuals) can co-occur in deposits formed by water currents (Hanson 1980).

Bones of small vertebrates also can be moved by wind action on beaches, dune fields, and ephemeral river beds. Dust-devils are effective mechanisms for transporting and scattering small bones in arid environments. Gravity assists in bone movements on steep slopes, as in caves and sinkholes. The low density of bones helps to keep them near the surface and exposed to slope wash and mass movements of sediment.

Orientation. The orientations of individual bones indicate the influence of hydraulic processes on the bone assemblage (see also Section 3.4.1). In strong currents, elongate bones generally orient parallel to the flow direction, with the heavier end upstream. In shallow water or in weak currents, such bones may orient perpendicular to the current and roll downstream around their long axis (Voorhies 1969; Behrensmeyer 1975; Shipman 1981). Determining flow direction from bone orientations must take both of these patterns into account. Large bones may act as 'traps' for smaller ones, which accumulate against the upstream side or in the downstream zone of flow separation (shadow). The orientation of the larger bones may influence those of associated smaller ones.

Concentration. Dense concentrations of fossil bones in river deposits are often attributed to hydraulic processes. However, experiments in modern rivers indicate that fresh bones are generally too light to form permanent patches or 'bone bars' unless there is a point source nearby and/or an obstruction that causes transport to cease abruptly. Repeated winnowing and reworking can concentrate denser elements (e.g. teeth) as part of the gravel 'lag' deposit in fluvial sediments. Previously fossilized bones with higher densities may be incorporated into such lags, mixing remains from periods of 100–10 000 or more years to create a time-averaged sample of the original vertebrate communities (Behrensmeyer 1984).

Abrasion. Hydraulic transport can abrade and break bones, but experiments in tumbling machines and in natural rivers indicate that it takes considerable bone–sediment interaction to cause significant damage to fresh bones and teeth (see also Section 3.1). Weathered bones are more vulnerable to abrasion and breakage in transport situations. Fresh experimental bones can travel over 3 km in a sand- and gravel-bed river with only minor loss of surface detail due to abrasion. Exposure to poorly sorted sand for up to 35 h in a tumbling machine is necessary to produce gross changes in fresh bones. Fossil dinosaur and crocodile teeth subjected to the equivalent of 360–480 km of transport in a tumbling machine with coarse sand showed negligible damage to enamel surfaces (Argast *et al.* 1987). Thus, bones and teeth can experience considerable trans-

port without showing significant abrasion. Conversely, stationary bones may be 'sand-blasted' by water or wind-borne sediment and heavily abraded without significant transport. Thus, it is very difficult to judge the transport history of a bone from its appearance.

Burial. The same physical processes that transport bones also bury them. In channels and on beaches, bones are buried and exhumed many times prior to destruction or fossilization as they move along with bedload sediment. They may be overtaken by moving bedforms (ripples, sand waves), and scour on their downstream sides also promotes burial. Permanent burial happens when the bone is removed from the active zone of sediment transport; this can occur when the channel abandons its course or when unusual flood conditions alter its bottom morphology.

The taphonomic history of bones should be analysed prior to ecological interpretations of species represented in a vertebrate fossil assemblage because they are readily transported by both physical and biological processes. The tendency for bones to be buried and reworked repeatedly in fluvial and shoreline environments also implies that transported remains may represent a substantial amount of time-averaging. Transported bone assemblages thus contain evidence of vertebrate palaeoecology for areas and time periods that often are not directly comparable with samples of vertebrate communities from modern ecosystems.

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3.5 Fossil Concentrations and Life and Death Assemblages

F. T. FÜRSICH

Fossil concentrations

A fossil concentration is defined as any relatively dense accumulation of fossils, irrespective of taxonomic composition, state of preservation, or degree of post mortem modification. Fossil concentrations are nearly exclusively accumulations of hard parts. They are therefore regarded here as synonymous with skeletal concentrations of fossil organisms (Kidwell *et al.* 1986). As the size of the biogenic hard parts is not restricted, this definition includes dinosaur bone beds as well as coral reefs, shell beds of bivalves and those of ostracodes (see also Section 3.4).

Fossil concentrations also include several types of Fossil-Lagerstätten, especially those formed by rapid burial or by condensation (Section 3.6).

Descriptive classification. Fossil concentrations can be described in several ways, stressing either taxonomic composition, bioclastic fabric (degree of packing), geometry, or the internal structure of the deposit (Fig. 1). Each of these aspects carries some genetic significance. The *taxonomic composition* largely depends on the ecology of the component taxa and, to a lesser degree, on the hydrodynamics of their accumulation. The *biofabric*, that is the three-dimensional arrangement of skeletal elements in

TAXONOMIC COMPOSITION	PACKING	GEOMETRY	INTERNAL STRUCTURE SIMPLE | COMPLEX
monotypic	matrix supported	stringer pavement pod clump	
polytypic	bioclast supported	lens wedge bed	
↓ ECOLOGY	↓ HYDRODY- NAMICS	↓ TOPOGRAPHY	↓ ECOLOGICAL & HYDRODYNAMIC HISTORY

Fig. 1 Major features used in the descriptive classification of fossil concentrations and their genetic significance. Shaded box = predominant; white box = rare. (After Kidwell *et al*. 1986.)

the matrix, includes skeletal orientation, degree of packing, and sorting by size and shape. The bio-fabric is strongly influenced by hydrodynamic conditions, whilst ecology and compaction may be additional factors. The *geometry* of a fossil concentration depends on the pre-existing topography of the depositional surface (e.g. burrow fills), the ecology of the hard part producers (e.g. clumps of mussels) and other organisms (e.g. shell-lined burrows), and on the hydrodynamic conditions which, at the time of hard part concentration, produce a topography (e.g. by the migration of ripples, excavation of scours, etc.). The *internal structure* provides information on the ecological and hydrodynamic history of the deposit. Simple (i.e. internally homogeneous or, at the most, with unidirectional trends) and complex skeletal concentrations can be distinguished. In the latter, features such as grain size, degree of articulation, and orientation vary in a complicated pattern.

Genetic classification. Fossil concentrations can also be classified genetically, based on the main concentrating processes. The formation of concentrations is governed by the interplay of net rate of sedimentation, net rate of production of biogenic hard parts, and to a lesser extent diagenetic processes. Accordingly, biogenic, sedimentological, and diagenetic concentrations can be distinguished (Fig. 2). *Biogenic concentrations* result from the gregarious behaviour of organisms with hard parts (e.g. mussel beds) or of organisms which concentrate skeletal elements (e.g. during the feeding process). *Sedimentological concentrations* are produced by hydraulic processes which may represent short-term events (e.g. storms) or long-term processes (e.g. background current and wave action). Examples include shelly storm lags or condensed shell beds. *Diagenetic concentrations* are the result of post-burial physical
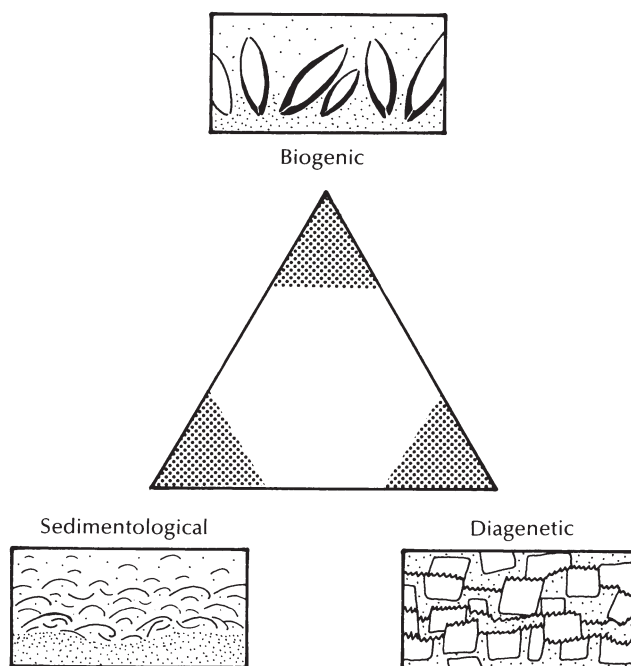

Fig. 2 Genetic types of fossil concentrations based on biogenic, sedimentological, and diagenetic processes. White area of the triangle represents concentrations of mixed origin. The longer the time-span involved in the formation of a concentration, the more likely it will be mixed in origin. (After Kidwell *et al*. 1986.)

or chemical processes, including compaction as well as selective pressure solution of matrix in bioclastic limestones. These processes act in most fossiliferous sediments, but are rarely as significant as biogenic or sedimentological processes.

Most fossil concentrations are formed by more than one process. For example, a storm-reworked mussel bed is of mixed biogenic and sedimentological origin; a strongly compacted layer of bivalves killed by drastic changes of salinity represents a diagenetically enhanced biogenic concentration.

Of particular importance for the formation of fossil concentrations is the combination of low net rates of sedimentation with high net rates of biogenic hard part production. Zero net rates of sedimentation (i.e. omission) and negative net rates (corresponding to erosion) result in different types of fossil concentrations which frequently exhibit sharp lower or upper contacts (Kidwell 1986). When subsequently undisturbed, such concentrations and their bed contacts can be interpreted very precisely. In reality, however, the contacts are commonly modified by burrowing organisms and/or diagenesis.

Geological and palaeontological significance. Fossil concentrations are a useful tool in basin analysis, furnishing information on bathymetry, rate of sedimentation, hydrodynamic regime, and environmental gradients. The prevalence of particular types of concentration, such as those produced by storms, and their frequency through time allow inferences about basin configuration and evolution. Along onshore—offshore gradients for example, sedimentological concentrations which dominate in shallow, nearshore environments are gradually replaced by biological concentrations in deeper shelf areas. Among sedimentological concentrations those exhibiting wave influence are most prominent in very shallow water, those of storm origin in shallow to intermediate shelf depths, whilst in lower shelf regions sediment starvation and condensation are the governing factors.

Biostratinomic features of the skeletal elements such as biofabric, articulation, sorting, fragmentation, abrasion, bioerosion, and encrustation provide additional data on residence time on the sea floor, wave versus current influence, degree of reworking, and sediment starvation (see also Section 3.3).

The palaeontological significance of fossil concentrations varies greatly depending on their genesis (see below).

Life and death assemblages

Definitions. The term *assemblage* has several meanings (Fagerstrom 1964). According to some authors, assemblages consist of organisms derived from more than one community (i.e. they exhibit signs of mixing). In another, broader definition adopted here, the term refers to any group of organisms from a geographical locality. A *life assemblage* accordingly is defined as any group of living organisms from a geographical locality. It may represent a whole community or only parts of it. A *death assemblage* (= *thanatocoenosis*) consists of the preserved elements of a life assemblage after its death and decay. As a rule, soft-bodied organisms are no longer represented in a thanatocoenosis. The species diversity of a thanatocoenosis is therefore much lower than that of the life assemblage. The trophic composition of a living community is commonly not adequately reflected in the thanatocoenosis. The term *taphocoenosis* (= *allochthonous thanatocoenosis* of some authors) refers to hard parts of organisms which became embedded together after having been subject to biostratinomic processes such as sorting, admixture of shells from adjacent habitats or from stratigraphically older units, mixture of skeletal elements resulting from time-averaging, or selective destruction by physical, chemical, or biological agents. A *fossil assemblage* differs from a taphocoenosis in that post-burial diagenetic processes have been operating which led to lithification or partial destruction of the hard parts.

In cases where biostratinomic and diagenetic processes did not play a significant role, the fossil assemblage will be roughly identical to the thanatocoenosis. The terms taphocoenosis and thanatocoenosis are often used as synonyms. In the definition given here they do, however, characterize different stages of the transition of a life assemblage to a fossil assemblage (Fig. 3).

Time averaging. The quality of a taphocoenosis (and thus often of the resulting fossil assemblage) largely depends on the time factor. Rapid *in situ* burial of a life assemblage (e.g. during storms) may produce a taphocoenosis which faithfully records species composition and age structure of the organisms with hard parts. Under normal circumstances, however, taphocoenoses represent time-averaged relics of life assemblages.

Time-averaging refers to the mixing of skeletal elements of non-contemporaneous populations or communities. This telescoping of biological data representing tens, hundreds, or even thousands of years into a single geological time plane drastically alters the quality of the data. Short-term fluctuations in species composition and in the morphological range of species, reflecting variations in salinity, oxygen, or other environmental factors, cannot be recognized from time-averaged assemblages. The occasional dominance of opportunistic species in a
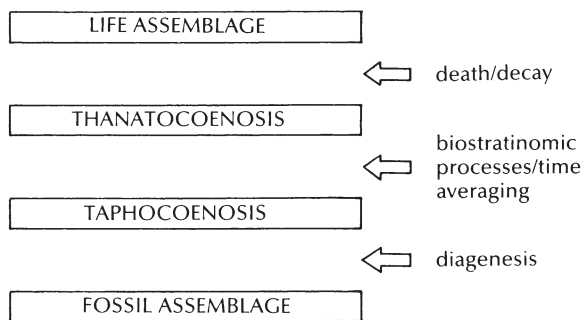
Fig. 3 Relationship of the various kinds of assemblages and the processes which shape them.

community will be considerably tuned down in time-averaged relics. Species richness and often also evenness in such taphocoenoses will be greater than that of the living communities (excluding soft-bodied organisms) from which they are derived (Fig. 4). Some attributes of live communities, such as trophic structure and taxonomic composition, stand a better chance of being preserved during time-averaging than others (e.g. numerical abundance) (Staff *et al.* 1986). Even very short time-averaging (e.g. 10—20 years) can produce significant differences between living communities and tapho-coenoses. For example, organisms living during different stages of community succession will invariably become mixed after death. Similarly, new taxa are introduced into the taphocoenoses by tapho-nomic feedback, i.e. the spectrum of live—dead interactions. In this case, biostratinomic processes need not be involved.

Palaeontological significance. Time-averaged tapho-coenoses have therefore a different quality than living communities and the two cannot be strictly compared. On the other hand, time-averaged tapho-coenoses often record the large-scale environmental conditions more faithfully and thus may be more indicative of long-term trends than living communities. Several studies (e.g. Warme 1971) have demonstrated that taphocoenoses do reflect the broad environmental framework and give an, albeit rough, account of the dominant taxa with hard parts living in and characteristic of these environments. The fidelity of taphocoenoses and resulting fossil assemblages for palaeoecological analysis thus largely depends on the degree of biostratinomic and diagenetic distortion, the degree of time-averaging, and on the frequency and degree of environmental fluctuations.
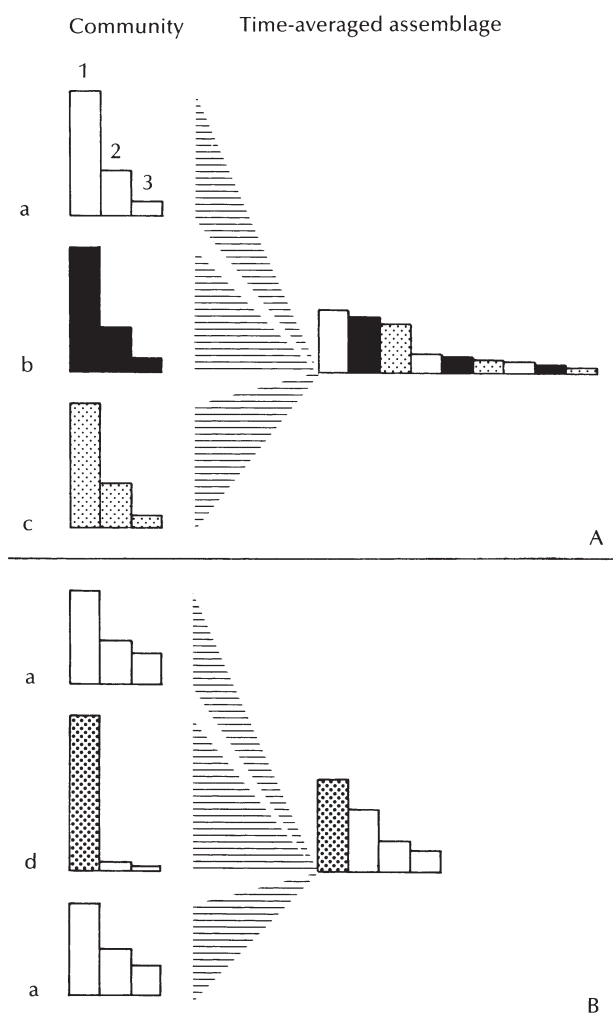

Fig. 4. Effects of time-averaging on species diversity: a, b , c, d, communities; and 1,2,3, different species of a community. Shaded areas represent slices of time. A, Time-averaging substantially increases both evenness and species richness. B, The dominance of an opportunistic species (stippled) is tuned down in a time-averaged sample. Similar changes take place in other community characters, such as trophic composition and composition of life habits.

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3.6 Obrution Deposits

C. E. BRETT

General characteristics

The term *obrution* refers to fossil assemblages preserved by very rapid burial of intact organisms and is approximately equivalent to 'smothered bottom assemblages' (Seilacher *et al.* 1985). Obrution deposits are generally considered to represent one endmember of extraordinarily preserved biotas, or conservation Lagerstätten (Seilacher *et al.* 1985); in contrast, stagnation deposits are produced by deposition of organic remains in anoxic environments (see also Section 3.11.1). However, decay of organic matter is exceptionally rapid (days to months) even in anaerobic environments (Section 3.1). Weak currents, which appear to be present even in black shale depositional settings, will then cause complete disarticulation and scattering of skeletal elements. Hence, rather than being a distinct endmember, obrution is involved in most, if not all, examples of exceptionally preserved, articulated fossils.

Examples of obrutionary Lagerstätten (Seilacher *et al.* 1985) include the famous echinoderm occurrences, such as the Mississippian Crawfordsville crinoid beds of Indiana or the Jurassic Gmünd horizon of southern Germany. Undoubtedly, many of the classic soft-bodied fossil Lagerstätten, such as the Cambrian Burgess Shale (Section 3.11.2), the Devonian Hunsrück Slate (Section 3.11.4), and the Jurassic Solnhofen Lithographic Limestones (Section 3.11.7), represent obrutionary stagnation deposits. Here the combination of rapid burial and anoxia facilitated preservation of soft tissues.

Taphonomic and sedimentological aspects

Obrution deposits are recognizable primarily from taphonomic aspects of their enclosed fossils. Preservation of completely articulated multielement skeletons in trilobites, echinoderms (Figs 1–3), and vertebrates normally requires rapid entombment. In addition, other sedimentological evidence may indicate rapid emplacement of sediment layers.

Each obrution deposit consists of two basic components: the *buried horizon* itself (smothered layer) and the *burial layer* (Fig. 2). The buried horizon represents a former sediment–water interface, and consequently may display a variety of features that indicate a span of non-deposition prior to final burial. The most obvious examples are obrution deposits associated with hardgrounds, in which the buried layer is an encrusted and bored pavement. Remains of the last community to inhabit the hard substrate may be extraordinarily well preserved, as in cases of complete edrioasteroids, cystoids, and crinoids remaining attached to hardgrounds (e.g. in the Middle Ordovician of Ontario; Brett & Liddell 1978). Where the buried horizon consisted of unconsolidated sediment, it may be recognizable as a concentrate or lag of shells, bones, or other skeletal elements, abruptly overlain by less fossiliferous or even barren sediments (Fig. 2). If such a skeletal lag is absent, buried horizons may be extremely cryptic. Well preserved remains of sessile or semisessile organisms may occur directly on the buried surface, while skeletons of infaunal organisms may be preserved directly beneath it in their original burrows.

In certain obrutionary layers there is also evidence of physical disturbance of the benthic environment shortly before sediment deposition: for example, shells with fragile encrusting epibionts may occur in inverted positions. This demonstrates that the shells were flipped, in some cases to concave upward positions, shortly before they were buried (Fig. 1C).

Skeletal remains on the buried horizon may be concentrated into windrows, aligned, or otherwise preferentially reoriented by the agent of final burial. Such features of these horizons may give clues as to the strength and direction of currents associated
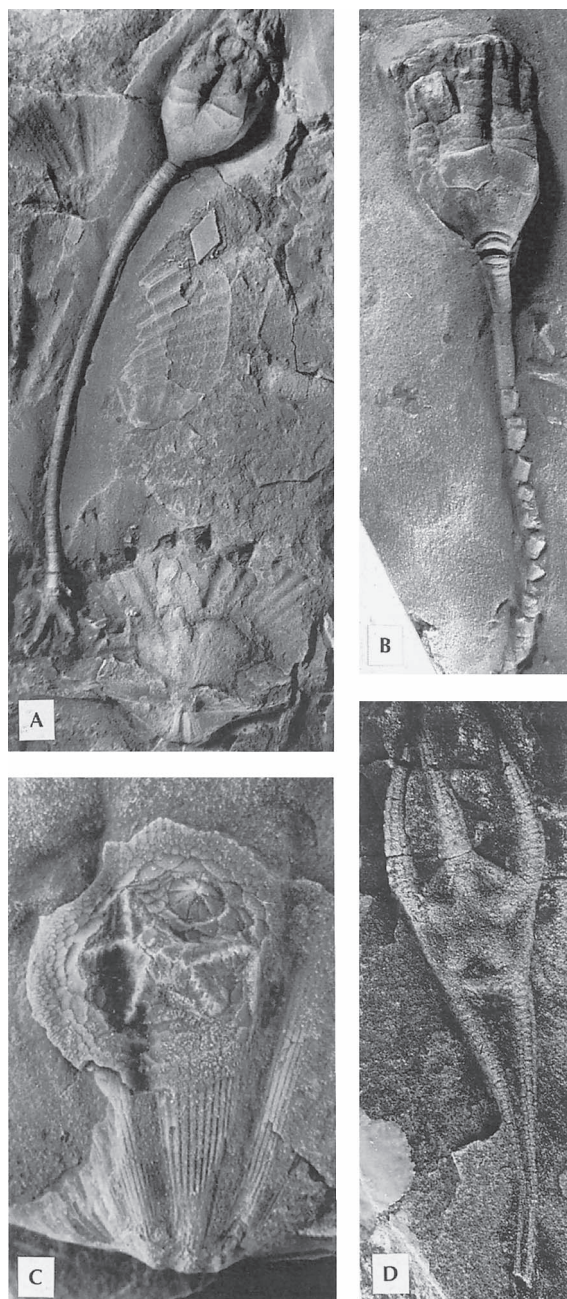
Biostratinomic features associated with an obrutionary echinoderm Lagerstätte; Lower Rochester Shale, *Homocrinus* beds, Lockport, Niagara County, New York. Figs A, B, D, × 2; Fig. C, × 3. A,B, Articulated specimens of the crinoid *Asaphocrinus ornatus*. A, Crinoid attached by its original holdfast to a brachiopod; note shell pavement of buried horizon. B, Specimen displaying incipient disarticulation; note staggering of individual segments which indicates that the crinoid had undergone some decay prior to burial. C, Edrioasteroid *Hemicystites parasiticus* attached to the fold of a *Striispirifer* brachiopod valve; specimen is on the undersurface of a shale bed — hence it must have been overturned shortly before burial. D, Ophiuroid *Protaster stellifer*, in possible crawling position; specimen is in sparsely fossiliferous mudstone overlying buried horizon and probably represents a failed escape attempt.

with the burial event (see also Section 3.4.1). Rarely, fossils in obrution deposits have been transported considerable distances from their living sites, as in the case of trilobites (*Triarthrus*) with preserved appendages from the Ordovician Frankfort Shale of New York, that occur within turbidites (Cisne 1973). Fossils in the famous Solnhofen Limestone show evidence for abrupt importation into an anoxic, probably hypersaline basin or lagoon; some organisms apparently were alive at the time, as indicated by evidence of a 'death struggle' (Seilacher *et al.* 1985; Section 3.11.7).

The burial layer consists of an interval of sediment overlying the smothered horizon, which was rapidly deposited, normally in a period of a few hours to a few days. It is typically unfossiliferous or sparsely fossiliferous, and may display features such as fining-upward size grading, and planar and cross lamination indicative of deposition from a waning current. Most commonly the burial layer consists of barren structureless mudstone or siltstone. If escape burrows or delicate articulated skeletons extend upward into this layer, it may be possible to determine the approximate thickness (with corrections for compaction) and rate of deposition of the burial sediment.

Geological agents that contribute to obrution deposits include turbidity currents, grain or debris flows, and, especially, major storms and the accompanying flood runoff. In many cases, fine-grained sediments, resuspended in shallow waters by storm waves, may be carried by gradient or turbidity flows into offshore areas, where they accumulate rapidly. Burial layers may consist of relatively coarse-grained sediment, in which case they are readily interpreted as rapid accumulations of suspended sediment loads. However, most of the best obrution Lagerstätten are preserved in and beneath layers of fine-grained sediments, for which extremely rapid sedimentation might seem an impossibility. The very rapid emplacement required for exceptional preservation may occur if muds were flocculated or pelleted. These sediments behave hydrodynamically as silts or even fine sands, rather than muds. Rapid entombment may also occur if the sediment suspensions are extremely dense, as in thick mud slurries.

Obrution deposits may be accentuated by early diagenetic mineralization (Fig. 2). For example, fossils may be encapsulated within carbonate concretions, as in the well known Carboniferous Mazon Creek sideritic nodules (Section 3.11.5). Carbonate precipitation is probably favoured both by in-
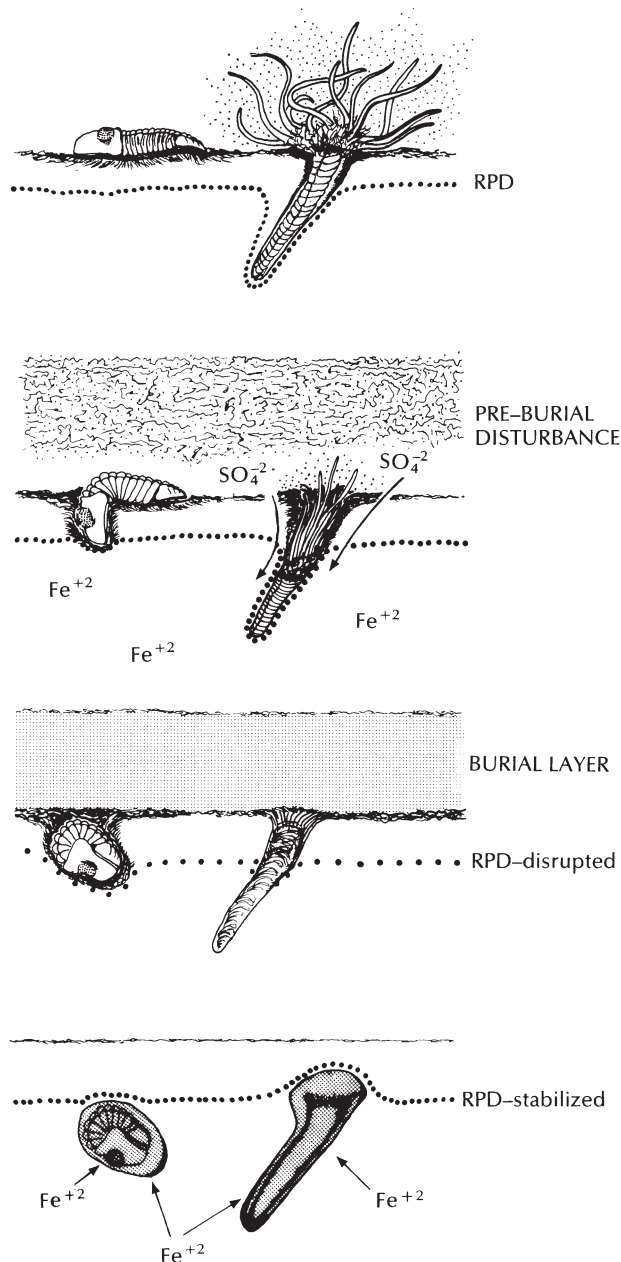
Fig. 2 Taphonomic history of an obrutionary deposit with enrolled, pyritized trilobites. Preburial disturbances of sea floor environment (including toxic conditions and/or high turbidity) induces trilobite enrollment. Burial of the sea floor entombs the trilobite and decay of organic matter causes redox potential discontinuity (RPD) to rise above the trilobite and associated tube-dwelling annelid. Local production of reducing sulphidic microenvironments around decaying organisms favours precipitation of iron sulphides at these sites. (After Speyer 1987.)

creased pH, as a result of ammonia formation, and bicarbonate concentrations produced as a by-product of bacterial sulphate reduction (Section 3.8.2). Fossils within obrution layers commonly display films or external moulds of pyrite (Fig. 2). This has been interpreted as a result of rapid entombment of organic nuclei within otherwise organic-poor, anoxic non-sulphidic sediments (Section 3.8.3). The Eocene Messel Lake deposits of Germany display soft tissues of bats, birds, and other organisms preserved by siderite-replaced bacteria (Section 3.11.8).

Obrutionary deposits are more likely to be produced in certain environments than in others. For example, shallow-water environments are conducive to episodic sedimentary events, which might preserve smothered bottom assemblages; however, these will rarely be preserved permanently in environments above normal wave base, as most will be cannibalized by later erosion. Relatively low-energy environments, slightly below normal storm wave base, are probably the optimal areas for preservation of obrution deposits. Obviously, obrution deposits will be more numerous in areas of heavy sedimentation than in regions of relative sediment starvation. However, very large inputs of sediment may have a diluting effect on fossil occurrence, and may inhibit the recognition of obrution deposits. Conversely, obrution layers may be common in condensed sedimentary sequences where they record the only permanent sediment accumulation. Seilacher *et al.* (1985) predicted that obrution deposits will be best developed in sediments overlying the caps of coarsening-upward cycles.

Biological aspects of burial

Organisms found in obrution layers may have been killed by asphyxiation due to the burial event itself or by some other agency prior to deposition of the sediment. In many cases there is evidence of pre-burial disturbance. For example, layers of enrolled trilobites, which in some instances are traceable for several kilometres, appear to record instances in which trilobites were able to respond to environmental stimuli, such as changes in the water temperature, chemistry, or salinity prior to the actual burial event (Speyer 1987; Fig. 2). Fossils in obrution deposits commonly display evidence that organisms had undergone incipient decay (e.g. minor disarticulation and/or displacement of skeletal ossicles) and, therefore, must have died at least several hours before final burial (Figs 1B, 3B). Such 'event separation' could occur during the course of a single large
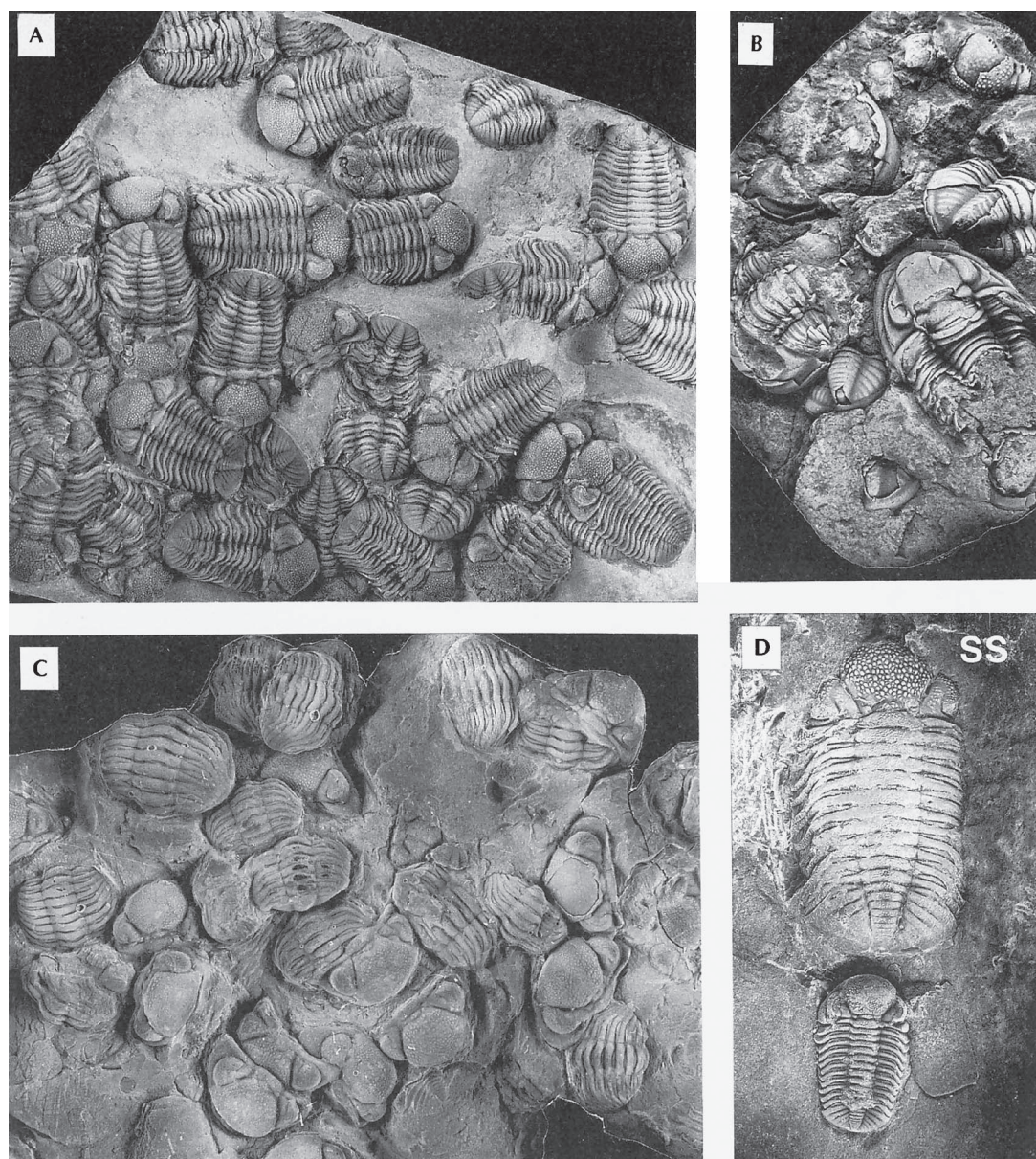
Fig. 3 Obrutionary deposits with implications for trilobite autecology. A, Large cluster of *Phacops rana* (Green) from the Middle Devonian of New York; species-specific clusters of this sort suggest gregarious life habits. B, Group of *Dechenella rowi* showing partial articulation; these specimens underwent minor decay prior to burial. C, Cluster of moult elements (thoracopygidium and cephalon) of *Phacops rana*. Such specimens indicate that some trilobites moulted in clusters. D, Two specimens of *Phacops rana* showing differential preservation. Upper specimen shows thin wrinkled cuticle and may represent a soft-shelled individual. All figures × 1. A, C, D, Windom Shale at Penn Dixie Quarry, Blasdell, Erie Co., New York; B, Wanakah Shale, Lake Erie Shore near Wanakah, Erie Co., New York. (From Speyer & Brett 1985.) (Reproduced with permission from the *Lethaia* Foundation.)

storm which might cause disturbances in water temperature, salinity, or chemistry during early stages, as well as later influxes of sediment. Specimens of ophiuroids and bivalves may be preserved in burrowing positions within the burial layer, overlying smothered benthic assemblages (Fig. 1D). Escape burrows likewise reflect a direct response to burial, in this case a successful one. Schäfer (1972) and Peterson (1985) observed that infaunal bivalves usually move upward and out of their burrows in response to burial. Commonly, they are unable to move upward through the water-rich burial sediments themselves, and die at the former sediment—water interface.

The thickness of burial layers required to trap and kill organisms varies not only with the type of organism, but with the grain size, density, and rate of deposition of the burial medium. Echinoderms may be particularly vulnerable to death by burial in that their water vascular system may be easily fouled by fine-grained suspended sediment (Fig. 1; Seilacher *et al*. 1985). Schäfer's (1972) seminal studies of preservation processes in the North Sea demonstrated that ophiuroids can escape from layers of sediment up to 5 cm thick in a matter of minutes, while echinoids can burrow out of substantially thicker layers. Kranz (1974) demonstrated that certain species of bivalves display differing 'escape potential'; deep and rapid burrowing forms could commonly escape from substantially thicker layers than those which were semisessile as adults. Peterson (1985) noted that juvenile bivalves are commonly better able to escape rapid burial because of their lower mass, which allows them to move upward through water-rich burial sediments.

Conclusions

The significance of obrution deposits is threefold: palaeobiological, sedimentological, and stratigraphical.

1 Obrution deposits are the most numerous type of conservation Lagerstätten (Section 3.11.1). As such they provide 'snapshots' of ancient sedimentary environments, with unique opportunities to study detailed morphology of fragile organisms that are not normally preserved intact. They may permit direct observations of certain types of organism—substrate associations and rarely, as in the case of clustered trilobites from the Palaeozoic (Fig. 3), they may even permit inference of life behaviours (Speyer & Brett 1985; Speyer 1987).

2 Obrution deposits are a type of sedimentary event deposit. Thus, they permit recognition of subtle 'mud tempestites', distal turbidites, and other types of event beds. The highly episodic nature of sedimentation, even in seemingly monotonous sequences, may be demonstrated by means of closely-spaced sampling and identification of obrution deposits. Taphonomy of such burial layers may provide important clues as to sedimentary dynamics in fine-grained sedimentary sequences.

3 Some obrution deposits are extremely widespread and, as such, provide a special type of stratigraphic marker. Inasmuch as they can be demonstrated to represent single events, they are probably isochronous over much of their range and display unique taphonomic and palaeontological features that permit their easy identification. Recognition and mapping of obrution deposits may greatly refine stratigraphic correlations in some sedimentary basins.

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3.7 Flattening

D. E. G. BRIGGS

Introduction

An analysis of the mode of flattening of fossils (including collapse due to decay, and compaction as a result of overburden pressure) is important for the information it reveals about their taphonomic history, and also as a basis for the restoration of the organism to its former three-dimensional appearance. Failure to understand the effects of compaction in different orientations to bedding has sometimes resulted in the establishment of separate taxa based only on preservational variants. Fractures which are due to compaction have, on occasion, been mistaken for the results of predation.

The degree and nature of flattening is determined by a number of factors: (1) the grain size and composition of the sediment (coarser-grained sediments are more resistant to compaction resulting from the supporting effect of the grains and the lower pore-water volume); (2) the morphology and mechanical strength of the organism; (3) the orientation of the buried organism to the bedding; (4) the nature and timing of diagenesis; and (5) the infilling of cavities.

Hard parts

Mineralized skeletons normally fracture when they are compacted. The pattern which results depends mainly on geometry. Ammonites, for example, are commonly buried with the plane of coiling parallel to bedding. They usually retain their original dimensions except in the aperture where the retaining forces of the skeleton are reduced. Compaction is a two-phase process (Seilacher *et al.* 1976) — the body chamber normally collapses before the phragmocone, which is strengthened by the septa (Fig. 1B, C). The junction between the body chamber and phragmocone is therefore marked by a pronounced radial fracture. Much of the compaction, however, is accommodated by prominent fractures running alongside the keel, which forms a thickened, strengthening structure. The two phases of collapse are particularly distinct where the shells are subject to dissolution. In the Jurassic Posidonia Shales of Holzmaden, southern Germany (Section

3.11.6), for example, the body chamber is fractured in the characteristic manner. By the time the phragmocone was compacted, however, most of the shell mineral had dissolved, and it therefore deformed by wrinkling (Fig. 1D). Compaction of ammonites in the Solnhofen Limestone led to the formation of a collapse caldera and pedestal (Section 3.11.7).

The thickness of skeletal material also affects the response to flattening. Thick shells fracture in well defined patterns. Thin-shelled forms (e.g. some brachiopods), however, fracture and imbricate in much more subtle ways; the effects may only be evident in thin section. The relatively thin cuticle of Cambrian olenellid trilobites, and their occurrence in fine-grained lithologies, accounts for the rarity of specimens preserving the original convexity. The bones of vertebrates are also subject to brittle failure.
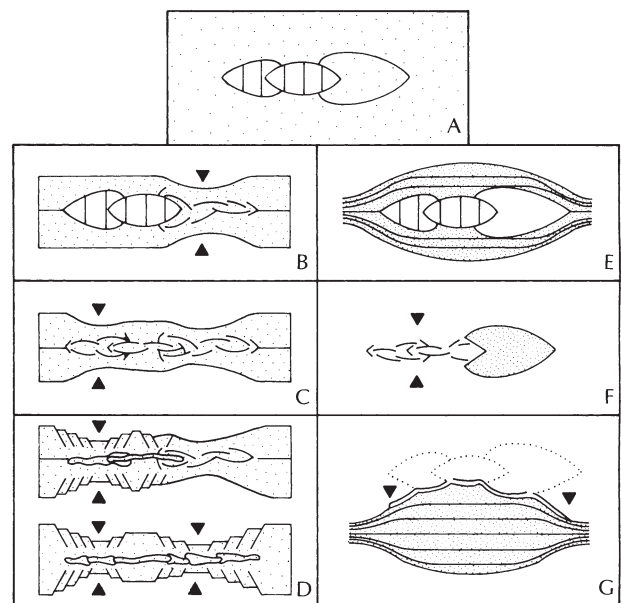
Fig. 1 Preservation and flattening of an ammonite, illustrated in diagrammatic section. A, Uncompacted shell preserved in a coarse early-cemented sediment. B, First of two-phase compaction, body chamber only. C, Second phase, phragmocone compacted. D, Delayed compaction of phragmocone (above), and entire shell (below), wrinkling due to decalcification. E, Compaction prevented by concretion formation. F, Body chamber concretion. G, Concretion external to the shell. (After Seilacher *et al.* 1976.)

Certain shapes are more resistant to compaction than others, and the solid margins of bones tend to be more resistant than the core.

Early diagenesis may have a significant influence on compaction. An entire shell or bone may be enclosed in a concretion (Fig. 1E). Alternatively, early diagenetic minerals may form only in the localized reducing environment promoted by organic decay within a cavity (Section 3.1). Sediment in the body chamber of ammonites, for example, may form a concretion, usually of phosphate (Fig. 1F). The chambers of the phragmocone may also resist compaction if sediment gains access to them and becomes phosphatized, or if they are reinforced by linings of early diagenetic pyrite or drusy calcite (Seilacher *et al*. 1976). Concretions may also occasionally form below the shell, retaining an external mould where it dissolves (Fig. 1G).

Plants

Most plant fossils are preserved as flattened 'compressions'. The more decay-resistant outer cuticle encloses altered organic material which shows no anatomical detail. In fine-grained lithologies, in particular, flattening obscures the original three-dimensional morphology of the plant (e.g. the arrangement of leaves on a stem), but this may be retained to some extent in coarser sediment (Rex & Chaloner 1983). Experimental work by Rex and Chaloner (1983) showed that flattening of plant structures infilled by sediment (e.g. the woody cylinder of a *Calamites* stem) results in a 'compression border' formed by the plant tissue which compacts to a much greater extent than the sediment-fill which it surrounds. This border represents the original thickness of the plant tissue; lateral expansion is prevented by the confining sediment. Compaction may also result in external features of the plant being 'printed' onto the sediment-infill or cast (e.g. leaf-cushions onto a cortical-infill).

In exceptional circumstances plants are preserved in three-dimensional detail. This occurs when they are permineralized (because of precipitation of calcium carbonate, silica, or pyrite), in which case they resist compaction (Section 3.10).

Soft tissue

Flattening of soft-bodied organisms is mainly the result of collapse due to decay. This exerts no pressure on the confining sediment and therefore no lateral expansion occurs (although fluids may seep beyond the outline of the specimen). Collapse takes place within a very short time-scale (days or weeks), compared with compaction resulting from overburden pressure. Hence soft-bodied organisms are preserved in three-dimensions only where diagenetic alteration has taken place almost instantly. This kind of spectacular preservation most commonly involves phosphatization (Sections 3.8.4, 3.11.3).

In a number of Konservat-Lagerstätten (e.g. the Burgess Shale and Hunsrück Slate; Sections 3.11.2, 3.11.4) turbulent transport and catastrophic burial (obrution; Section 3.6) have resulted in the preservation of specimens in a variety of orientations to bedding. Studies of the Burgess Shale arthropods have shown that while the majority of the specimens come to rest with their most pronounced planar dimension near-parallel to the bedding (i.e. resulting in lateral flattening in the case of bivalved arthropods, dorso-ventral in trilobites), a significant proportion are oblique, lateral, or even vertical (Whittington 1985).

Restoration of flattened fossils

In organisms with mineralized skeletons the results of compaction are usually clearly evident as fragmentation, fracturing, or distortion of the shape. The original three-dimensional appearance can be established by comparison with the same or similar taxa preserved in more competent lithologies. Soft-bodied and lightly skeletized organisms, however, are rarely preserved except in a flattened configuration, and other methods have to be employed to restore them (Briggs & Williams 1981).

As expansion of the outline does not occur, soft-bodied fossils are only distorted by flattening normal to the plane of bedding. Thus a suite of fossils preserved in various orientations represents different projections of the three-dimensional organism onto a two-dimensional bedding plane. In this respect they are equivalent to a series of photographs of the original organism taken from different angles (Briggs & Williams 1981). (This is the case even if the flattened fossil is not strictly two-dimensional — many of the Burgess Shale fossils, for example, consist of discrete layers separated by a thin veneer of sediment.) Based on this realization, models can be used to assist the restoration of flattened fossils. A simple three-dimensional model is made and then photographed in a variety of orientations (Fig. 2). These photographs are directly analogous to flattening the organism onto a bedding plane. A systematic
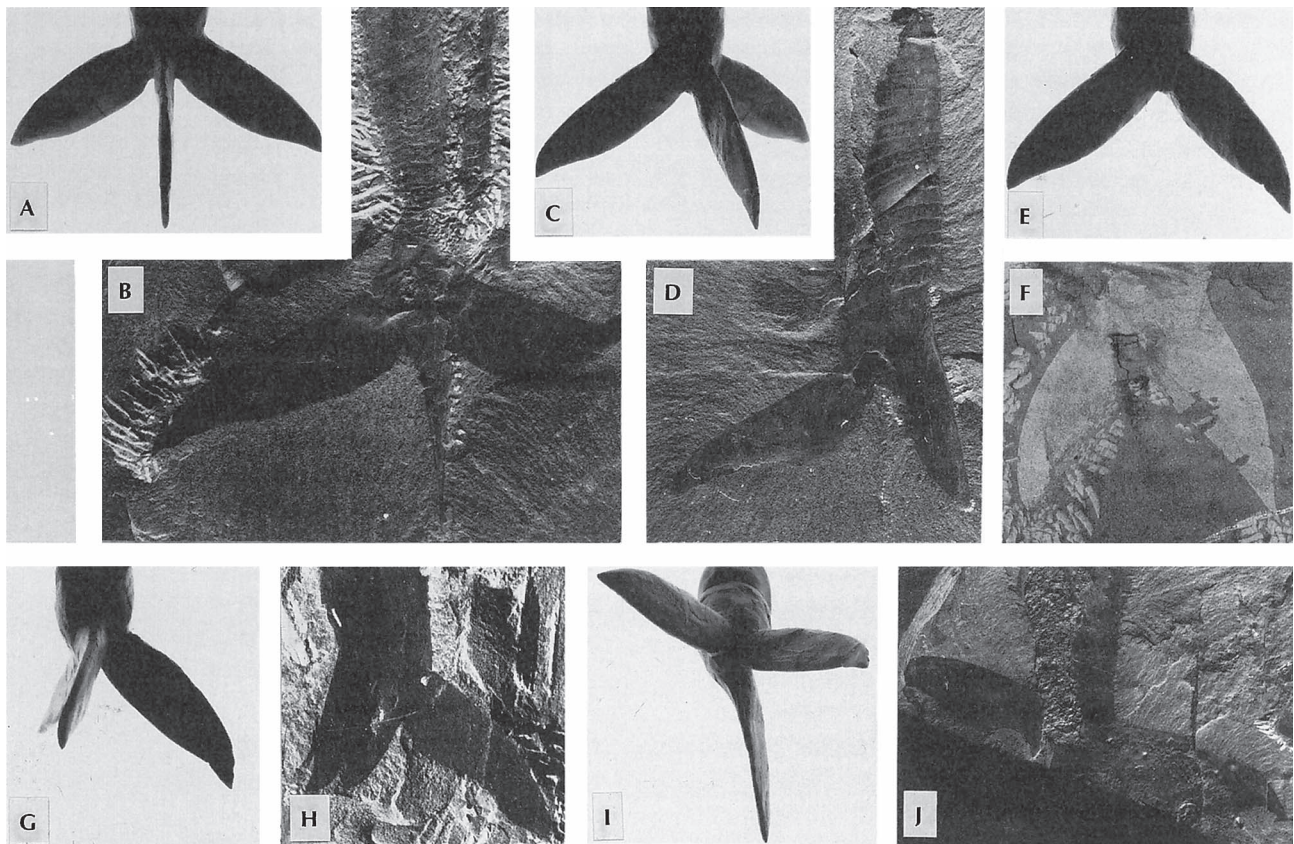
Fig. 2 Flattening of the telson of the Burgess Shale arthropod *Odaraia alata*. A, C, E, G, I, Model of telson photographed in different attitudes. B, D, F, H, J, Specimens of the telson preserved in different orientations to the bedding for comparison with the adjacent figure (B, D, ×1.2; F, H, ×1.8; J, ×0.9). The similarity of the specimens to the photographs of the model indicates that the restoration is essentially correct. (From Briggs & Williams 1981.) (Reproduced with permission from the *Lethaia* Foundation.)

comparison of the photographs with specimens preserved in different orientations allows the restoration to be tested, corrected, and refined (Briggs & Williams 1981). This approach has been used, for example, with Burgess Shale fossils, and graptolites. The tilt correction control on a scanning electron microscope can be used also to restore small deformed fossils visually.

The same approach can be applied using numerical methods. Doveton (1979) employed standard matrix algebra to compute three-dimensional restorations of fossils based on morphological distances measured from specimens flattened in particular orientations to bedding. This involved a series of steps: (1) digitizing specific reference points on the fossils with reference to coordinates; (2) computing the estimated distances between these points; (3) computing a cross-product matrix and its eigenvalues and eigenvectors and generating a linear

coordinate solution; (4) modifying this solution, as appropriate, using non-linear mapping; and (5) displaying perspective views of the non-linear solution to allow comparison and refinement with reference to other material.

Fossils may be distorted tectonically, of course, in directions other than normal to bedding. They can be restored using computer-graphical methods. Such fossils (e.g. trilobites, brachiopods, crinoid ossicles) are useful in the analysis of strain in deformed rocks (Ramsay & Huber 1983). If the fossil was initially spherical (e.g. Radiolaria), the shape of the strain ellipsoid can be determined directly. Deformed fossils are often flattened, however, in which case strain can be assessed in only one section through the strain ellipsoid (that parallel to bedding). While the principal axes can usually be identified, it may be possible to determine the magnitude of strain only semiquantitatively.

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3.8 Diagenesis

3.8.1 Skeletal Carbonates

M. E. TUCKER

Introduction

Many organisms have skeletons and shells composed of calcium carbonate. The carbonate occurs in a great range of crystal sizes, fabrics, and mosaics, depending on the organism group. The skeletons of many organisms are composed of either aragonite or calcite, but some have both (Table 1). After death, the carbonate skeleton is commonly altered to a greater or lesser extent during near-surface and burial diagenesis. In studies of fossils, an understanding of the diagenetic processes which have taken place is necessary to interpret the original mineralogy and structure of skeletons and shells. It also contributes to an interpretation of the organisms in terms of taxonomic affinity, palaeoecology, and taphonomy. Thus there has been much discussion, for example, of the original mineralogy of extinct groups such as rugose corals, archaeocyathids, and stromatoporoids.

Aragonite is the mineralogy of many mollusc shells, all scleractinian coral skeletons, and many green calcareous algae, and it is mostly in the form of needle-shaped crystallites and tablets less than 20 μm in length. The aragonite in marine organisms is characterized by quite high strontium levels, from a few 1000 ppm in molluscs to 800–10 000 ppm in corals and green algae. Skeletal calcite is commonly divided into two groups on the basis of magnesium content: low magnesium calcite with less than 4 mole percent $MgCO_3$ and high magnesium calcite with 11–19 mole percent $MgCO_3$. The magnesium content depends not only on the organism but also on environmental factors, such as temperature and salinity. Red calcareous algae like *Lithothamnion*, for example, commonly show a decreasing magnesium content into higher latitudes. In addition to red algae, bryozoans and echinoderms have skeletal elements of high magnesium calcite. Some molluscs (oysters and scallops, for example), brachiopods, coccoliths, and many foraminifera have low magnesium calcite shells and tests. The majority of the calcite crystals in these skeletal grains are on the scale of microns, but echinoderm calcite does consist of large, single crystals several millimetres across and coarse fibrous calcite crystals also on the millimetre scale occur in some skeletons (such as belemnites, certain foraminifera, and brachiopod spines).

The diagenesis of carbonate skeletons depends mainly on the original mineralogy, and also on the nature of the pore-fluids. Aragonite is a metastable polymorph of $CaCO_3$ and is only preserved under special conditions, such as within impermeable, generally organic-rich mudrocks. In the majority of cases, within sandstones and limestones, aragonite is altered to calcite. Calcite, on the other hand, is the more stable form of $CaCO_3$, and so is generally preserved. However, the magnesium content is usually reduced considerably, and there may be more diagenetic alteration of high magnesium calcite grains than those originally of low magnesium calcite.

Table 1 The mineralogy of carbonate skeletons. x = dominant mineralogy, (x) = less common. During diagenesis these mineralogies may be altered or replaced; aragonite, in particular, is metastable and is almost always replaced by calcite, and high magnesium calcite loses its magnesium. (From Tucker 1981.)

Organism	Aragonite	Low Mg calcite	High Mg calcite	Aragonite + calcite
Mollusca:				
Bivalves	x	x		x
Gastropods	x			(x)
Pteropods	x			
Cephalopods	x		(x)	
Brachiopods		x	(x)	
Corals:				
Scleractinian	x			
Rugose + tabulate		x	x	
Sponges	x	x	x	
Bryozoans	x		x	x
Echinoderms			x	
Ostracodes		x	x	
Foraminifera:				
Benthic	(x)		x	
Pelagic		x		
Algae:				
Coccolithophoridae		x		
Rhodophyta	x		x	
Chlorophyta	x			
Charophyta		x		

Diagenesis of skeletal aragonite

Skeletal aragonite is commonly altered to calcite and this takes place in two main ways: by wholesale dissolution and later filling of the void by calcite cement, and by a neomorphic replacement process of dissolution−reprecipitation across a thin film, referred to as calcitization (Bathurst 1975).

Wholesale dissolution of aragonite mostly occurs where pore-fluids are well undersaturated with respect to $CaCO_3$; this is generally the case in near-surface meteoric diagenetic environments, particularly in the vadose zone (above the water table) where there is a high throughput of water. Dissolution of the aragonite leaves a void, with the original shape maintained either by an earlier, calcitic cement fringe around the shell or by a micritic envelope, a thin zone of alteration around the shell produced by endolithic algae (Fig. 1). When pore-fluids become supersaturated with respect to $CaCO_3$, calcite is precipitated within the skeletal voids. This calcite is actually a cement, and so commonly shows a drusy fabric of increasing crystal size towards the void centre. The timing of the calcite precipitation is variable. It may be early, soon after the dissolution, possibly in the lower vadose zone or phreatic zone (below the water table) if the meteoric waters have quickly become saturated in $CaCO_3$. Alternatively, the skeletal voids may not be filled until later in diagenesis, during burial. This may be evident from the fracture of micritic envelopes and cement fringes into the voids, indicating some degree of compaction by overburden pressure before calcite precipitation.

Calcitization of aragonite skeletons and shells produces textures which generally retain relics of the original structure. The most common relic is that of growth banding (Fig. 1A), preserved in the form of organic particles in the replacement calcite crystals. Relic fragments of the original aragonite itself may be preserved in the calcite, and these are best seen with the scanning electron microscope after very delicate etching (e.g. 0.5% formic acid for 30 s) of a polished thin section (Sandberg & Hudson 1983). The aragonite relics may have been protected from dissolution by an organic sheath. The calcite
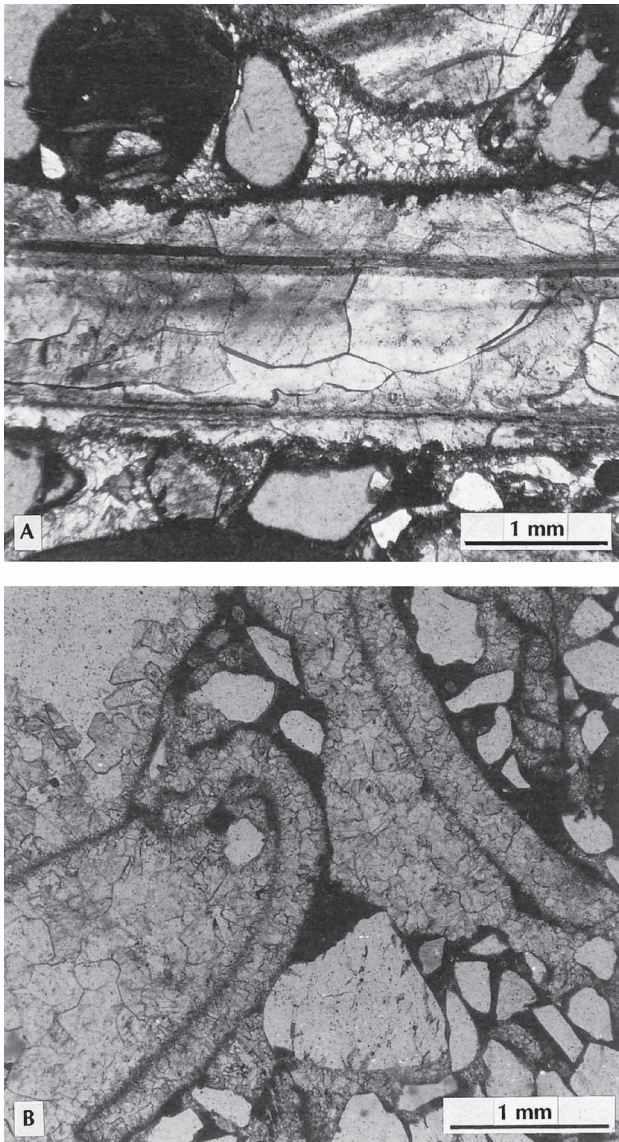
within the original shell; they may develop along the growth banding for example, but cross-cutting relationships are common (Fig. 1A).

The replacement calcite is commonly a pale amber to brown colour, and in thin section a pseudopleochroism (a variation in colour intensity when the stage is rotated) is usually seen, attributed to the effects of minute particles of organic matter. The timing of calcitization is also variable. It may occur in near-surface or in burial diagenetic environments, and if in the latter, a post-compaction origin can be deduced from the nature of fracture surfaces (following original shell structure) if there was sufficient overburden to break the grains.

Since in calcitization the replacement of skeletal aragonite takes place across a thin film, probably a few microns thick, with dissolution of aragonite on one side and precipitation of calcite on the other, most of the CaCO$_3$ is derived from the shell. The replacement calcite is thus commonly enriched in strontium (over calcite cement), inherited from the aragonite. Changes in pore-fluid chemistry or fluid flow during the replacement process may lead to an increase in width of the replacement front, to such an extent that dissolution of the aragonite may proceed faster than precipitation of the calcite, and a significant void may be developed. This may be filled later by calcite cement. Thus some originally aragonitic skeletons may show both types of preservation: calcite cement in dissolution voids and neomorphic spar through calcitization.

Diagenesis of skeletal calcite

In general, ancient carbonate skeletons and shells originally composed of calcite are still composed of calcite (unless silicified or dolomitized) and show good to perfect preservation of the original skeletal structure. Biogenic grains originally composed of high magnesium calcite, however, may show some alteration, and even low magnesium calcite shells, such as brachiopods, under the close scrutiny of cathodoluminescence, may be seen to have patches of recrystallized calcite with different iron and manganese contents. With high magnesium calcite skeletal elements, the Mg^{2+} content is reduced to a few mole percent MgCO$_3$, but commonly small crystals (5–20 μm) of dolomite are produced within the skeleton through stabilization to low magnesium calcite. These microdolomites can be seen in thin section, but they are best viewed under cathodoluminescence or with the scanning electron microscope as slightly etched polished surfaces.

Fig. 1 A, Formerly aragonitic bivalve shell replaced by calcite. Large neomorphic calcite crystals contain relics of the original shell structure. The bivalve was bored prior to replacement and is surrounded by a micrite envelope. Diagenesis took place in the meteoric vadose zone, as indicated by the meniscus calcite cement between the two bioclasts. B, Two bivalve shells originally of aragonite which underwent dissolution; calcite spar was then precipitated within the shell voids. Both shells have micrite envelopes which maintained the shell shape. Calcite spar is also the cement between the bioclasts and was precipitated from meteoric water. Both from the Pleistocene, Miami, Florida. Photographed in plane-polarized light.

crystals replacing the aragonite are generally coarse, certainly much larger than the original aragonite crystals, and they do not show any drusy fabric. The crystals may in part follow lines and planes

Microdolomite is a common constituent of ancient echinoderm fragments, confirming an original high magnesium calcite mineralogy. The identification of an original high magnesium calcite skeleton is still possible, even where microdolomites are absent: the calcite may retain a 'memory' in the form of several mole percent $MgCO_3$, and this is generally significantly higher than originally low magnesium calcite grains, which usually contain less than 1 mole percent $MgCO_3$ after diagenesis. Originally high magnesium calcite grains may also preferentially take up iron (Fe^{2+}) during diagenesis (identified by staining), if this is available in the pore-fluids. Rarely, recrystallization fabrics (patches of coarse calcite crystals) may develop in high magnesium calcite grains, and even small cavities and voids may form as a result of localized dissolution.

Calcitic skeletons and shells are commonly the sites of syntaxial (in optical continuity) cement precipitation. The most familiar are overgrowths on echinoderm grains, whereby large cement crystals are formed. Fibrous calcite cements are commonly precipitated syntaxially on brachiopod, trilobite, and pelagic bivalve shells, and much hard chalk and chalkstone is the result of calcite overgrowth on coccolith debris.

Many limestones, and the fossils they contain, have been subjected to dolomitization. The preservation of carbonate skeletons again depends not only on their original mineralogy, but also on the timing of the stabilization of aragonite and high magnesium calcite to low magnesium calcite. If dolomitization occurs before $CaCO_3$ mineral stabilization, carbonate skeletons of high magnesium calcite commonly display perfect fabric retention. Echinoderms, benthic foraminifera, and red calcareous algae fall into this category. Aragonite shells, on the other hand, are usually dissolved out and the voids filled with dolomite cement. Low magnesium calcite is much more resistant to dolomitization and commonly survives, or is replaced with fabric destruction. If dolomitization takes place after a carbonate sediment has been stabilized to calcite, then mostly the skeletons show very poor structural preservation.

There is a broad pattern of change in the mineralogy of carbonate skeletons through the Phanerozoic. Calcite dominates in the Palaeozoic, aragonite becoming increasingly important in shallow-water carbonate skeletons and shells from the Mesozoic into the Cenozoic. Such changes may reflect subtle changes in seawater chemistry (Tucker 1989).

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3.8.2 Carbonate Nodules and Plattenkalks

P. A. ALLISON

Preservation of soft parts is more commonly associated with carbonate mineralization than with any other authigenic mineral. Such preservation occurs in localized concentrations of authigenic carbonate referred to as concretions or nodules, and also in fine-grained bedded limestones known as *plattenkalks*.

Nodules

Fossil-bearing carbonate (siderite or calcite) nodules are usually associated with organic-rich argillaceous sediments. The fossils within such nodules are often preserved in three dimensions and occasionally include preserved soft parts. Fossil-bearing carbonate concretions are commonly 10–30 cm in size, although examples up to 10 m long enclosing complete plesiosaurs have been recorded. The shape of concretions is controlled by sediment porosity. In sandstones, where porosity in both vertical and horizontal planes is equal, nodules are spherical. In argillaceous sediments, on the other hand, porosity is greater in the horizontal plane and the nodules that form are greater in dimension parallel to bedding. If sediment permeability in the horizontal plane is uniform then the nodules tend to be discoidal; if not, an ellipsoidal form occurs with the long axis aligned in the direction of greatest permeability.

Concretionary carbonate is rarely replacive and is usually precipitated in sediment pore-spaces. The presence of undeformed delicate biogenic structures

such as burrows and faecal pellets shows that mineral precipitation did not force sediment particles apart. Thus, the volume of nodule-forming mineral is equal to sediment porosity at the time of carbonate precipitation (Raiswell 1976). Sediment compaction in mud rocks is proportional to depth of burial; hence an assessment of original porosity in carbonate concretions is also an indication of diagenetic timing. In the case of carbonate concretions, this original porosity will be approximately equivalent to the acid soluble fraction of the nodule. Using this method, internal porosities of certain concretions can be shown to be as high as 80–90% at the centre (Raiswell 1976). Since such porosities in mudrocks only occur in the upper 10 m of the sediment, an extremely early diagenetic origin can be inferred. Internal porosities at the rim of the concretion, however, may be as low as 50%. Thus it is clear that nodule growth is often initiated early in the burial history of a sediment and continues during sediment compaction. Fluctuations in minor and trace element chemistry and in stable isotopes between the centre and the rim of a concretion therefore indicate variations in pore-water chemistry during burial.

Early diagenetic mineralization, such as that responsible for nodule formation, is the only process capable of retarding information loss during decay and fossilization. For this reason fossils preserved in nodules generally exhibit a higher level of preservation than those in the host sediment (Section 3.1). For example, the Upper Carboniferous Mazon Creek biota of Illinois, U.S.A. (Section 3.11.5) includes a variety of plants and animals with soft parts, but these only occur in siderite nodules and are unknown from the host shale. Similarly, ammonites preserved within concretions in the Upper Lias of Yorkshire are typically uncompacted, whereas those in the host sediment are often flattened with compaction cracks (see also Section 3.7).

Concretions characteristically display a network of radial and concentric fractures known as septaria (Fig. 1). It was once thought that these accommodated the reduction in volume brought about by dewatering of clay minerals during diagenesis. However, Astin (1987) has shown that such fracture systems are merely a response to overburden pressure during burial and can form at depths of less than 50 m.

Process of formation. The input of organic detritus to a sedimentary sequence and its subsequent decay (see also Section 3.1) are the primary factors control-
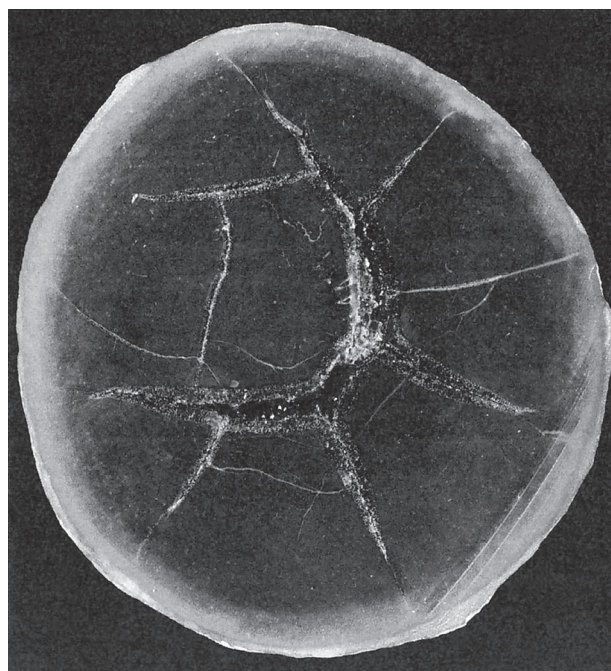

Fig. 1 Septarian cracks in calcareous concretion from Jurassic of Lyme Regis, Dorset. Specimen is 20 cm in diameter.

ling degree of anoxicity, Eh, pH and thereby mineral paragenesis. In the presence of oxygen, organic carbon in sediment is broken down by aerobic microbial respiration and CO_2 is produced. In pore-water solution this produces carbonic acid which promotes carbonate dissolution. In the absence of oxygen the sediment microbiota utilize a series of alternative oxidants in the respiration process, such as manganese, nitrate, iron, or sulphate. These reactions have different free-energy yields and this governs their occurrence in sediment. In the ideal case they are layered (Fig. 2) with those liberating the greatest amount of free energy at the top of the sediment pile. The depletion of the oxidants initiates the next most efficient reaction. When all the oxidants have been depleted fermentation reactions dominate and methane is produced.

A common denominator in all of these anaerobic reactions is the production of the bicarbonate ion. If this reacts with any suitable cations, such as calcium, iron, magnesium or manganese, then a carbonate mineral may form. The formation of early-diagenetic carbonate concretions is therefore associated with anaerobic decay of organic carbon. The mineral formed is dependent upon the dominant decay pathway at the site of deposition. In a marine system calcium is normally present in supersaturation levels; calcite is the most stable mineral phase and

AEROBIC $CH_2O + O_2 \rightarrow CO_2 + H_2O$

	Nitrate reduction	$5CH_2O + 4NO_3^- \rightarrow 2N_2 + 4HCO_3^- + CO_2 + 3H_2O$
	Manganese reduction	$CH_2O + 3CO_2 + H_2O + 2MnO_2 \rightarrow 2Mn^{++} + 4HCO_3^-$
	Iron reduction	$CH_2O + 7CO_2 + 4Fe(OH)_3 \rightarrow 4Fe^{++} + 8HCO_3^- + 3H_2O$
	Sulphate reduction	$2CH_2O + SO_4^{2-} \rightarrow H_2S + 2HCO_3^-$
	Methanogenesis	$2CH_2O \rightarrow CH_4 + CO_2$

ANAEROBIC

Fig. 2 Idealized bacterial reduction zones in organic-rich sediment. (After Berner 1981.)

iron reacts preferentially with sulphide ions (from sulphate reduction) to produce pyrite (Section 3.8.3). In a freshwater system, however, sulphide ions are almost absent and concentrations of iron ions may exceed those of calcium to a degree which allows siderite to form (Berner 1981). Although there are exceptions (Sellwood 1971), siderite can be considered an indicator of freshwater conditions. The manganese content of pore-water is rarely high enough for manganous mineral species to form. Manganese ions liberated near the anoxic–oxic boundary by anaerobic respiration are therefore more commonly incorporated into other mineral species such as calcite or siderite. Since manganese reduction is one of the earliest reduction zones in the sediment pile, concentrations of manganese in pore-water solution are greatest near the anoxic–oxic interface. Thus, those phases of the concretion which form first (the centre) have a higher manganese–calcium ratio than those which form later (the rim of the concretion).

Berner (1968) suggested a model for the localized precipitation of carbonate (forming concretions) based upon a series of actualistic experiments using decomposing fish. He monitored the decay of fish in jars containing anoxic seawater and noted the effect on pore-water chemistry. As fish decayed, ammonia and bicarbonate were liberated to solution and produced an alkaline environment; at the same time calcium stearate (a soap) formed at the bottom of the jars containing the fish. Berner (1968) suggested that this stearate was the most stable calcium-bearing mineral phase around a decomposing carcase. He believed that the authigenic carbonates were formed from the additional bicarbonate generated by further decomposition after the depletion of available stearate. Precipitation in this case would be favoured by the high pH microenvironment around the decomposing carcase.

Raiswell (1976), however, based an alternative model upon a geochemical and petrological study of ammonite-bearing concretions from Lower Jurassic shales in North Yorkshire, England. Stable isotope analysis of these concretions showed that the carbonate fraction had been generated as bicarbonate ions during bacterial sulphate-reduction and methanogenesis. However, the decay of the enclosed organisms (e.g. ammonites, belemites) could not have liberated sufficient bicarbonate to produce the volume of calcite forming the concretions. The bicarbonate was generated by the decay of disseminated organic carbon, and it migrated to nucleation sites such as skeletal carbonate. Localized precipitation of authigenic carbonate around such sites produced concretions.

In an open geological system, where calcium levels can be replenished, carbonate species can form in the decay aureole of decomposing organisms. Carbonates precipitated in this fashion may function as nucleation centres for additional bicarbonate in pore-water solution. Problems arise, however, in modelling the growth of carbonate concretions around plants in fossil peat swamps (see also Section 3.10). When plants decompose they liberate humic and fulvic acids and produce low pH pore-waters which inhibit carbonate formation. It is possible that bicarbonate ions produced during anaerobic decay achieve a sufficiently high concentration to buffer acid pore-waters and promote carbonate formation. Alternatively, nodules may form in peat swamps which have been flushed by non-acidic pore-waters. Evidence to date is inconclusive.

Plattenkalks

Plattenkalk deposits (also referred to as lithographic limestones) occur in both lacustrine and marine settings and are characteristically fine-grained and well

bedded. Examples include the Eocene Green River Formation of central North America, the Cretaceous Haqel and Hjoula Limestones of Lebanon, and the celebrated Solnhofen Limestones of the Jurassic of Bavaria (Section 3.11.7). The carbonate in these deposits may originate from a biogenic source (such as calcareous algae) or as a chemical precipitate. The formation of such deposits is therefore favoured by a reduced supply of terrigenous sediment and a high rate of organic production.

Plattenkalk deposits are famous sources of well preserved fossils, which in some cases include soft parts. Exceptional preservation in this case is favoured by rapid burial and a general absence of benthos. Soft-bodied fossils from such deposits are usually flattened parallel to bedding; thus lithification occurred after decay-induced collapse of soft-tissues (such as skin and muscle) and compaction of lightly skeletized structures (such as arthropod cuticle).

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3.8.3 Pyrite

P. A. ALLISON

Process of formation

Sedimentary pyrite is frequently encountered as a minor component of both modern (Berner 1972) and ancient (Baird & Brett 1986; Allison 1988) fine-grained marine clastic sediments. Of all the early diagenetic mineral phases, the formation of pyrite is best understood. Studies of recent sediments have shown that the formation of authigenic pyrite can occur very early in the diagenetic history of a sediment and may be initiated only a few centimetres below the sediment–water interface (Berner 1984). In the presence of oxygen, microbes feed on organic carbon in sediment and respire aerobically (Section 3.1). With increasing organic content and/or depth of burial the diffusion of oxygen into the sediment is impeded and the microbes are forced to respire anaerobically. In a marine environment the principal anaerobic decay pathway is that of sulphate-reduction (Berner 1972, 1984). This process can be represented by the following equation:

$$2CH_2O + SO_4^{2-} \rightrightarrows H_2S + 2HCO_3^-.$$
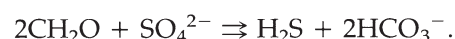
However, according to Jørgenson (1982) this reaction actually progresses through a variety of stages, including the breakdown of organic biopolymers (by bacterial fermentation) to simpler organic molecules that can fuel sulphate-reducing reactions. A principal by-product of this reaction is hydrogen sulphide (H_2S) which can combine with reactive iron-bearing minerals to produce finely-particulate iron monosulphides (FeS) such as greigite and mackinawite (Fig. 1). Bacterial breakdown of H_2S liberates sulphur (S) to solution which can react with FeS to produce pyrite. Should these sulphur-bearing chemicals diffuse upwards into aerobic waters they can be broken down by oxidizing bacteria to liberate sulphates to pore-water solution (Fig. 1).

Fossil preservation

Mineralization is the most frequent means of halting the information loss associated with the decay of macro-organisms (Section 3.1). Organisms that are permineralized early in the diagenetic history of a sediment frequently exhibit higher levels of preservation than those that form later (Allison 1988). Early diagenetic minerals (such as pyrite) are therefore an important preservational medium for fossils. The preservation of fossils is a result of the interplay between decay and mineralization. This can be simply illustrated with respect to pyrite.

Soft tissues. With rapid mineralization and/or an impediment to the decay processes, soft tissues such as muscle may be pyritized. Examples of this type of preservation include the appendages of trilobites from the Ordovician: Beecher's '*Triarthrus*'
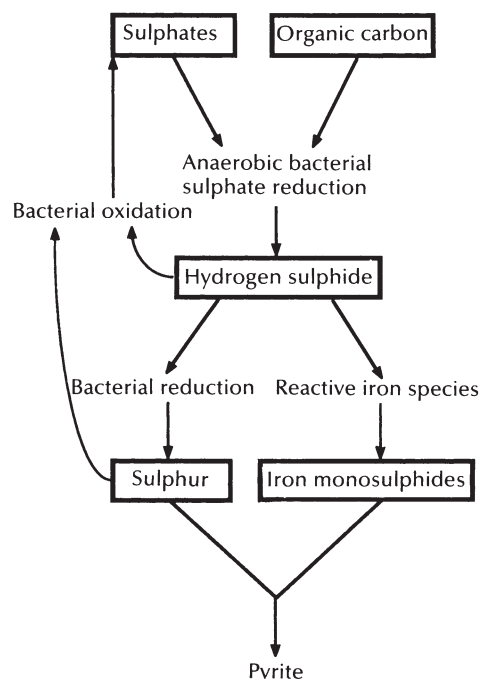
Fig. 1 Summary of the geochemical processes involved in the formation of pyrite. (From Berner 1972.)

by sulphate-reducing bacteria and is replaced by pyrite; even polished thin-sections show little or no cellular detail. The late wood, however, being more resistant to the action of sulphate-reducing bacteria, forms a coalified residue which preserves cell walls infilled with pyrite (Fig. 2C).

Shell and bone. Biogenic hard parts such as shell (calcium carbonate) and bone (calcium phosphate) are some of the most decay-resistant biological structures, and as such are the most commonly occurring fossil types. Of the two, calcium carbonate is the more unstable and is therefore the more likely to be replaced by pyrite. Preservation of shells may include replication of original shell lamination (Fig. 2D).

Mineral form

Sedimentary pyrite occurs in a variety of morphologies (Allison 1988).

Trilobite Bed of New York State, U.S.A., and the preservation of trilobites and the soft-tissues of cephalopods from the Devonian Hunsrückschiefer of the Bundenbach district of West Germany (Section 3.11.4).

Refractories. With more decay and delayed pyrite formation, soft tissues will be destroyed and only decay-resistant biological compounds (termed refractories) such as cellulose and lignin are preserved. Of the two compounds, lignin (a complex aromatic molecule) is the most refractory; thus lignified plant remains have a higher preservation potential than purely cellulosic tissues. This decay-rate differential can result in a preservational bias between different anatomical elements of a plant. For example, growth rings are composed of two elements: early wood, laid down at the beginning of the growing season (spring); and late wood, laid down later in the season (summer). Early wood is characterized by large thin-walled cells with a low lignin content, while late wood is usually composed of smaller thick-walled cells with a higher lignin content. Early wood is therefore more amenable to decay than late wood and in a sulphate-reducing environment is more likely to be pyritized. Pyritized wood from the Eocene London Clay of Kent, England displays just such a bias (Allison 1988). The early wood has been completely degraded
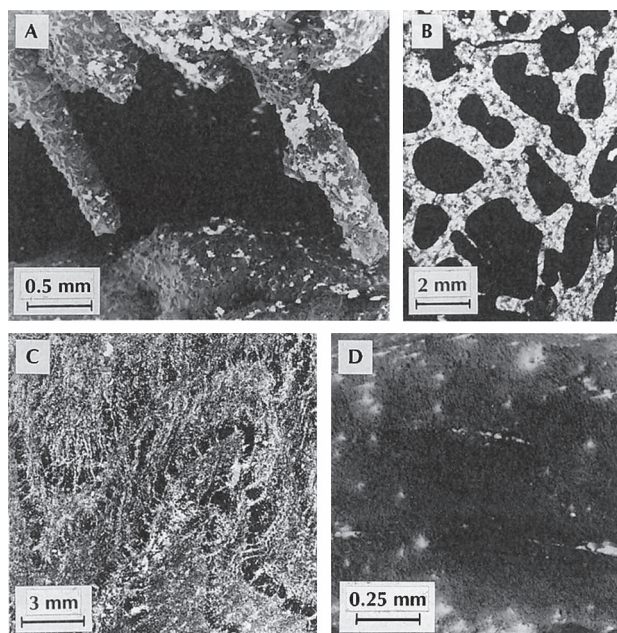

Fig. 2 Examples of pyrite morphotypes from the Eocene London Clay of Kent, England. A, Pyrite stalactites hanging from the inside of a gastropod shell. B, Thin-section of bone (light-grey) with pyrite-infilling of cavities. C, Preservation of grain in wood. Light-coloured layers are pyritized early-wood, dark layers are coalified late-wood. D, Pyritized gastropod shell, outer margin of shell towards top of picture. Note preservation of original shell lamination (left-to-right) in pyrite. (From Allison 1988.)

Framboids. Spherical aggregates of microcrystalline cubes and octagons are commonly encountered in mud-grade sediments. They vary in size from a few microns to about 1 mm in diameter and are referred to as framboids (from the French *framboise* meaning raspberry). They may occur as isolated elements or as conjoined aggregates, the latter occurring as linear (picking out original bedding) or sub-spherical amalgamations.

Pyritized sediment. Sediment infills of biogenic cavities which have been cemented by pyrite are referred to as pyritized sediment. Pyrite may replace detrital grains.

Cavity linings. Euhedral pyrite linings of cavities are common in mud-grade sediments. Examples of such cavities include the living space of molluscs and brachiopods, and vesicles in bone (Fig. 2B). They may be completely infilled or only partially lined with pyrite. In some cases pyrite stalactites (Fig. 2A) hang down from these linings and form geopetal structures.

Pseudomorphic textures. Pyrite may replace detrital and authigenic minerals as well as fossils. In the Eocene London Clay of Kent (Allison 1988) pyrite pseudomorphs authigenic cavity-lining calcite and phosphate concretions. In the latter, pyrite commonly extends from pyrite-infilled septaria and replaces the authigenic phosphate and detrital minerals of the concretion. Such pyritization includes the preservation of sedimentary textures such as original bedding, burrows, and faecal pellets.

Overpyrite. Encrusting pyrite on the surface of fossils is termed overpyrite.

Concretions. Pyrite concretions adopt a variety of habits and crystal textures. It is generally assumed that tabular examples formed later in the diagenetic history of a sequence when porosity was greater in the horizontal plane than in the vertical plane. Cone-in-cone pyrite is common and is thought to have formed as a result of the interference between overburden pressure and pressure of crystallization during mineral formation.

Reworked pyrite. As an early diagenetic mineral that can form in the upper few centimetres of sediment, pyrite is extremely susceptible to reworking. However, it was long assumed that reworked pyrite would be oxidized and destroyed during the pro-

cess. Recent work in the Devonian Leicester Member flooring the black shales of the Genesee Formation of New York State (Baird & Brett 1986), however, has demonstrated the presence of reworked pyrite remanié horizons. It is thought that these deposits were concentrated during brief erosive phases in an otherwise anaerobic environment.

Palaeosalinity

The formation of pyrite is controlled by the concentration of organic carbon, dissolved sulphate, and detrital iron minerals (Berner & Raiswell 1984). In a normal marine environment iron minerals and sulphates are present in abundance, and pyrite formation is controlled by the supply of organic carbon. In freshwater environments, however, the formation of pyrite is limited by low sulphate concentration. Euxinic environments, on the other hand, are characterized by an abundance of H_2S (from anaerobic sulphate reduction); the limiting factor for pyrite formation in this type of environment is therefore the availability of detrital iron minerals. The factors controlling pyrite formation in these different environments produce characteristic ratios of carbon and pyrite sulphur in a sediment, which can be used in the determination of palaeosalinity (Berner & Raiswell 1984).

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3.8.4 Phosphate

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Phosphorus is an element critical to life. It is concentrated either in hard tissues, such as bones or some cuticles, or more often in soft parts (which have an almost constant composition: C_{80}, N_{18}, P_1). Therefore it is not surprising that it is involved in fossilization. Bones, teeth, and scales, being primarily phosphatic, have a high preservation potential. Skeletons in other material (e.g. calcite, silica), and soft tissue, may be diagenetically altered to phosphate if there is enough organic matter available.

Fossil preservation

Primary phosphate. The vertebrate skeleton is composed mainly of hydroxyapatite ($Ca_{10}(PO_4)_6(OH)_2$). Locally, especially in teeth, some of the OH^- ions may be replaced by F^- ions, resulting in a less soluble hydroxy-fluorapatite. Phosphatic invertebrate shells have variable but similar compositions. The composition of fossil bone generally differs in having substantially more fluorine. For example, the average fluorine content of the bones of marine and freshwater fish is 4300 ppm and 300 ppm respectively, whereas those of their fossil counterparts contain 22 100 ppm and 19 900 ppm fluorine. Some PO_4^{3-} is replaced by CO_3^{2-} (one PO_4^{3-} replaced by $CO_3^{2-} + F^-$, or $2PO_4^{3-}$ replaced by $2CO_3^{2-} + 1$ vacancy of Ca^{2+}) and all the OH^- by F^-. The primary hydroxyapatite is transformed into less soluble carbonate-fluorapatite by simple ion exchanges between solution and mineral, without the necessity of a dissolution stage. This alteration occurs without any modification of the shape and structure of the object.

Calcium carbonate. Shells and tests composed of calcium carbonate, either calcite or aragonite, may be preserved in sediment if the physico-chemical properties of the interstitial waters remain similar to average marine or freshwater conditions (Section 3.8.1). Such carbonate debris may also be altered to apatite without affecting external morphology (Fig. 1). In natural environments, this diagenetic alteration occurs mainly in association with phosphate deposits (Prévôt & Lucas 1986). Bacterial transform-

ation of calcareous organisms into apatite has been demonstrated in the laboratory (Lucas & Prévôt 1985). These observations and experiments suggest the following possible mechanism: (1) the phosphorus needed to replace carbonate by apatite is added to the sediment by organic matter; (2) various micro-organisms (e.g. bacteria, algae, fungi) promote decay, liberating PO_4^{3-} ions and making the interstitial water acidic. This acidification, which may be very localized, results in the dissolution of carbonate; and (3) the newly liberated PO_4^{3-} combines with Ca^{2+} to form apatite. Apatite forms preferentially at the carbonate–micro-organism interface and replaces the dissolved carbonate. Crystallization of apatite preserves the external shape of the originally calcareous shell. Here, as in the fossilization of primary apatite, fluorine also plays an important role, for the final composition is carbonate-fluorapatite.

Phosphatization of primary silica also occurs in radiolarian tests, e.g. in phosphate deposits. This process is poorly understood.

Unmineralized organic material. Microscopic examination of phosphorites shows that numerous micro-
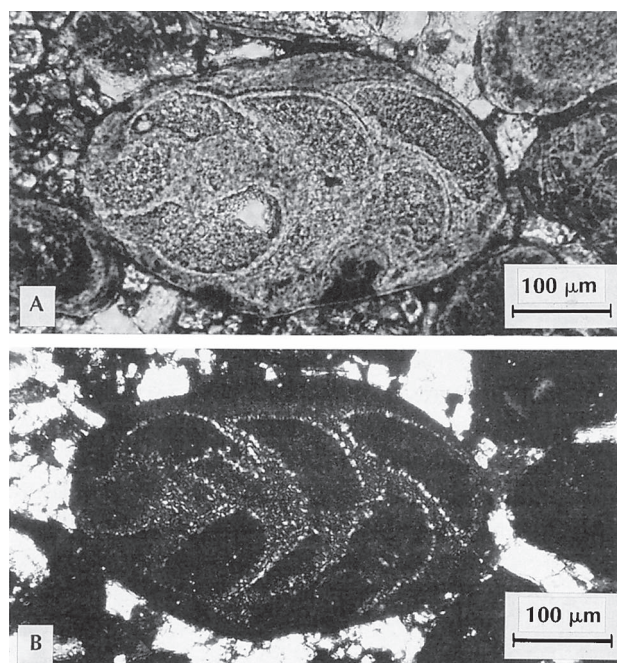

Fig. 1 Foraminiferan, originally calcium carbonate, transformed into apatite in a phosphorite from Ganntour Basin (Morocco). Thin section photomicrographs. A, Plane-polarized light. B, Crossed polar light. The walls are in anisotropic apatite and the chambers filled with isotropic apatite.

organisms without shells (e.g. algae, fungi, bacteria) are fossilized in apatite, although they did not contain any mineral precursor. Phosphatized coprolites (see also Section 4.12) are well known. The organic matter itself is replaced by apatite which retains the exact shape of the object as shown, e.g. by the constriction striae on some coprolites. Even phosphatized soft tissues of arthropods (copepods, ostracodes) may occur in calcareous nodules and phosphatic nodular limestones, or in big vertebrate coprolites. The cuticle is replaced and/or coated by carbonate-fluorapatite (Müller 1985; Section 3.11.3). In this case the mechanism is less clear, but may be similar to that in laboratory experiments where apatite is precipitated from solution by introducing phosphorus as a soluble organic complex, and calcium as a soluble mineral salt. The mechanism must be extremely rapid to account for the preservation of faeces and of the finest details of microscopic arthropods (Section 3.11.3) without deformation.

Conditions for phosphatization

Both the study of phosphorites and the results of experimental apatite synthesis allow an estimate of the most likely conditions for apatitic fossilization. Because of its stability requirements, apatite forms preferentially in an oxygen-depleted environment, sometimes even in fully reducing conditions, as indicated by the frequent association of pyrite with phosphates. This environment is easily produced by abundant organic matter, which is also required as the main source of phosphorus. The concentration of fluorine, essential to the formation of the more stable fluorapatite, is generally higher in marine than in freshwater. Its concentration in sedimentary apatites is so high that a constant supply is indicated, suggesting a marine origin. However, seawater contains a high concentration of magnesium, well known to inhibit apatite formation. This cannot be eliminated under normal marine conditions, but may be removed in the pore-water of a mud during early diagenesis. These conditions of early diagenesis with an organic-rich marine mud also

control the formation of sedimentary phosphorite deposits, archetype of the environment for phosphogenesis. In the deposits of the Cretaceous–Tertiary transition, for example, phosphate-rich levels often contain abundant bones and teeth of marine vertebrates. Rare invertebrate skeletons are phosphatized. In contrast, the interbedded carbonates are rich in shells but almost devoid of phosphatic remains. This separate distribution of phosphatic and calcareous remains is due only to different conditions of fossilization: calcareous skeletons are well preserved in carbonate-rich levels, apatitic remains in phosphate-rich levels. For the same reason bones and teeth are only found in the phosphorite 'patches' (including nodules and coprolites) within the Cretaceous chalk of the Paris Basin, and not in the chalk itself.

Though carbonate-fluorapatite appears most frequently in natural environments during early diagenesis, it is not the most stable of the apatites. Therefore it tends to evolve slowly into the more stable fluorapatite. The primary apatite loses its CO_2 very slowly; to reach the final stage takes several hundred million years.

Phosphatic fossils occur mostly in phosphate deposits, and there the mechanisms of apatite genesis can be investigated. Knowledge of the palaeogeographical, palaeoclimatic, and other conditions which result in apatite formation in phosphate basins is now increasing. It is still puzzling how these conditions converge locally to form phosphatic nodules in chalk, or to protect an isolated bone fragment. Apatite formation is far from fully understood.

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3.9 Taphofacies

C. E. BRETT & S. E. SPEYER

Taphofacies, or taphonomic facies, consist of suites of sedimentary rock characterized by particular combinations of preservational features of the contained fossils (Brett & Baird 1986). As such they are similar to, but distinct from, biofacies (Section 4.18) which are defined on the basis of recurring organisms, generally species or genera, which are inferred to have lived together in the geological past. Similarly, taphocoenoses, or death assemblages, are simply groupings of organisms found together in fossil assemblages, whereas thanatocoenoses are interpreted as variously biased derivatives of once-living communities, or biocoenoses (see also Section 3.5). In contrast, taphofacies are not defined on the basis of fossil taxa, but rather on the basis of consistent preservational properties. These preservational features include the following: (1) orientation of fossils, including life orientations; (2) relative degree of articulation of skeletons; (3) relative fragmentation of fossils; (4) proportion of convex-up to convex-down skeletons; (5) proportions of various skeletal elements from multiple-element skeletons (e.g. pedicle—brachial valve ratios in

brachiopods); (6) degree and type of abrasion, corrosion, or bioerosion of skeletons; (7) type of shell fillings or coatings; (8) evidence for early dissolution of skeletons; and (9) any special features of preservation. By defining indices based upon taphonomic properties (e.g. ratio of articulated versus disarticulated skeletons), it is possible to quantify various modes of fossil occurrence and to provide a basis for comparing the preservational grade of fossil assemblages. The differential preservation of similar fossils between facies reflects different biostratinomic and/or diagenetic processes active in various environments. The most useful fossils for comparative taphonomic study are eurytopic taxa that occurred in a variety of sedimentary environments. Comparative study of taphofacies permits recognition of certain environmental parameters which influence preservation. These factors include particularly: (1) the relative frequency of episodic storms and other disturbances; (2) the relative rates of background sedimentation; (3) the environmental energy, including intensity and direction of currents; and (4) the geochemistry and level of

Table 1 Relationship of biostratinomic features of various types of fossil skeletons to sedimentation rate and environmental energy. (From Brett & Baird 1986.)

Environmental energy	Skeletal type	Sedimentation rates		
		Episodic, very rapid $(10-50 \text{ cm}/10^2 \text{ years})$	Intermediate—rapid $(10-100/\text{cm}/10^3 \text{ years})$	Low—intermediate $(1-10 \text{ cm}/10^3 \text{ years})$
High	Fragile; ramose	Minor fragmentation	Strong fragmentation	Absent
	Bivalved shells	Mostly articulated; rarely *in situ*	Partially articulated; some fragmented	Disarticulated; fragmented; abraded
	Multielement skeletons	Mostly articulated; rarely *in situ*	Partially articulated; pieces sorted	Disarticulated; pieces sorted
Low	Fragile; ramose	Intact; not fragmented	Some fragmentation	Strong fragmentation; corrosion
	Bivalved shells	Articulated; some *in situ*	Mostly disarticulated; complete valves	Disarticulated; minor fragmentation; corrosion
	Multielement skeletons	Completely articulated; some *in situ*; intact moults	Partially articulated; non-sorted	Disarticulated; non-sorted

Table 2 Relationships of early diagenetic features of fossils (e.g. types of shell fillings, coatings, authigenic minerals) to sedimentation rate and oxygenation of bottom water and sediment. (From Brett & Baird 1986.)

Water oxygenation	Sediment geochemistry	Sedimentation rates		
		Episodic, very rapid $(1-50 \text{ cm}/10^2 \text{ years})$	Intermediate–rapid $(10-100 \text{ cm}/10^3 \text{ years})$	Low–intermediate $(1-10 \text{ cm}/10^3 \text{ years})$
Aerobic $O_2 > 0.7$ ml/l	Oxic–depth; organic-poor	No sediment fillings; late diagenetic mineral fillings; minor pyrite	Sediment steinkerns	Partial sediment steinkerns; rare chamositic, hematitic coatings
Aerobic–dysaerobic $O_2 = 0.7-0.3$ ml/l	Anoxic with oxic microzone; organic-poor (non-sulphidic)	Pyrite steinkerns, overpyrite (euhedral); $CaCO_3$ concentrations	$CaCO_3$ concretionary mud steinkerns; minor overpyrite	Phosphatic and/or glauconitic steinkerns, often reworked; rare overpyrite
Dysaerobic– anaerobic (euxinic) $O_2 < 0.3$ ml/l	Anoxic–surface; commonly organic-rich (commonly sulphidic)	No fillings: minor pyritic replacement; rarely, traces of soft parts	Mud steinkerns; pyrite patinas; periostracal remnants	Highly compacted mud steinkerns

oxygenation of the lower water column and upper sediments (Tables 1, 2; Brett & Baird 1986).

The concept of taphofacies has been applied recently to the subdivision and interpretation of ancient sedimentary environments. For example, Speyer & Brett (1986) used a combination of qualitative observations and semiquantitative indices of preservation in widespread phacopid trilobites to recognize nine distinctive taphofacies in the Middle Devonian Hamilton Group of New York State (Fig. 1). Preservation indices included relative frequency of fragmentation, up-and-down orientations of concavo-convex skeletal parts, cephalon–pygidium ratios, percentage of articulated trilobites and moult remains, and percentage of enrolled versus outstretched individuals. The taphofacies recognized display a broad range of preservational grades. Taphofacies 1 is characterized by almost completely disarticulated, sorted and highly fragmented trilobite remains, which are indicative of low rates of deposition in high-energy environments. In contrast Taphofacies 3 and 4 display high proportions of complete outstretched skeletons, or moult assemblages. In addition to biostratinomic characteristics, observations on early diagenetic minerals in the fossil trilobites were analysed and used in the interpretation of sediment geochemistry and oxygenation. For example, abundant pyrite was found to be associated with other evidence for dysaerobic but not anoxic settings, where moderate rates of sedi-

mentation prevailed (Fig. 2). Similarly, Fisher and Hudson (1987) compared pyrite geochemistry and fossil preservation in ammonoid shells and distinguished three taphonomically separate groups of fossil assemblages from the Jurassic Oxford Clay of Britain. Flattened, highly compressed ammonites with very minor pyrite are typical of black shale environments, in which relatively weak gradients existed between organic remains and their surrounding sediments; in contrast, grey bioturbated facies provided excellently preserved, uncompacted pyrite steinkerns of fossils (see also Section 3.7).

A similar approach is illustrated by Martill's (1985) study of modes of preservation in marine vertebrates, also from the Oxford Clay of the U.K. He was able to distinguish five distinct types of preservation among crocodilians, ichthyosaurs, and fish; these included completely articulated to variously disarticulated skeletal remains, isolated bones and teeth, worn bones, and coprolitic accumulations. Martill observed a correlation between the organic content of the sediment and the degree of skeletal articulation, and noted trends in vertebrate preservation throughout transgressive–regressive cycles that reflect variations in sedimentation rates.

Norris (1986) and Flessa & Fürsich (1987) recognized gradients of taphonomic indices, such as fragmentation and abrasion, amongst Neogene molluscan assemblages. Taphonomic gradients were arrayed approximately perpendicular to the
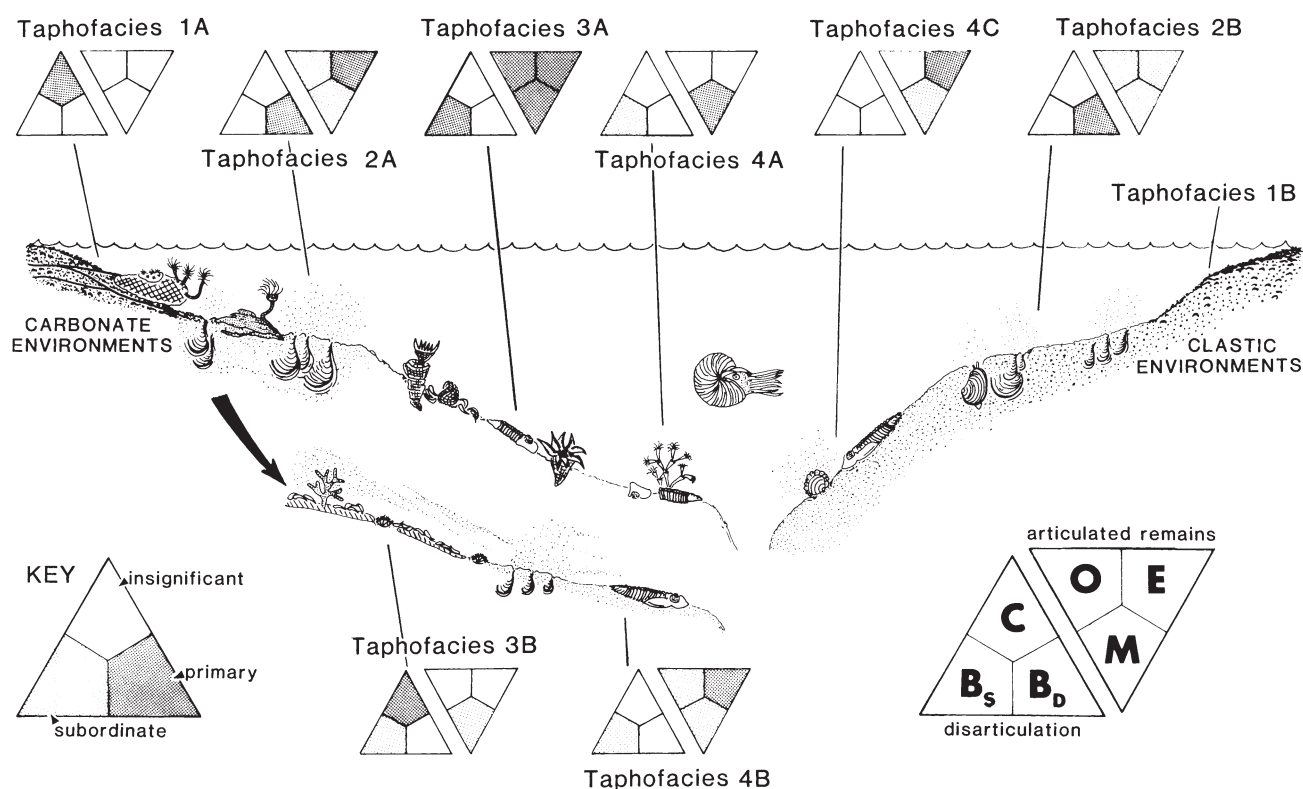
Fig. 1 Reconstructed panorama of Hamilton Group (Middle Devonian, New York State) trilobite taphofacies and summary of taphonomic attributes. Disarticulation was mediated by current-related processes (C), surficial bioturbation (B_S), and/or deep, intrastratal bioturbation (B_D); these agents are differentiated on the basis of sclerite orientation. Articulated remains are categorized according to body posture (O = outstretched, E = enrolled) and mode of generation (M = moult).

Taphofacies 1A and 1B display modes of fossil preservation that indicate a taphonomic history involving long-term lag accumulation and deposit reworking in a nearshore setting. *Taphofacies 2A and 2B* are characterized by pervasive *Zoophycos*-like bioturbation and a relative abundance of enrolled corpses; sedimentation rate was moderately high and substratum was water saturated, well oxygenated, and easily suspended. *Taphofacies 3A* displays abundant disarticulated but non-fragmented remains; because of insignificant sediment supply, these accumulated to form thin, laterally persistent layers. *Taphofacies 3B* is characterized by prominent shell layers in which shell concentration was the result of sediment bypass; sediment was carried to and deposited in deeper-water settings. *Taphofacies 4A* reflects very low rates of sedimentation in deep, quiet water conditions; trilobite debris accumulated between depositional events and may have served as substrate for various sessile organisms. *Taphofacies 4B* indicates higher rates of sedimentation, probably as a result of bypass in more proximal environments (e.g. Taphofacies 3B); sediment chemistry favoured early pyrite diagenesis, which indicates dysaerobic-anaerobic conditions. *Taphofacies 4C* represents very high sedimentation in a deep-water setting and is characterized by anaerobic sediment chemistry, low-diversity faunas, and an unstable substratum.

Comparative taphonomic analysis enhances our perception of stratigraphic facies as dynamic environmental units that are distributed in an orderly fashion with respect to specific physico-chemical parameters. This reconstruction is a generalized synthesis of bathymetrically and sedimentologically related environments on the basis of observed taphonomic products and inferred sedimentary processes. (From Speyer & Brett 1986.)

shore line, and reflected decreasing severity of re-working events in an onshore direction for tidal flats (Flessa & Fürsich 1987) and an offshore direction for a Miocene shelf (Norris 1986).

Speyer and Brett (1988) used a deductive approach to produce a hypothetical model of taphofacies for various environmental settings of ancient epeiric seas (Fig. 3). Hypothetical distributions of tapho-nomic properties, such as articulation ratio, convex up-and-down orientations of shells, and relative degree of fragmentation and abrasion, were contoured along gradients of depth and sedimentation rates to produce generalized three-dimensional block diagrams (Fig. 3). For example, disarticulation and fragmentation should be highest in areas where sedimentation rates are at a minimum and where the sea floor is continually reworked by current or wave disturbances. Optimal levels of articulation
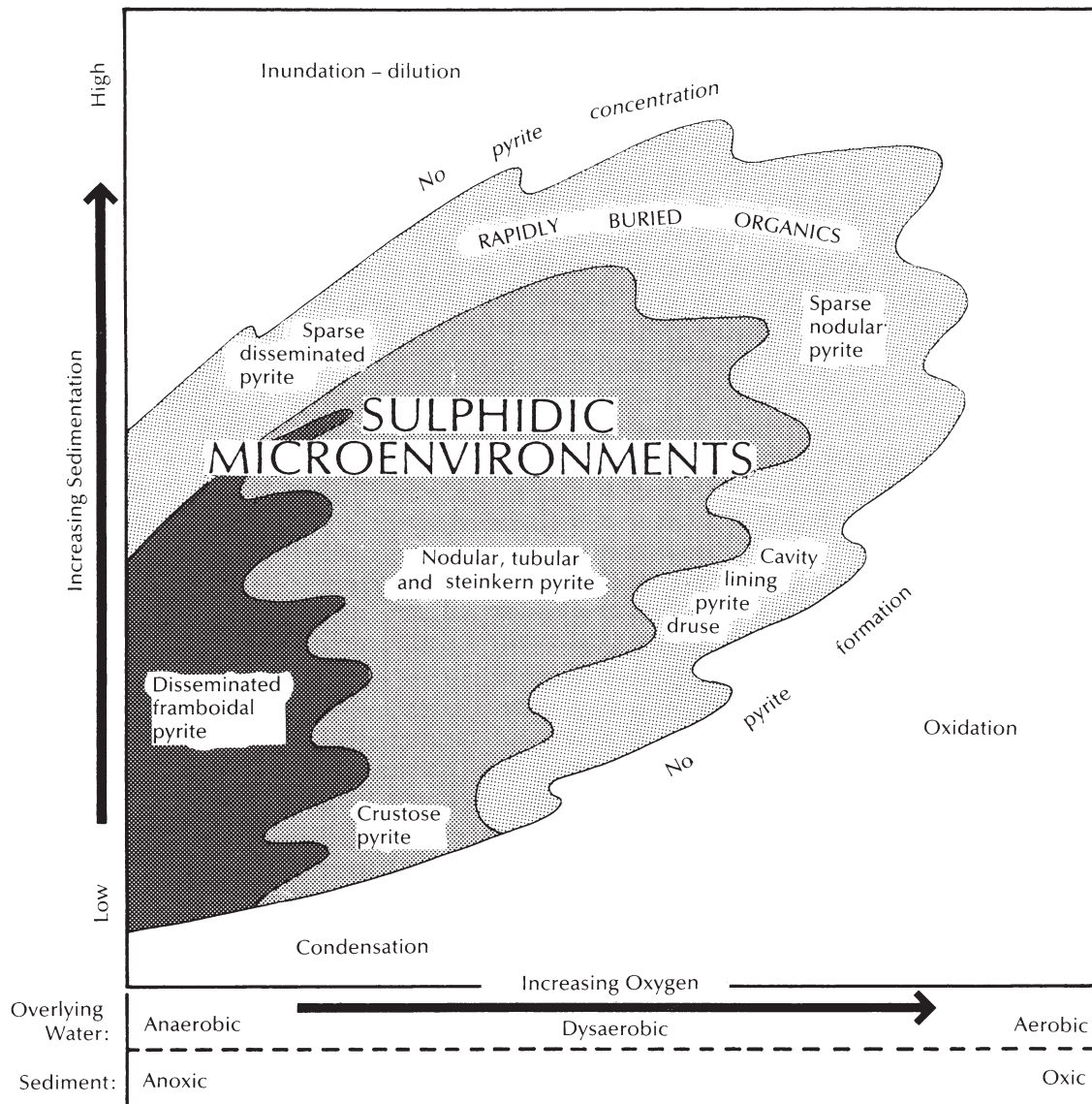
Pyrite Taphofacies Model

Fig. 2 Schematic diagram illustrating the range of conditions that favour formation of various forms of early diagenetic pyrite (see also Section 3.8.3). Note that pyrite formation is enhanced in sulphidic microenvironments, within nonsulphidic sediments, and with moderate sedimentation rates. Little or no concentration gradient exists in anaerobic, organic-rich (sulphidic) muds, while fully aerobic conditions in the upper sediment clearly militate against pyrite formation. Organic matter must be buried in sediment to initiate bacterial action; however, too high a rate of deposition will swamp early diagenetic reactions by diluting the necessary concentrations. (After Brett & Baird 1986.)

and minimal fragmentation would occur in low-energy environments with high sedimentation rates. Trends in the frequency or percentage of event deposits (such as storm-generated shell layers) can also be contoured using a similar diagram and provide an additional type of taphonomic data which can be used in interpreting ancient facies. Synthesizing these simple deductions, it was possible to construct taphofacies models (Fig. 4)

which approximate distribution patterns of tapho-facies observed in empirical studies (e.g. Speyer & Brett 1986).

The concept of taphofacies requires further testing in many modern marine settings, as well as in various ancient depositional environments. However, if taphofacies can be recognized consistently, it should be possible to reconstruct patterns of ancient sedimentation rates and other factors,
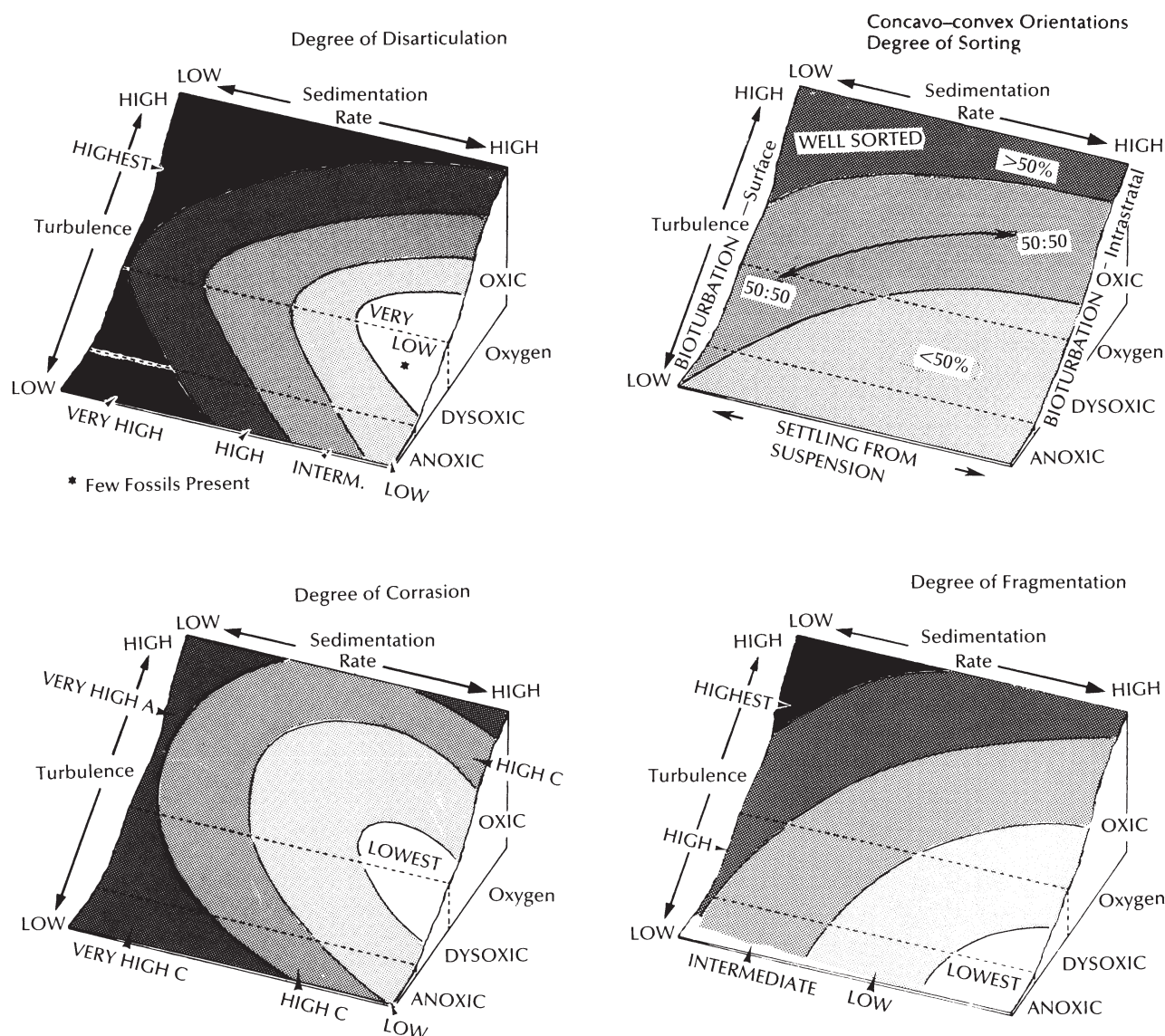
Degree of Disarticulation

Concavo–convex Orientations
Degree of Sorting

Degree of Corrasion

Degree of Fragmentation

Fig. 3. Biostratinomic gradients with respect to three generally defined environmental parameters: sedimentation rate (decreases right to left); turbulence (i.e. current energy, decreases downslope from top to bottom); sea-floor oxygen (decreases downslope — oxic, dysoxic, anoxic). Duration of surface exposure is inversely proportional to sedimentation rate and is important in regulating the magnitude of illustrated taphonomic properties. A = Abrasion, C = Corrosion.

and hence to refine interpretations of ancient sedimentary environments.

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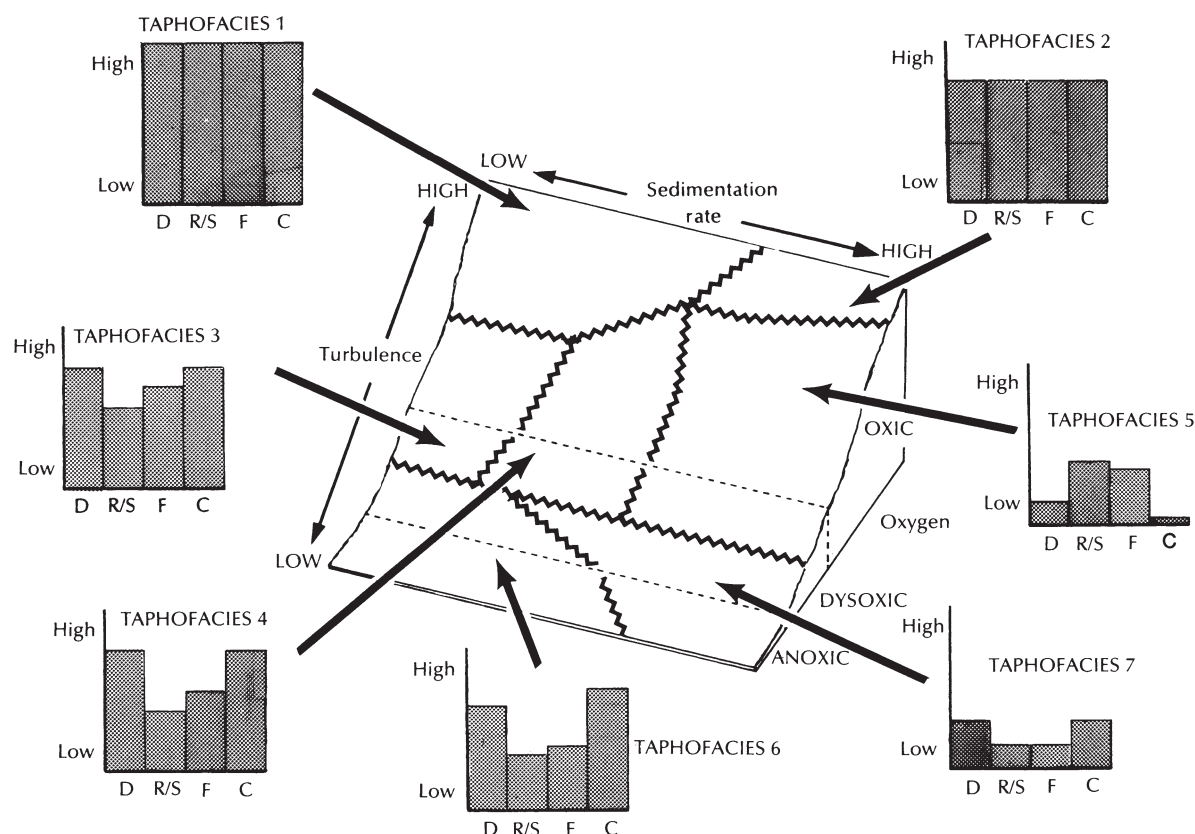
Fig. 4 General taphofacies for Palaeozoic epeiric seas. Seven distinct taphofacies are recognized on the basis of differences in four taphonomic properties: D = disarticulation, R/S = reorientation and sorting, F = fragmentation, C = corrasion, i.e. corrosion/abrasion. These seven taphofacies, in turn, reflect environmental conditions in corresponding fields of the general block diagram. Environmental conditions are coarsely represented by the three indicated parameters (sedimentation rate, turbulence, and oxygenation). (From Speyer & Brett 1988.)

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3.10 Anatomical Preservation of Fossil Plants

A. C. SCOTT

Introduction

Plant fossils may be preserved: (1) as compressions; (2) anatomically, as fusain (fossil charcoal) where the cell walls have been converted to pure carbon by fire; and (3) as permineralizations, where original cell walls are still preserved, or as petrifactions, where cell walls have also been replaced (usually by silica, carbonate, or pyrite). While compressions are both common and useful, they preserve no internal structure, and it is anatomically preserved plants that provide most data (Fig. 1).
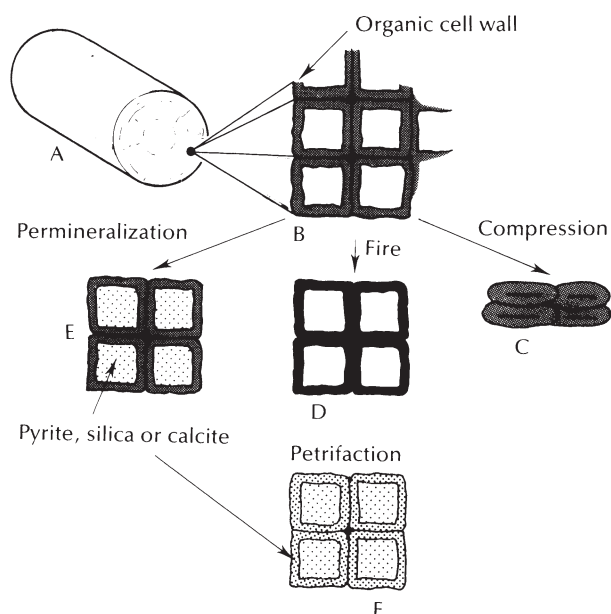
Fig. 1 Anatomical preservation of fossil plants. A, wood (plant cells lacking living contents). B, Detail of transverse section showing cell walls. C, compression with the closure of cell lumina. D, Conversion of cell wall to almost pure carbon by fire (charcoal). E, Early infiltration of cell lumina by permineralizing fluids with crystallization of calcite, silica, or pyrite (giving cell internal moulds). F, Decay of organic cell walls and secondary crystallization of calcite, silica, or pyrite to produce a petrification (giving casts of cell walls). (After Scott & Collinson 1983.)

Fusain

By far the most widely distributed anatomical mode of plant preservation, both geographically and stratigraphically, is fusain. It occurs widely in post-Silurian sediments (Scott & Collinson 1978). During burning, the cell walls are converted to pure carbon and above 300°C the middle lamella of the cell is homogenized with the rest of the cell wall (Cope & Chaloner 1985) (Fig. 2F). The cellular structure is beautifully preserved and may be studied particularly well by scanning electron microscopy (Fig. 2D, E); being pure carbon the cell walls are resistant to bacterial decay and acquire rigidity. Many smaller plant parts, including not only leaves and fruits but also delicate flowers, have been preserved in this way. Only larger plant organs break up during burning and because of physical damage during transport. Several important plants, including Cretaceous flowers and the earliest Carboniferous conifers, are preserved as fusain (Scott 1989).

Permineralization

Permineralization is where the cell spaces are infiltrated by mineral-rich solutions and precipitation takes place (Fig. 1E), preserving the organic cell walls (Schopf 1975). The most common precipitating mineral is calcium carbonate, followed by silica and pyrite. Calcareous permineralization is best known from the Upper Carboniferous coal balls of Europe and North America (Fig. 2B), but coal balls are also known from the Permian of China. Coal balls are limestone concretions encountered in coal seams, and are permineralized peat (Scott & Rex 1985). Calcium and magnesium carbonate infiltrated the peat before significant decay or compaction took place (see also Section 3.8.2), giving an exceptionally preserved fossil plant assemblage. Coal balls preserve fine anatomical and histological details and even cell contents such as starch grains, nuclei, germinating spores, gametophytes, pollen drops, pollen tubes and plant apices. Several hypotheses have been put forward to explain the occurrence of coal balls but the presence of marine bands overlying the coal seams strongly suggests a marine influence. The calcite is precipitated as radiating fibrous crystals which nucleate on cell walls (Scott & Rex 1985). Coal balls may occur singly and in rare cases may nearly replace a seam. Palaeoecological studies have identified changing plant communities in vertical profiles of coal balls through a seam.

Calcareous permineralizations may be found in a wide range of environments, including marine rocks, freshwater mudstones, siltstones, and sandstones (Fig. 2C), and are also commonly associated with basaltic volcanic rocks. Basaltic ashes often yield abundant anatomically preserved plants. Here the calcite was probably released from the breakdown of various minerals in the ashes.

Some of the most famous anatomically preserved plants are permineralized by silica (Knoll 1985; see also Section 1.2). The silica is usually the product of volcanic activity, but in rare cases silica permineralizations are found in marine radiolarian cherts. Both peats (Fig. 2A) and individual plants may be preserved in this manner and the Early Devonian Rhynie chert is a good example.

Occasionally, upright trunks in fossil forests are preserved, such as the Purbeck fossil forest in southern England. Often the original cell walls are also replaced in minute detail by a second generation of silica, forming a true petrification where no organic material remains (Schopf 1975) (Fig. 1F). The Triassic Arizona fossil forest and that from
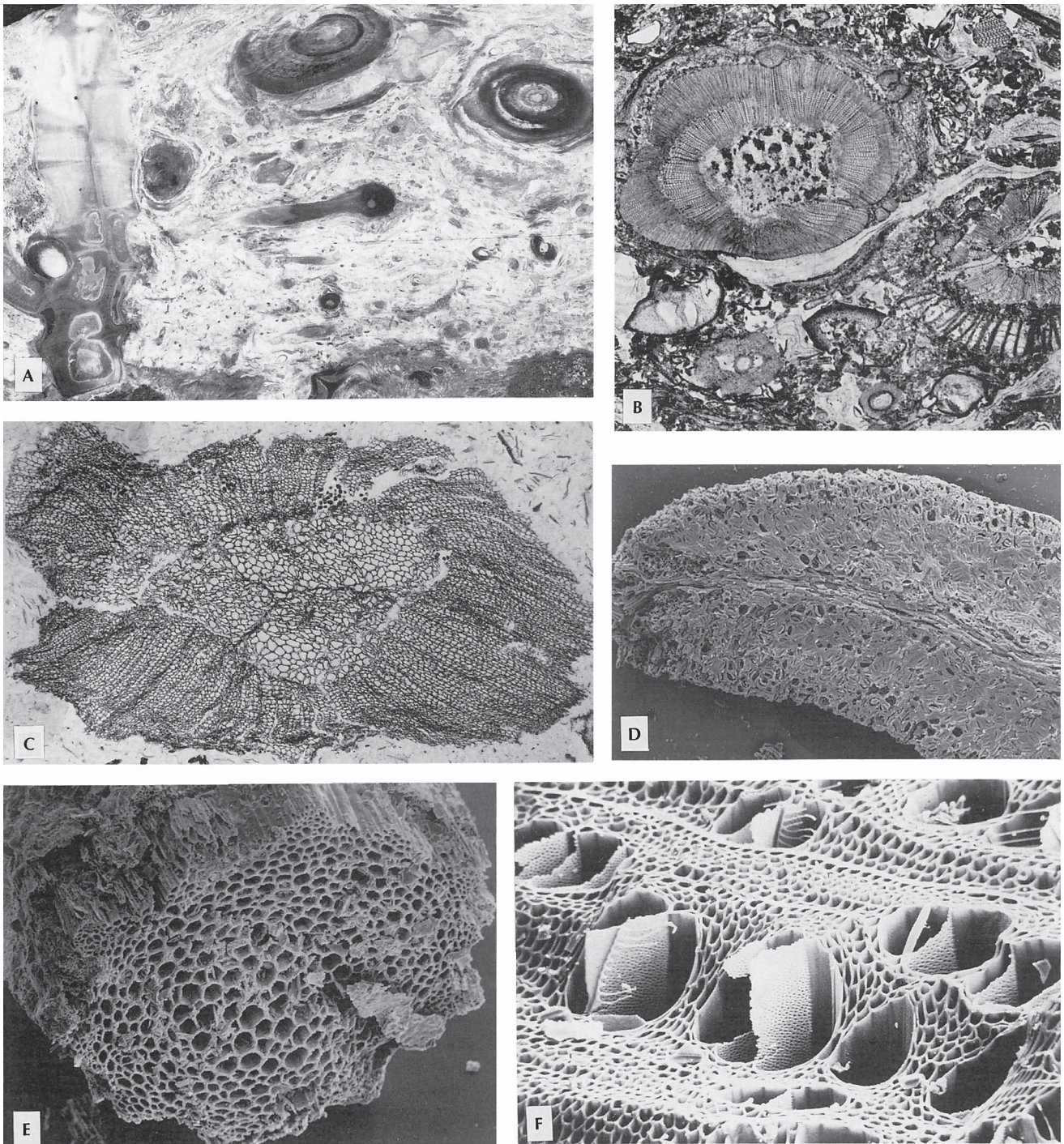
Fig. 2 Anatomically preserved fossil plants. A, Siliceous permineralized and partly petrified peat (× 1) composed mainly of the seed plant *Glossopteris* with branches showing growth rings and its roots (*Vertebraria*). Permian, Bowen Basin, Australia. (From Collinson & Scott 1987.) B, Carboniferous coal ball (× 2). Calcareous permineralized peat showing pteridosperm and fern axis with stigmarian rootlets, Westphalian A, Lancashire. (From Scott & Rex 1985.) C, Calcareous permineralization of pteridosperm stem, *Stenomyelon tuedianum* (× 10) from non-marine calcareous sandstone, Lower Carboniferous, Scotland. D, Scanning electron micrograph of fusainized leaf of the Lower Cretaceous fern *Weichselia* (× 30) from the Isle of Wight, U.K. E, Scanning electron micrograph of fusainized xylem cylinder of the herbaceous lycopod *Oxroadia* (× 10) from the Lower Carboniferous of Donegal, Ireland. (From Scott & Collinson 1978.) F, Scanning electron micrograph of modern beech charcoal (*Fagus*) after a man-made fire on Box Hill, Surrey, showing fine preservation of vessel-to-vessel pitting (× 200).

Yellowstone National Park (Tertiary) are good examples of this type of preservation.

Plant compressions often show partial permineralization by pyrite. Pyrite may form in stagnant conditions and is often associated with bacterial activity (see also Section 3.8.3). It may fill cell spaces and often occurs as framboids. In many cases several generations of pyrite are present which have infiltrated spaces left by decaying organic material. Complex casts and moulds of cell walls may be produced and may be difficult to interpret (Grierson 1976). In some cases the pyrite has been converted to limonite. Permineralized plant compressions are especially useful as they provide data on both morphology and anatomy.

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3.11 Taphonomy of Fossil-Lagerstätten

3.11.1 Overview

A. SEILACHER

Terminology and goals

The term 'Fossil-Lagerstätten' (singular Lagerstätte) is derived from the German mining tradition. 'Lagerstätte' is any rock or sedimentary body containing constituents of economic interest. Accordingly, a Fossil-Lagerstätte is any rock containing fossils which are sufficiently well preserved and/or abundant to warrant exploitation — if only for scientific purposes. The problem with this term is that it defines no boundary. Just as low-grade mineral deposits may become economic as market prices rise, so almost any fossiliferous rock may rise to the level of distinction in the eyes of an inquisitive researcher.

What matters here is the concept behind the term. Basically, the preservation of any fossil is an exceptional event that deserves our attention. As Raup and Stanley (1978) pointed out, a single square metre of sea floor could, during a few million years, produce enough shells to swamp the museums of the world, were all of them to be preserved. Also the calcium budget of the ocean would rapidly collapse without taphonomic recycling.

Since, however, we cannot hope to solve the case history of every single fossil, our attention focuses on occurrences that are extraordinary by geological standards. Nevertheless, we should not treat them as a separate class of rocks, but as end members of related groups of sedimentary facies, different only in that their additional palaeontological information may reveal interesting details about the environmental, depositional, and diagenetic history of the whole guild. Admittedly, this has not always been the view of collectors. Well preserved fossils have an attraction of their own and may reveal new

palaeobiological details in isolation from their geological context. However, as in archaeology, controlled excavation methods are gradually replacing the old treasure-hunting approach.

Given that preservation is not random, extraordinary fossil occurrences (the term 'biota' should be avoided when considering taphonomic conditions) should fall into genetic groups, defined with reference to typical examples. In the classification outlined in Fig. 1, concentration deposits and conservation deposits are distinguished as main categories (see also Seilacher *et al.* 1985). They are discussed below, proceeding from the more normal to the extreme cases.

Concentration deposits

Of the two main categories, *concentration Lagerstätten* are the less spectacular group because the quality of individual preservation may not be extraordinary in any way. But preservation is unusual not only if soft parts are preserved; the episodic prevention of hard part recycling may be just as noteworthy.

For example, to explain the common *coquinas*, in which the shells of gastropods, burrowing bivalves, or ammonites have accumulated, as representing periods during which the particular community thrived more than usual would be unrealistic. All three mollusc groups have aragonitic shells, which are chemically unstable and would have been destroyed by the combined action of shell borers, algae-nibblers, and dissolution, had they been lying unprotected on the sea floor for thousands of years (see also Sections 3.3, 3.8.1).

In a famous *ammonite coquina* in the Middle Jurassic of the Normandy coast, the shells are so perfectly preserved that they still have a nacreous lustre (Fürsich 1971). Yet the decimetric bed contains a mixture of ammonites from two stratigraphic zones representing *c.* 2 million years! A combination of two processes was therefore required: (1) sedimentation to seal the shells, before they could become corroded, in a well buffered and non-cementing sediment; and (2) one or a few concentration and mixing events brief and gentle enough not to destroy the delicate shells. These contradictory conditions are met in mud bottoms below normal storm wave base, when sedimentation rate is reduced by transgression. But the site still had to be within reach of the effects of the few largest storms (in two million years!) that did the mixing and concentration by winnowing away the finest fraction, yet deposited enough mud on top of the tempestite to provide

a new seal. The association of these Normandy ammonites with large bivalves (*Ctenostreon*) is also important. Their thick valves and outriggers indicate that they were passive recliners on muddier sediments than are now preserved. But they also indicate that sedimentation rates were low and storms rare enough to allow such a lifestyle.

Another common class of multiple-event coquinas are *oyster beds* (Seilacher 1985). Significantly they consist always of reclining or mud-sticking soft bottom species. Since oysters have calcitic shells, it is probable that the embedding sediment was more corrosive than in the previous case and eliminated the aragonitic shells that should normally have been found in association. Also revealing is the accumulation of such oysters into mounds. It shows that the storm reworking involved little transport, so that preferred sites could grow up like Mesopotamian tells in spite of periodic destruction.

Still another kind of storm coquinas are *bone beds*, which commonly occur in the final stages of larger regression cycles (the Silurian of Ludlow; top of the German Muschelkalk), or in the initial transgression. Here an unusual concentration of phosphatic vertebrate remains occurs, usually in a matrix of coarse sand or small lithoclasts. The idea of a mass mortality (as during red tides) would again be misleading, because, along with teeth and ganoid fish scales, there is a high concentration of coprolites. Some of them, as well as the few associated bones, show ancient fracture surfaces that are angular — different from the way the fresh objects would have broken. In this case the biomaterials were not only sealed in the sediment between reworking events, but also became *prefossilized* by early phosphatization (Section 3.8.4). This indicates that the original host muds were anoxic — although no sedimentary clues to this survived the final storm.

This theme extends to include coquinas made up of crinoid remains (originally consisting of high magnesium calcite stereom that may become prefossilized into more stable calcite and into massive crystals), or to brachiopod and trilobite coquinas. In all cases early diagenesis is likely to have played a role, but also to have considerably distorted the original spectrum of the fauna (see also Section 3.8.1). Nevertheless, such beds provide us with valuable information about sedimentary regimes, both in the background facies and during perturbation events.

Not all concentration deposits are stratiform. In terrestrial, but also in marine environments, we

may find local concentrations of fossils in protected cavities — varying in size from body chambers of ammonite shells to fissures and caves. Such *concentration traps* provide primarily mechanical protection, but they may also shield their contents from diagenetic dissolution, either by inducing early concretion formation or by buffering the pore-water.

Conservation deposits

In this case it is not the quantity but the individual quality of preservation that matters (see following sections). Some of the most famous conservation deposits (e.g. Solnhofen; Section 3.11.7) are in fact rather barren. To appreciate what is going on, we must consider some of the processes that cause unusual preservation.

Preservation processes. Normally, carcasses quickly decompose through the activities of scavengers and microbes. As a result, soft parts are lost and composite skeletons disarticulate. But also the organic components of the skeletal parts (bone collagen, periostracal coating of mollusc shells, chitin of arthropod cuticles; lignin and cellulose in plants) will eventually be consumed by microbes.

The incompleteness of this biological recycling (*necrolysis*; Section 3.1) is what makes for unusual preservation. Causes vary from case to case, but they encompass all the methods that humans use to keep their food from decomposing: in the Pleistocene, mammoth carcasses were deep-frozen in clefts in the glacial permafrost of Siberia, while a contemporary woolly rhinoceros in Galicia became pickled in a salty oil swamp, and ground sloths in South American desert caves were mummified by desiccation.

On a smaller scale, Tertiary insects became sealed in resin that matured into amber (Section 3.11.9) — a material whose low density allows for secondary concentration into sedimentary placers. Other insect remains were saved from destruction by being enclosed in the excrement of their consumers. In low oxygen lithotopes this matrix was prone to early bacterial phosphatization. Since the resulting coprolites are heavier than ordinary sedimentary particles, they again tend to form secondary placers, which facilitate the search for insects in them.

Bacteria, however, may also be a positive factor. They were probably responsible for the selective phosphatization of small chitinous arthropods in the Cambrian 'Orsten' (Section 3.11.3), which can be freed from their calcareous matrix by etching, without damage even to the fine setae. A similar interaction appears to be involved in the preservation of vertebrate skin contours of aquatic vertebrates (Wuttke 1983). Bacterial pyritization is another process that may selectively preserve small arthropods, although this process is more familiar in ammonites, whose empty chambers became lined with framboidal pyrite before the aragonitic shell was dissolved.

The examples cited so far reflect localized preservational conditions, which could be grouped as *conservation traps*. In contrast, *stratiform conservation deposits* comprise larger rock units in which incomplete necrolysis was a general phenomenon. Although local microenvironments and bacterial interactions are by no means excluded, these stratiform deposits call for larger scale causes, of which sediment smothering (obrution; Section 3.6) and anoxic conditions (stagnation) in the water column are most prevalent. In most instances both factors are involved, but the dominance of one or the other makes a great difference with respect to the ecological spectrum preserved. Therefore, the separation of *obrution* and *stagnation deposits* is well justified, however ambiguous it may be in particular cases.

Obrution deposits. In principle, smothering (Section 3.6) is an episodic process that affects mainly bottom-living organisms. But it is selective not only in an ecological sense, but also taxonomically. This is because some groups of animals are, by virtue of their general organization, more vulnerable to such catastrophes. Such a group are the echinoderms, probably because their ambulacral system communicates with the ambient seawater and becomes easily clogged by fine sediment. This means that sudden mud sedimentation can kill and preserve the victims simultaneously.

A classic example of echinoderm obrution is found in southern Germany at the very base of the Jurassic transgression (Rosenkranz 1971). Except for a few small oysters, the perfectly preserved thanatocoenosis contains exclusively echinoderms, in spite of different life styles: predatory starfish, scavenging brittle stars, grazing echinoids, and filter-feeding stalked crinoids. Their burial at the top of a thin basal conglomerate and below a decimetre layer of dark shale is significant. It indicates that a local hard bottom fauna (probably also containing members of other, less vulnerable phyla) was hit by a storm-generated mud fall. It is also possible that the change in sedimentation coincided
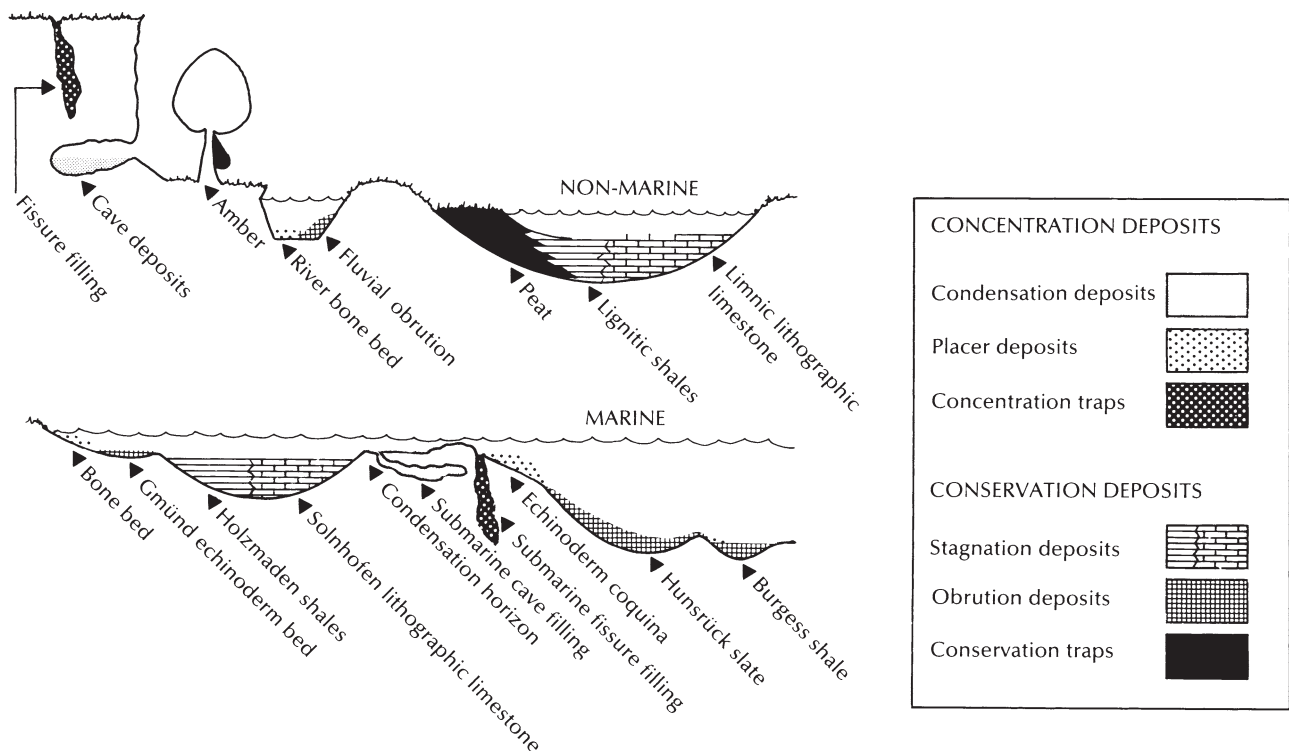
Fig. 1 Synopsis and classification of fossil-Lagerstätten. (After Seilacher *et al.* 1985.)

with a drop in local oxygen levels, because extensive bioturbation would otherwise have jumbled the buried echinoderm skeletons afterwards.

Obrutional echinoderm layers are known from many epicontinental carbonate basins (see also Section 3.6). They are always located between the coarser and the muddy phase of storm layers, but it is the amalgamated rather than the single-event tempestites in which they are most commonly found. To cite another example from southern Germany, the *crinoid beds* of the Upper Muschelkalk are particularly telling. Here the bed itself is a typical crinoid coquina representing the dissociated ossicles of many crinoid generations that flourished during a long interval of starved sedimentation. But it was only the terminal storm and the onset of heavier mud sedimentation that left an obrution deposit of perfectly preserved crinoids on top of the coquina of earlier populations. Echinoderm layers are also common in the Palaeozoic, whereas in other settings trilobites appear to have been a similarly vulnerable group (Section 3.6).

A more complex example of obrution is the Hunsrück Slate (Hunsrückschiefer) (Section 3.11.4). Lithologically the slates resemble black shales. They also preserve non-mineralized arthropod cuticles; but largely through pyritization (probably bacteria-mediated), which is absent in truly anoxic shales. On the other hand, the Hunsrück Slate contains trace fossils and other remains of a rather diversified autochthonous bottom fauna. Still, as in other obrution deposits, echinoderms are overrepresented.

Even more ambiguous is the dark-coloured Burgess Shale (Section 3.11.2), because in this case there are no trace fossils to attest to an autochthonous bottom fauna. Still, most of the well preserved soft-bodied organisms, as well as the trilobites, were probably benthic, while their perfect preservation indicates low oxygen levels at the place of their burial. This brings the Burgess Shale genetically close to the lithographic limestones of Solnhofen discussed below.

Stagnation deposits. While anoxia is usually associated with black, bituminous sediments, the famous *lithographic limestones* (Solnhofen; Section 3.11.7), however, may be cited as a striking counter-example. In spite of being very pure (and now white) limestones, they contain a predominantly water- and airborne fauna in perfect preservation. Traces do occur, but (except in better aerated marginal zones) they were produced by benthic organisms which were swept into the deeper abenthic

zone and died at the ends of their trackways. It is also remarkable that not only *Archaeopteryx*, but also fish skeletons show a characteristic dorsal curvature of the vertebral column. This phenomenon typically occurs in carcasses dried out on land. It could also have resulted from dehydration in a brine, which in this case might have been the reason for a stratified water column and anoxia in the basin centre.

Similar lithographic limestones are known from other geological levels. While showing varying preservational histories, most of them are associated with relatively small depressions formed by reef growth (e.g. Triassic, Alcover; Hemleben & Freels 1977), tectonic pull-apart (Cretaceous, Lebanon; Hückel 1970), or other processes (Hemleben 1977).

Bituminous shales, in contrast, may occur over very large areas, indicating that they needed vertical rather than lateral sediment supply. The Upper Liassic Posidonienschiefer (Holzmaden; Section 3.11.6) was laid down in an area covering large parts of Europe. Here the fauna is again predominantly pelagic. In contrast to Solnhofen, however, we occasionally find individual bedding planes covered by benthic fossils, whose perfect preservation (bivalves with the two valves still articulated in the butterfly position; echinoids with spines attached) indicates autochthonous burial — as in obrution deposits. These benthic events were originally thought to correspond to short phases of higher oxygenation. Savrda & Bottjer (1987; Section 4.19.4) suggested that they represent an epibenthic window that opened every time the system passed from dysaerobic through 'exaerobic' to anaerobic conditions, or vice versa. The probable reason is that under dysaerobic conditions, bioturbation produced a fuzzy interface and a nepheloid layer adverse to epibenthic life. As soon as bioturbation stopped, biomats could make the mud habitable for epibenthic specialists that either grazed on the bacteria or used them for chemosymbiosis before oxygen levels became once again too low.

Taphonomy, however, goes beyond necrolysis of soft parts and the sedimentological fate of the hard parts, to include diagenesis. Solnhofen and Holzmaden share a preservational history of ammonite shells that differs significantly from diagenetic pathways in either limestones or dark shales, to which either example is more closely related in a lithological sense.

In conclusion, the comparative palaeoecology and taphonomy of Fossil-Lagerstätten is a promising field of research, but one in which palaeobiology has to be linked with other disciplines, such as sedimentology, geochemistry, marine biology, and — last but not least — actuopalaeontology.

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3.11.2 Burgess Shale

S. CONWAY MORRIS

Introduction

Study of the soft-bodied biota of the Middle Cambrian Burgess Shale has opened a unique window into Cambrian life, providing new insights into the nature of the major adaptive radiations amongst metazoans, the relative importance of shelly taxa, and the role of different

trophic groups in the palaeoecology of early communities (Whittington 1985; Conway Morris 1989; see also Section 1.5). As originally exploited by C. Walcott between 1910 and 1921, the fossils came from two quarries on the west slope of a ridge that connects Wapta Mountain and Mount Field, near the town of Field, British Columbia. These excavations are in the basinal shales of the Stephen Formation, and the term 'Burgess Shale' is one of only local significance.

The lower Walcott Quarry, exposing the so-called Phyllopod bed, has been by far the most prolific source of fossils, yielding over 65 000 specimens (Conway Morris 1986). The higher, known as the Raymond Quarry, has been less productive but it provides a distinct assemblage distinguished by a lower diversity and different proportions of taxa in comparison with the Phyllopod bed. In addition, recent searches for comparable soft-bodied biotas elsewhere have yielded a rich harvest. In the vicinity of the Burgess Shale many new localities have been found. More importantly, discoveries elsewhere in the U.S.A., Greenland, and south China have led to a realization that there is a distinctive Burgess Shale-type fauna with a specific and recurrent character that ranges through the Lower and Middle Cambrian.

However, in terms of taphonomic information little is yet known about most of these deposits, and existing insights depend largely on studies of the Phyllopod bed. All the occurrences of Burgess Shale-type biotas share the character of burial in fine-grained sediment, often in catastrophic circumstances, but it would be unwise to assume that their taphonomic histories were similar.

Biota and sedimentary environment

Although studies of the Phyllopod bed biota, which includes both a benthic and pelagic fauna together with associated algae, are not complete, existing estimates of both the number of taxa and individuals (Conway Morris 1986) (Fig. 1) probably will not require radical revision. The benthic fauna (see Conway Morris 1979, 1986; Whittington 1985) is dominated by arthropods, of which only a small fraction are trilobites. In addition, other major groups include priapulid and polychaete worms, cnidarians, sponges, molluscs, echinoderms, and a variety of groups of uncertain taxonomic position (Conway Morris & Whittington 1985; Whittington 1985). As might be expected, the fauna is dominated by relatively few taxa, some nine species accounting

for about 90% of the total. The pelagic fauna is identified largely on adaptations suitable for either a planktic or nektic existence, such as prominent fins, streamlined bodies, or abundance of gelatinous tissue (Conway Morris 1979). In the Phyllopod bed there is strong evidence that much of the biota owes its preservation to catastrophic burial, including occurrence in graded beds, variable orientation of specimens relative to the bedding plane, and seepage of sediment between appendages or other extensions of the body. Because the laminations of the Phyllopod bed lack disturbance or other evidence of bioturbation, it is concluded that the environment of deposition was inimical to metazoan life, and this is confirmed by the exquisite preservation. The excluding factor was most probably anoxic conditions with H_2S, and an alternative possibility of hypersaline waters seems less likely because the specimens do not show obvious osmotic shrinkage or swelling.

The biota clearly lived elsewhere, because it was transported into a hostile environment, and it is useful to recognize this pre-slide environment (Conway Morris 1986). Its exact location is conjectural, but it is probably significant that all the soft-bodied localities in the Stephen Formation, including the Phyllopod bed, were deposited in relatively deep water immediately adjacent to an enormous carbonate bank which rose vertically and acted as a rim to extensive carbonate shoals and lagoons that extended hundreds of kilometres to the east. There is no evidence that any substantial fraction of the biota was derived from the reef top or margins, and it is likely that the pre-slide environment was also adjacent to the reef base. There is also some evidence that the distance of transport between pre- and post-slide environments was relatively small, perhaps a kilometre or so. This figure is based on inferences of local palaeotopography, inferred position of the photic zone relative to the post-slide environment, and survival of partially decayed specimens whose delicate nature could survive only limited transport.

Taphonomic history

The taphonomic history of the Phyllopod bed biota began, therefore, with the failure of the sea bed and its descent towards the post-slide environment. The area of sea floor may have been small, and additional specimens may have been trapped *en route*. As the flows were probably rather weak, extensive erosion and scouring out of the infauna
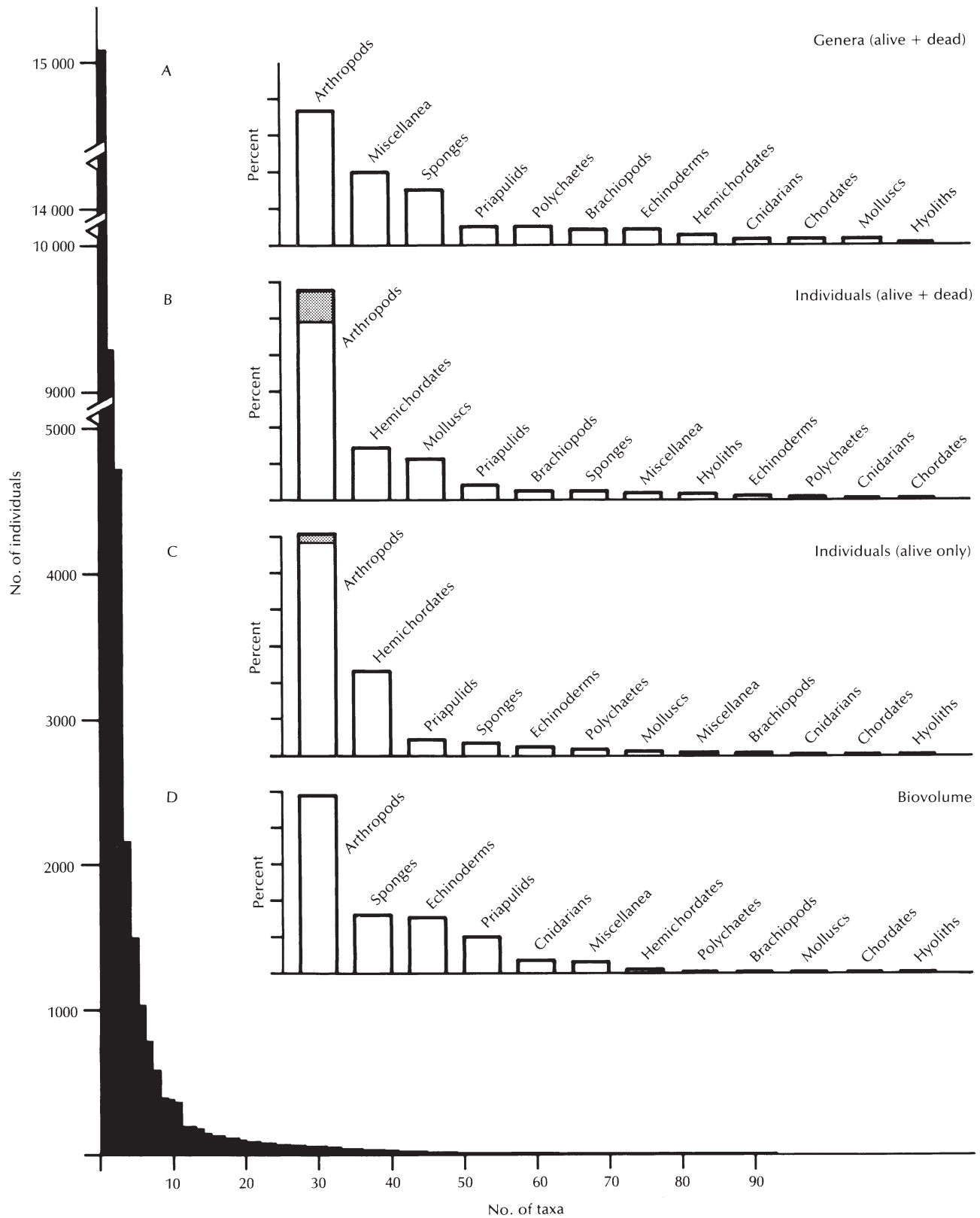
Fig. 1 Frequency distribution of the 93 species that contribute to the benthic community of the Phyllopod bed. Note characteristic 'hollow curve' distribution, and also breaks in scale of ordinate. Inset histograms show relative percentages of the major groups in the Phyllopod bed. A, Genera. B, Individuals, alive and dead (i.e. empty exuviae). C, Individuals alive at the time of burial. D, Estimated biovolumes. Stippled zone in arthropod column represents proportion of trilobites.

seems unlikely, but addition of epifauna and pelagic elements that had strayed close to the sea bed probably occurred. However, other pelagic elements may have descended into the post-slide environment, and there is little doubt that the sampling of this assemblage is very incomplete.

An important principle is that although the benthic flows contained many specimens alive at the time of transport, it also carried a cargo of resistant skeletal parts that had either been discarded (e.g. by ecdysis in trilobites) or remained on death (e.g. in brachiopods, monoplacophorans, and hyoliths). If an accurate census of the original living community is to be undertaken, it is, of course, necessary to subtract these exuviae and empty shells from the specimen totals (Conway Morris 1986). In the case of hyoliths, with attached opercula and helens, and some inarticulate brachiopods with mantle setae extending beyond the valve margins, it is possible to establish whether the individual had been alive at the time of burial. In other cases, such as the monoplacophorans, it is not possible to determine vitality. However, by making reasonable assumptions it can be shown that the shelly component was an insignificant part of the living community, perhaps as little as 2%.

Reasons for death are probably linked to arrival in the inhospitable post-slide environment, but it is likely that much of the fauna was either stunned or dying by the time of deposition. This is because animals placed in an anoxic environment often coil tightly as they enter a metabolic stasis; this feature has not been observed in the Phyllopod bed specimens. Moreover, the lack of evidence for escape activity also supports the notion that the fauna was incapacitated during transport.

In the post-slide environment the majority of specimens were buried, but occasional individuals that show scattering of parts may have lain on the sea floor, where they were disturbed by weak currents. After burial decay commenced, and this is best seen by a dark stain that surrounds an individual and appears to represent body contents that oozed out into the sediment (Whittington 1985). However, decay was evidently limited and, for reasons that are not understood, the processes of fossilization began.

Diagenesis. At present the soft parts of fossils are composed of carbon films (Butterfield 1990) coated by silicate films, principally chlorite and potassium micas (Fig. 2A). In terms of the hard parts, those of calcareous organisms are replaced by similar silicates, although in some cases pyritization has been extensive (Fig. 2C). However, phosphatic species, including the inarticulate brachiopods (Fig. 2B), retain their original composition, while in some cases the sponges retain the siliceous composition of their spicules (Fig. 2D). In many soft-bodied Lagerstätten the role of bacteria is being realized now as a key step in exceptional preservation, especially in the form of coatings that may be subject to rapid mineralization. Although their role in phosphatization has received particular attention (Section 3.11.2), recent work has shown how iron aluminium silicates can also arise during microbial activities (Ferris *et al.* 1987). Fossilized bacteria are now widely known, but have not been recognized

Fig. 2 Back-scattered electron micrographs of Burgess Shale fossils. A, *Eldonia*, surface with potassium mica (dark) and a coating of calcite (light), with a nodule of barium sulphate (very bright), × 65. B, Transverse section of inarticulate brachiopod (*Dictyonina*) with original phosphatic shell and blades of potassium mica, × 125. C, Transverse section of trilobite (*Olenoides*) with exoskeleton partially replaced by pyrite (very bright) enclosing calcite (grey) and elsewhere silicates (light coloured chlorite and dark potassium mica), × 70. D, The sponge *Choia*, surface showing spicules composed of silica and scattered nodules of cerium phosphate (very bright), × 160. (Photographs based on unpublished work with K. Pye.)
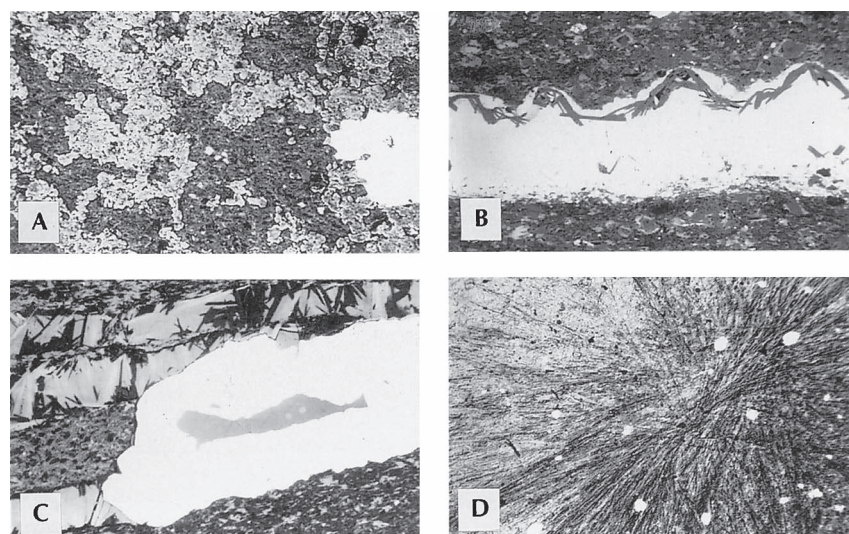
in the Phyllopod bed, perhaps being obliterated during subsequent diagenesis. Indeed, the diagenetic alteration of the Burgess Shale has only received limited study, but in addition to the changes in the silicates, nodules of barium sulphate (Fig. 2A) and cerium phosphate (Fig. 2D) also formed.

The taphonomic history of the Phyllopod bed continued with increasing depths of burial beneath substantial thicknesses of younger sediments. Thrust sheets (including the Cambrian sections with the Stephen Formation on the Simpson Pass thrust sheet) were propelled eastwards as part of a major orogeny during the Mesozoic to Early Cenozoic. Associated with these movements was the development of a strong penetrative cleavage in the argillaceous units. More basinal equivalents of the Stephen Formation were thus affected, and were it not for the massive dolomites of the Cathedral Escarpment providing a tectonic shadow zone, the soft-bodied localities adjacent to this reef would have also been deformed, making recovery of fossils impossible. The final stage of taphonomy, that of its discovery, is to the credit of Walcott, whose chance stumbling on this superb fauna has answered some questions, but set many more.

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3.11.3 Upper Cambrian 'Orsten'

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Introduction

The Upper Cambrian Alum Shale of southern Sweden first yielded small arthropods with preserved cuticular organs in 1975. Since then, a large variety of such fossils has been recovered at 22 localities from at least five trilobite zones or subzones. They have been discovered over a wide area in Northern and Central Europe, mainly in Västergötland (Kinnekulle, Hunneberg, Falbygden), Skånia, on the island of Öland, in a borehole in northwestern Poland, as well as in drift boulders throughout northern Germany. The fine preservation (Fig. 1) permits detailed comparison not only between the various 'Orsten' animals, but also with extant arthropod orders. Thus the material is important for considerations of the phylogeny of early arthropods and of the relationship between the Recent orders.

Sedimentary environment

'Orsten' is a sulphurous anthraconitic limestone, occurring either as concretions of about 0.1–2.0 m in diameter, or as large flat lenses within the Alum Shale, which may appear as beds in small outcrops. It is commonly banded, because of the fossil layers containing an abundant and varied trilobite fauna represented mainly by exuvia, and/or because of an alternation of lighter, often more sparitic bands with darker, finer-grained ones. There is no apparent difference in the composition of the fauna from either lithology. In general the limestone is rather carbonaceous and often petroliferous. When dissolving such a sample in acid, the oil usually concentrates on top of the liquid. Less carbonaceous beds are beige to light grey. Quartz grains are lacking in both the Alum Shale and the 'Orsten'. Most sediment deposition was under very low-energy conditions. Finely dispersed pyrite indicates the absence of oxygen at the time of deposition. Higher energy sediments composed of fossil hash are rather limited and have not yielded specimens with preserved soft integument.

There is an abundance of calcareous shelly remains; phosphatic fossils are less frequent. Conodonts generally have a dark brown–blackish
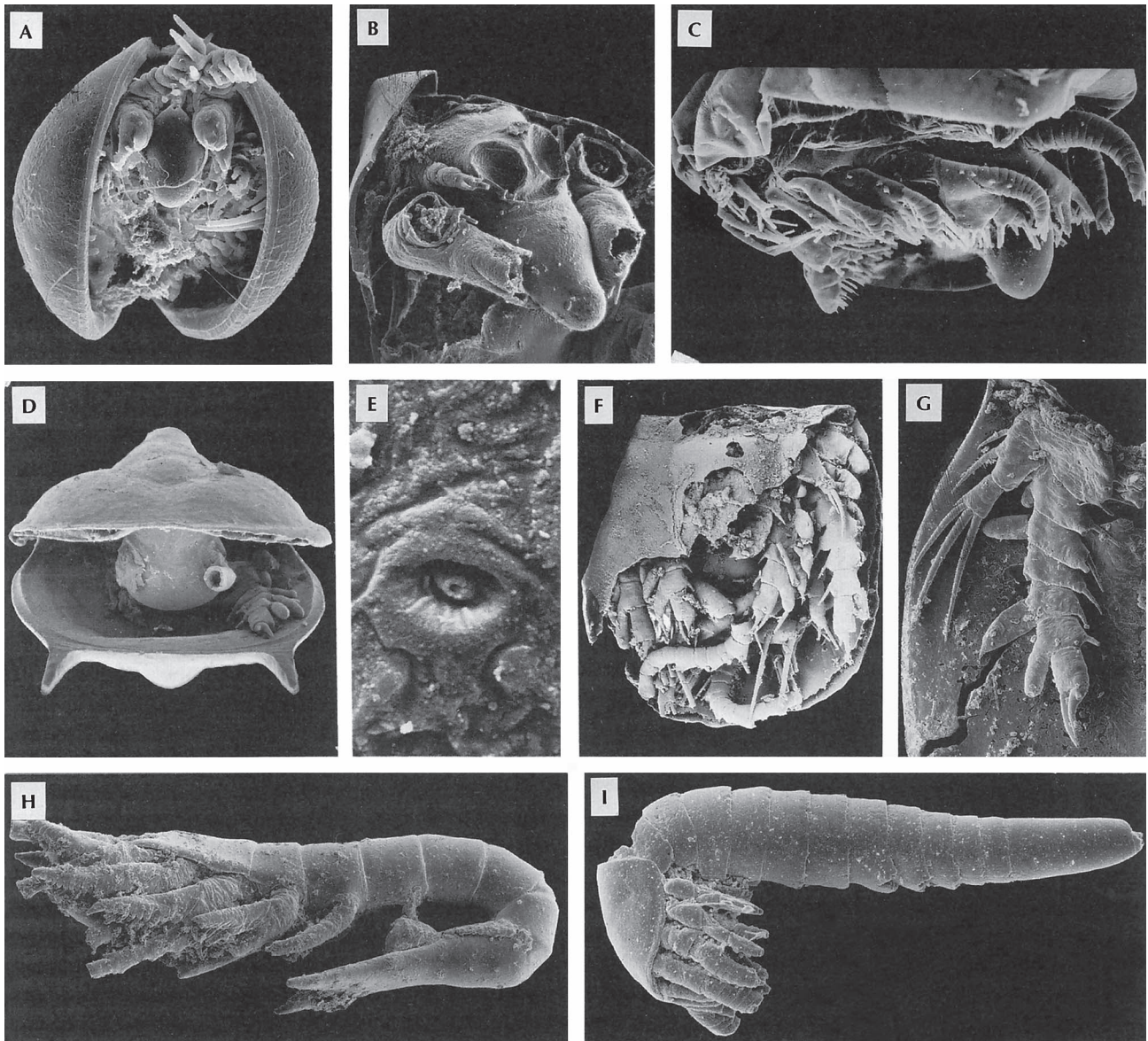
Fig. 1 Examples of 'Orsten' arthropods from the Upper Cambrian of Sweden. A—C, Ostracoda. A, *Falites*, a small growth stage, probably just hatched (× 180). (From Müller 1979.) B, *Hesslandona unisulcata*. Detail with the naupliar eye on collapsed labrum. Small first and large biramous second antennae (× 77). (From Müller 1982.) C, *Vestrogothia spinata*. Preadult stage with six pairs of completely preserved appendages (× 155). (From Müller 1979.) D—G, *Agnostus pisiformis*. (From Müller & Walossek 1987.) D, Larval stage 1b. Hypostome (centre) with proximal parts of antennulae between cephalic and pygidial shields. Left first trunk appendage also evident (× 77). E, Pore on a holaspid (× 1695). F, Larval stage 2a with the appendages snugly packed between the shields (× 220). G, Trunk appendage of meraspid. Note the fusion of proximal podomeres of endo- and exopodites (× 175). H, *Martinssonia elongata* stage 4 (× 77). (After Müller & Walossek 1986.) I, *Skara minuta* (× 90). (After Müller & Walossek 1985 (Reproduced with permission from the *Lethaia* Foundation.)

colour corresponding to the Colour Alteration Index 4—5 (Section 6.2.5). This colour can be produced experimentally by heating the rock to about 300°C. Recrystallization has destroyed the texture in the limestone.

Diagenesis

Dissolution of the limestones in weak acetic acid yields two different types of phosphatic fossils. The first consists of the primarily phosphatic hard parts

of groups such as conodonts, inarticulate brachio-pods, phosphatocopine ostracodes, and various problematica. The other type includes secondarily phosphatized fossils or fragments. A thin coating of phosphate may be deposited on the entire surface, in some cases repeatedly. Alternatively, the original chitinous substance may have been replaced by phosphatic matter. Preservation of this kind is gen-erally rare and, except for certain somewhat more widely distributed phosphatocopine ostracodes, most taxa are restricted to a few samples only. The detail preserved by phosphatization varies con-siderably within samples, let alone between the various occurrences.

The mechanism of phosphatization has not yet been determined (see also Section 3.8.4). It is un-likely that it occurred in the open sea. Many of the 'Orsten' fossils seem to have been phosphatized prior to decay. As even the finest structures have survived, the animals are assumed to have been buried alive or immediately after death.

Extensive picking of residues has produced sev-eral thousand specimens with preserved soft in-tegument. Ostracodes such as *Hesslandona unisulcata* (Fig. 1B) are represented by more than one thousand specimens. On the other hand, some other arthro-pods have yielded only hundreds, tens, or even single individuals. In at least some cases, this dif-ference in preservation potential between the taxa may be attributed to patterns on the cuticle or to variations in original abundance.

The extremely fine preservation even of minor details is due to secondary phosphatization of the body wall, which in most (or all?) cases was chitin-ous. This may explain the restriction of such preser-vation to arthropods or arthropod-like organisms and to certain worm-like remains, possibly annelids (see also Section 3.8.4). Other organic matter be-longing to an unidentified phylum was not phos-phatized at all. The occurrence of internal soft organs is rare.

Most specimens are three-dimensional and show little if any distortion. Others are wrinkled, and were collapsed or inflated before burial. This is perhaps the result of osmotic differences between body liquid and seawater. Flattening or stretching is not evident, and individuals were not compressed significantly after deposition. This enhances the scope for detailed study compared to that afforded by flattened fossils such as those of the Burgess Shale (Section 3.11.2).

Biota

Most representatives of the 'Orsten' arthropod as-sociation appear to have been benthic or epibenthic. Their body and appendages indicate that the ma-jority were actively swimming. Forms with legs suitable for walking have not been observed.

A suitable habitat may have been a flocculent bottom layer with a high content of nutrients and low currents. The various morphotypes developed adaptations to different life strategies. They may have lived at different levels on or within the soft bottom layer. The 'Orsten' arthropods represent a thanatocoenosis (death assemblage) (see also Section 3.5). Some of them may be autochthonous, while others have been introduced.

The most widespread soft-bodied fossils are the phosphatocopine ostracodes (Fig. 1A-C). Their ap-pendage morphology indicates that they were filter feeders. *Dala peilertae* and *Rehbachiella kinnekullensis* may have been similar in this respect.

The Skaracarida were cephalomaxillipedal sus-pension feeders. The more than 100 specimens of the two species of *Skara* (Fig. 1I) represent only adult stages.

Bredocaris admirabilis was most likely a suspension feeder. The retention of many larval features into the adult stage indicates that both larvae and adults fed largely on the same source. This is corroborated by the common occurrence of larvae and adults in the same samples. The paddle shape of thoracopods indicates a swimming mode of life. The habitat may have been on, or closely above, the flocculent bottom layer.

Martinssonia elongata (Fig. 1H) was a bottom dweller that stirred up food with its limbs and its pleotelson-like tail. 'Larva C', a rare form with affin-ities to the Chelicerata, was ectoparasitic.

The trilobite *Agnostus pisiformis* (Fig. 1D-G) is represented by growth stages from the first instar up to the first holaspid (Müller & Walossek 1987). Although their calcareous exoskeletons are often so abundant as to be rock-forming, phosphatized specimens are extremely rare. *Agnostus* shows characters quite different from the metameric trilobites.

The organization of the Upper Cambrian arthro-pods as a whole is surprisingly well advanced. Although they are primitive in important respects, many are closely comparable with Recent taxa, even if a direct evolutionary connection is not very likely. In the absence of evidence for the origin of the arthropods in the Precambrian, it is more likely that

the major evolutionary steps were condensed into a time-span of about 80 million years in the Lower and Middle Cambrian.

Small arthropods with preserved soft integument, mainly ostracodes, also occur elsewhere. Similar phosphatization has been found in the Lower Cambrian limestone of Comley, U.K., the Upper Devonian cephalopod limestone in the Carnic Alps, Italy, the Triassic of Spitsbergen, and in the Lower Cretaceous Santana Formation, Brazil. It is likely that further occurrences will be discovered if the techniques used in processing 'Orsten' limestone are more widely applied to such lithologies.

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3.11.4 Hunsrück Slate

J. BERGSTRÖM

Introduction

The Hunsrück Slate (Hunsrückschiefer) occurs mainly in a belt almost 150 km long, south of the River Mosel in West Germany. It is Early Devonian (Early Emsian) in age. Due to synsedimentary tectonism the thickness varies from less than 200 to 3000 m. In the northwest, 'Rhinean' shallow-water sediments are dominated by brachiopods; in the southeast are 'Bohemian' distal sediments with the 'classic' faunas. Much of the clay and silt filling the troughs was derived from a land area to the northwest. Sedimentary structures and trace fossils indicate a depth of more than 200 m (Seilacher & Hemleben 1966), while the well developed eyes of arthropods and vertebrates indicate that the water was probably not much deeper than this (Stürmer & Bergström 1973).

The Hunsrück Slate fossils are pyritized and often preserved as more or less flattened complete individuals. In addition to mineralized skeletal parts, the pyritization has affected unmineralized skeletons and true soft parts (Fig. 1B, C). The latter include cnidarian polyps, arthropod muscles and intestines, and soft parts of annelids and molluscs. The sediment has been transformed to a slate as a result of the Variscan Orogeny, but the cleavage is commonly more or less parallel to bedding, so that the fossils are largely unaffected.

The Hunsrück Slate is a conservation Lagerstätte resulting from rapid burial (or obrution) (see also Sections 3.6, 3.11.4). The dark colour of the rock is partly due to organic carbon, but the sediment is basically a mineral clay and silt deposit.

Sedimentary environment

The average sedimentation rate ranged to a maximum of a couple of millimetres a year. Thus the various well preserved organisms must have been embedded not by normal sedimentation but by very rapid episodic burial. The animals buried in this way were probably alive in many cases; in others they may have been killed by the current transporting the suspended sediment (Stürmer & Bergström 1973; Kott & Wuttke 1987). This explains why many specimens are lying at a high angle to the bedding planes (Fig. 1A). It also explains the strong dominance of benthic organisms in the fauna. A large proportion of the specimens are complete and articulated. It is well known that echinoderms disintegrate within hours of death, and their excellent preservation also indicates rapid burial. Judging from the vertical and lateral distribution of faunas, such events seem to characterize much of the up to 3000 m thick Hunsrück Slate, although fossils are abundant only in the Bundenbach area. Few of the benthic animals seem to have been able to avoid
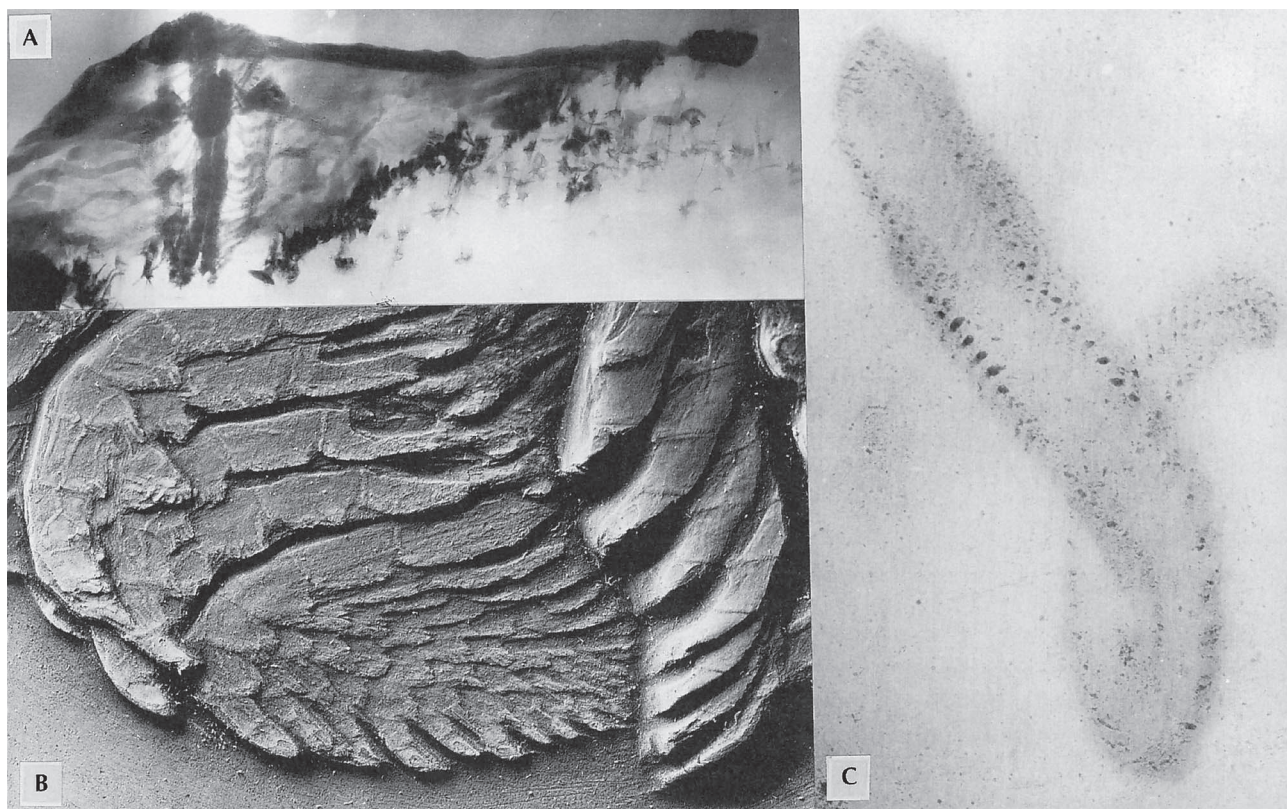
Fig. 1 A, Radiograph of undescribed somasteroid species from Bundenbach. Part of single arm ripped off from rest of body; note isolated skeletal elements on the lower side. The arm is much shortened due to deposition at an angle to sediment surface; tip of the arm above. Contrast due to pyritization of skeleton, × 0.9. (After Stürmer *et al*. 1980.) B, *Phacops* species from Eschenbach. Careful preparation has exposed fine details of pygidial and four thoracic legs of the right side, × 2.9. (Photograph courtesy of S. Stridsberg.) C, Undescribed annelid worm from Bundenbach. Segmental pattern indicated by strongly pyritized chaetae, × 3.5. (Radiograph courtesy of W. Stürmer; no. 12852, Senckenberg Museum, Frankfurt am Main.)

being caught by the suspension currents. Occasionally the currents appear to have been powerful enough to tear bodies apart (Kott & Wuttke 1987) but these may have been weakened by partial decay. A good example of this is illustrated in Fig. 1A, showing a single arm of an undescribed new somasteroid echinoderm.

Part of the Hunsrück Slate sequence includes quite thin lenses and extensive laminae of silt. These are interpreted as indicating a distal density current or turbidite (Seilacher & Hemleben 1966). The undersides of the silt laminae show frequent signs of current activity, such as flute casts and tool marks. These features, in combination with trace fossil evidence, indicate sedimentation in basins in the shelf. The more homogeneous shale is devoid of diagnostic sedimentological features.

Diagenesis

The fossils are usually strongly compressed because of the fine-grained sediment. However, early pyritization has preserved much relief (Fig. 1B), more than in other argillaceous deposits, such as the Burgess Shale (Section 3.11.2). Deposition of small organisms, in particular at high angles to bedding, adds to the deformation caused by compaction. Sliding movements also occurred inside decomposing carcasses. In the arthropod *Cheloniellon*, for example, the ventral side has moved in relation to the dorsal, making the discrimination of the segments difficult (Stürmer & Bergström 1978).

Some authors have suggested that the pyrite was formed mainly in those parts of the animals which contained much organically bound sulphur, e.g. in

the shape of conchiolin, keratin, cystin, spongin, etc. (Fig. 1A, C). The microbial production of H_2S played an important role (Section 3.8.3). In many arthropod specimens the limbs are more extensively pyritized where they extend beyond the carapace, than where they are covered by it. This is probably mainly a function of the high surface area : mass ratio of the exposed limbs, which promotes the reduction of sulphates, compared with that of the main part of the body and adjacent structures.

Biota

In addition to one acritarch and 47 spores, about 400 species of macrofossils are known from the Hunsrück Slate (Mittmeyer *in* Stürmer *et al.* 1980). The fauna is dominated by benthic and nectobenthic species. Thus, echinoderms form the largest group with some 125 species, closely followed by molluscs with around 115 species. Of the molluscs, 92 species are gastropods or bivalves and 31 more or less heavily shelled cephalopods. There are 63 listed species of brachiopods, 31 arthropods, 17 vertebrates, 12 cnidarians, six tentaculite-like forms, six conularids, three bryozoans, one ctenophore, and one red alga. All the arthropods belonged to the benthos, and many of the cephalopods could have done so. The vertebrates are species of agnathans and placoderms which were flattened in life. The flattening provides good evidence that they lived on the substrate. In addition, there is a species of lungfish. A few species form exceptions to this benthic association. These are six species of psilophytes, which must have been derived from a nearby land area, and one pelagic species of each of the hydrozoans and ctenophores.

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3.11.5 Mazon Creek

G. C. BAIRD

Introduction

The Mazon Creek area fossil localities in northeast Illinois yield a diverse biota of Middle Pennsylvanian plants, terrestrial animals, and numerous aquatic taxa including both estuarine marine and non-marine animals. This biota, preserved in sideritic concretions, includes the most important assemblage of soft and lightly skeletonized invertebrate animals known from the Late Palaeozoic (Nitecki 1979). Moreover, it also includes one of the most diverse land plant floras known from North America. Over 350 species of plants, 140 species of insects, and over 100 additional non-marine taxa, including bivalves, millepedes, centipedes, scorpions, spiders, eurypterids, xiphosurans, branchiopods, ostracodes, shrimp-like crustaceans, fish, and tetrapods comprise the non-marine component which is termed the Braidwood Biota (Baird *et al.* 1985a). Estuarine marine organisms, comprising the Essex fauna, are similarly diverse and varied; this component includes medusae, hydrozoans, a siphonophore, chitons, cephalopods with soft parts, diverse polychaetes and crustaceans, a xiphosuran, a holothurian, several agnathan vertebrates, numerous fish species, and various problematical taxa (Fig. 1).

Stratigraphy. Concretions containing the Mazon Creek fossils occur in the Francis Creek Shale Member of the Carbondale Formation which was deposited during the Middle Pennsylvanian Westphalian D stage. The Francis Creek Member is underlain by the widespread and commercially important Colchester (No. 2) Coal Member; strip mining and deep mining of this coal unit account for the numerous spoil dumps which are the usual collecting sources for these fossils. Where the Francis Creek is thin, it is overlain by the Mecca Quarry Member, a thin, fissile, black shale unit which is
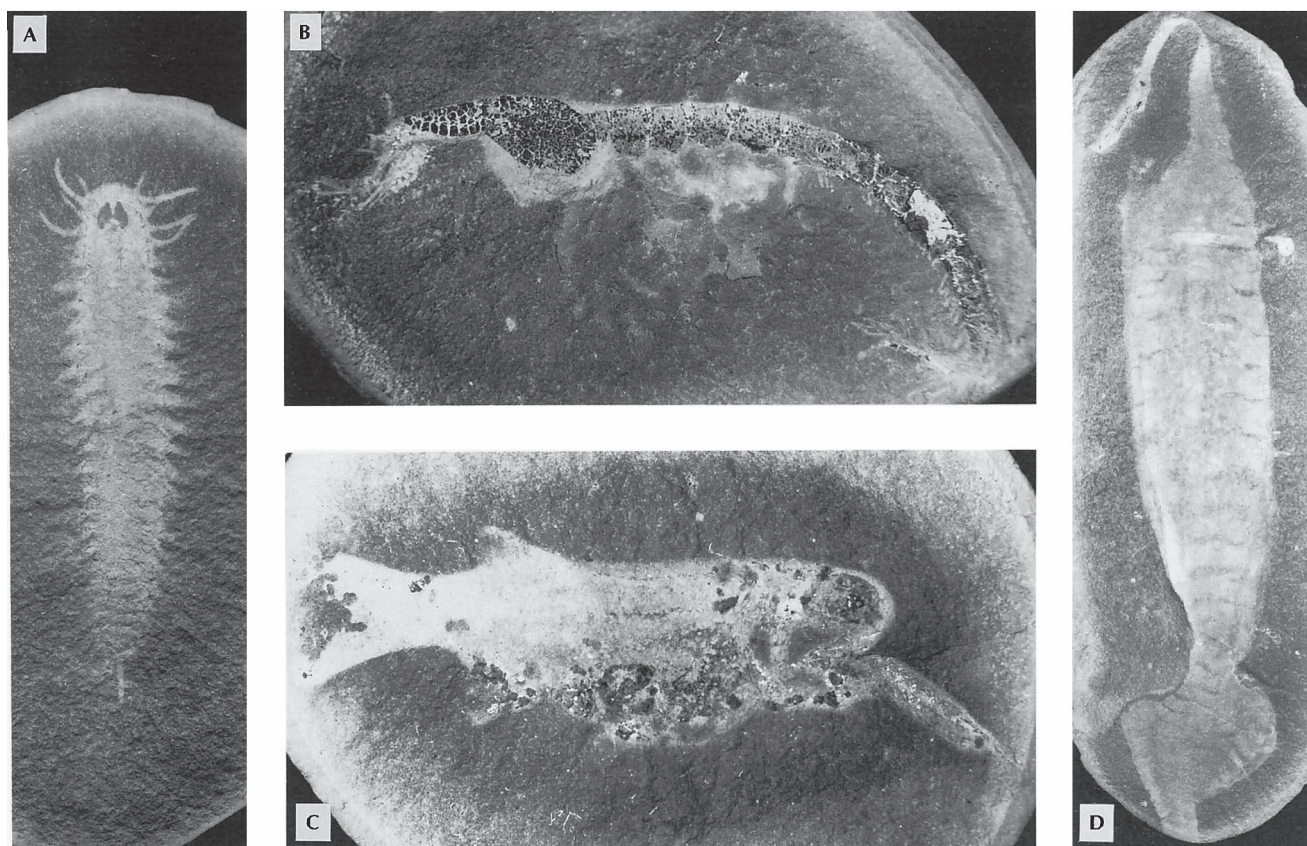
Fig. 1 Marine animals (Essex fauna) from Mazon Creek area, northeast Illinois. All specimens from a large strip mine 'Pit 11' near Essex, Illinois. A, Polychaete annelid *Fossundecima konecniorum* with conspicuous chitinous jaws, × 1.25. B, Phyllocarid crustacean *Kellibrooksia macrogaster*, × 1.4. C, Palaeoniscoid fish *Elonichthys peltigerus*, which has choked on an acanthodian fish, × 1.8. D, Problematic organism *Tullimonstrum gregarium* ('Tully Monster'), × 0.7. (All specimens courtesy of Northeastern Illinois University, Mazon Creek Paleontology Collection.)

locally famous for the occurrence of well preserved marine vertebrates; this unit is absent where the Francis Creek Shale exceeds 10 m in thickness.

The Francis Creek Shale is variable in thickness regionally, and is absent in many parts of Illinois. It reaches a maximum thickness of 25–30 m in northeast Illinois; in the Mazon Creek area it is composed of silty mudstone with local development of coarser deposits, particularly in the upper part of the unit. Fossiliferous sideritic concretions are characteristic of the thickest Francis Creek deposits, and they are usually common in its lowermost four metres. Thin (0–5 m) Francis Creek deposits west and southwest of the Mazon Creek area are composed of grey, argillaceous, and distinctly bio-turbated mudstone deposits which typically lack sideritic concretions (Baird *et al*. 1986).

Localities. More than 100 collecting localities for Mazon Creek fossils exist within the Mazon Creek area, which includes parts of Grundy, Will, Kankakee, Essex, and LaSalle counties. Natural out-crops of the fossiliferous strata are almost completely restricted to Mazon Creek itself near Morris, Grundy County. Virtually all remaining localities are spoil dumps of abandoned strip mines and underground mines exploiting the Colchester Coal. Most fossil collecting is done in strip mine areas, most notably in one large mine area ('Pit 11') near Essex, Illinois. Concretions are continually exposed as the back-piled tip heaps weather and erode; many of these nodules break open along the fossil plane by re-peated frost wedging, but others must be split with a hammer.

Sedimentary environment

The Francis Creek Shale Member in the Francis Creek area is believed to be an estuarine-deltaic deposit recording the progradational advance of

one or more major distributary systems into a shallow epeiric sea (Baird *et al.* 1985a). The presence of numerous thick, distributary channel sandstones with associated crevasse splay and interdistributary bay deposits indicates that an active coastal delta-distributary complex was present. Braidwood aquatic animals inhabited interdistributary bays and waterways bordering this delta complex.

The stratigraphic occurrence of Essex animals in the basal Francis Creek across much of the Mazon Creek area indicates that the delta prograded into a large marine water area. However, the diminutive character of most Essex taxa, the total absence of normal marine shelf organisms (such as corals, bryozoans, articulate brachiopods, trilobites, and crinoids), plus the character of the associated deposits, collectively indicate that Essex organisms inhabited a large river-influenced estuary (Baird *et al.* 1986). Examination of mudstone deposits associated with these organisms reveals the presence of distinctive cyclic repetitions of mudstone and siltstone laminae which appear to record sequential flood- and ebb-tide events within the estuary (Baird *et al.* 1985a).

Detailed census collecting at all Mazon Creek area localities shows that an abrupt boundary separates areas yielding abundant Essex animals from regions yielding no Essex taxa (Baird *et al.* 1985a); non-marine localities near the northeast margin of the census area are abruptly bounded by marine localities to the southwest. However, one-way mixing of plants and non-marine Braidwood animals into areas of Essex animal abundance does occur; this is believed to reflect southwestward (seaward) transport of non-marine taxa by currents from upstream sources (Baird *et al.* 1985a).

Diagenesis

Mazon Creek aquatic animals generally died as a result of episodic incursions of turbid freshwater during periods of flooding (Baird *et al.* 1986). Rapid sedimentation is indicated by engulfment of upright trees, the edgewise burial of plant leaves, and by occasional evidence of escape attempts by bivalves and other organisms (Fig. 2). The rarity of large animal specimens partly reflects a near-absence of large taxa and/or the successful escape of large animals, but it is also a result of the limited availability of interstitial iron and organic nutrients required to produce concretions of sufficient size to enclose large organisms.

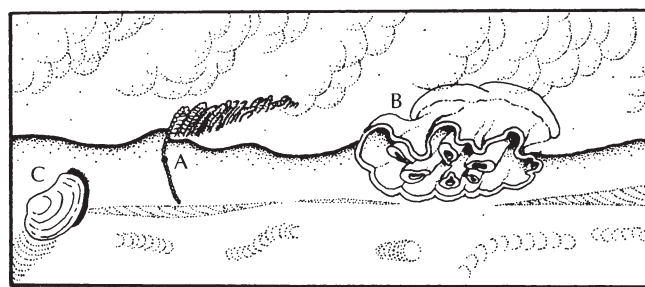Mazon Creek fossils are preserved as variably

Fig. 2 Burial of Mazon Creek organisms. Flood event with torrential sedimentation and incursion of freshwater. Organisms include: A, up-ended pinna of *Pecopteris*; B, partially engulfed medusoid *Essexella asherae*; C, bivalve *Edmondia* attempting to escape smothering. (From Baird *et al.* 1986.)

compressed moulds within concretions. Plant fossils occur as moulds infilled by calcite, kaolinite, or sphalerite with a residue of coaly organic material often present (Baird *et al.* 1986). Mollusc shells, cephalopod and chiton radulas, and holothurian pharyngial rings are also preserved as moulds. Medusae are typically composite moulds which reflect compressive superposition of top surface detail onto the lower surface following burial; convex-downward relief on such impressions reflects weight pressing (loading) of the jellyfish lower surface into subjacent muds (Fig. 2). Most arthropods and some worms retain thin surficial films of variably degraded organic cuticle.

Sideritic concretions enclosing fossils serve as a taphonomic 'window' through which important biological information can be obtained because synjacent mudstone deposits yield few well preserved fossils. These concretions formed very early following fossil burial; they contain up to 80% carbonate, indicating that they formed in water-rich surface muds (Woodland & Stenstrom *in* Nitecki 1979). Most Francis Creek concretions are believed to have nucleated around buried organisms prior to significant decay, and the growth of some may have been triggered or enhanced by decay processes (Fig. 3; see also Section 3.8.2). Precipitation of the siderite is believed to have commenced following depletion of interstitial seawater sulphate by sulphur-reducing bacteria; once it was exhausted, bacterial methanogenesis would have commenced, leading to siderite precipitation (Woodland & Stenstrom *in* Nitecki 1979). Rapid sedimentation, a weak or unsteady sulphate supply within the estuary, and the entrapment of iron and abundant
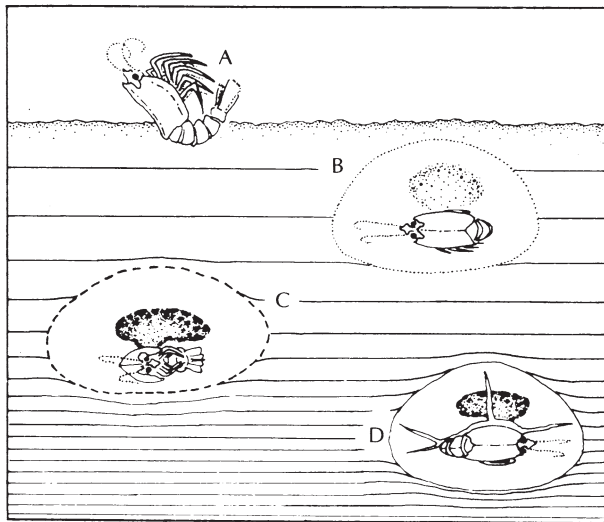
Fig. 3 Early diagenetic events. A, Burial of organism. B, Bacterial sulphate reduction proceeds in local decay centre ('gas vent' zone) above organism prior to depletion of interstitial sulphate. Subsequent bacterial activity produces siderite. C, Continued siderite precipitation hardens proto-concretion which resists compaction. D, De-watering of surrounding muds causes laminae to deform around nodule. Syneresis (de-watering) within concretion produces fractures which break preformed pyrite (or iron monosulphide) halo around decay centre. (From Baird et al. 1986.)

organic material, are believed to explain the abundance of sideritic concretions in this deposit (Baird et al. 1986).

A regional preservation gradient is observed within the area of Essex animal occurrence; preservation quality of jellyfish, shrimp, worms, and holothurians decreases to the south and west of Grundy, Will, and Essex counties. In eastern LaSalle County jellyfish occur as diffuse and often micro-burrowed impressions, and holothurian remains are sometimes identifiable only from the presence of the coherent pharyngial ring. In western LaSalle County body fossils are rare and the mudstone is highly bioturbated; slower sedimentation near the seaward margin of the delta complex, combined with extensive bottom churning by infauna, account for this poor preservation. Study of similar but younger deposits in Illinois shows that trace-fossil diversity increases seaward of deposits yielding Essex animals, but that body fossils are uncommon between regions of sideritic concretion abundance and normal marine, shell-rich sediments deposited far from shore (Baird et al. 1985b; Baird et al. 1986).

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3.11.6 Holzmaden

R. WILD

Introduction

The small village of Holzmaden is situated on the northwestern fringe of the Schwäbische Alb, about 30 km southeast of Stuttgart in Baden-Württemberg, West Germany. It lies in an area of Liassic sediments, of which the Lower Toarcian Posidonienschiefer (Fig. 1) contains an abundant, excellently and completely preserved fossil flora and fauna. Fossils have been known since the end of the sixteenth century, at first from Boll, later from the neighbouring Holzmaden region. In this area, which is protected, some quarries still work and fossils are discovered up to this day.

Sedimentary environment and diagenesis

The Posidonienschiefer at Holzmaden consists of 6—8 m of thick black bituminous marls and shaly marls with intercalated bituminous allochthonous limestones. The dark colour of the marls is caused partly by diffusely distributed pyrite and partly by organic material. In some layers the latter exceeds 10%, indicating that stagnant conditions persisted for a long period of geological time. The limestones, calcareous nodules and concretions, however, represent rapid deposition, as shown by obliquely or even vertically embedded uncompressed fossils.
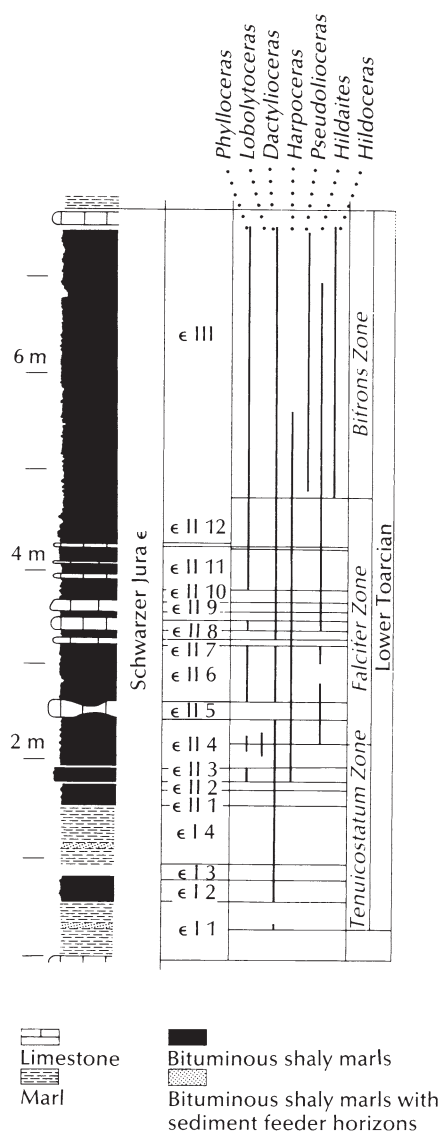
Fig. 1 Stratigraphy of the Posidonienschiefer and distribution of the stratigraphically important ammonites in the quarry G. Fischer, Holzmaden. (After Urlichs *et al*. 1979.)

Limestone
Marl
Bituminous shaly marls
Bituminous shaly marls with sediment feeder horizons

The marls are laminated over a distance of kilometres, as a result of an alternation of clay minerals and enriched organic material, consisting mostly of coccolithophorids. They were deposited slowly, primarily as low-density, water-enriched muds, which were later compacted to about 0.17–0.1 of their original thickness. During this early diagenetic process, the pore-water dissolved the aragonite and also partly the calcite of shells, or destroyed micro-organic hard tissues, so contributing to the lamination (Einsele & Mosebach 1955). Compaction also resulted in the condensation of shell fragment layers (ε II 3, ε II 12). The enclosed organisms were compressed, broken and flattened, except where they are preserved in calcareous nodules, which originate from the decaying organic material. These layers are often enriched by pyrite (see also Sections 3.8.2, 3.8.3). Bioturbation horizons (ε I 3, ε I 4, top of ε III), consisting mainly of the trace fossil *Chondrites*, indicate that temporary periods conducive to epibenthic life interrupted the otherwise predominantly euxinic conditions. In some beds aligned and mainly juvenile ammonites, or oriented belemnite rostra, point to weak bottom currents. These are also evidenced by the disarticulation of vertebrate skeletons, or those parts of them, which projected above the embedding mud surface.

Benthic organisms are extremely rare in the Posidonienschiefer. They are restricted to some diademoid echinoids, ophiuroids, a few burrowing bivalves (such as *Solemya, Goniomya, Cucculaea*), and possibly the crustacean *Proeryon*. The reduced benthic life, the proportionally high percentage of bitumen, the undisturbed sedimentation and the preservation of soft tissues, led to the proposal of a stagnation depositional model for the Holzmaden Posidonienschiefer, and comparison with the quiet-water conditions of the modern Black Sea. An upper water body rich in oxygen and life was underlain by euxinic near bottom water. Kauffman (1979), however, supported a depositional model of black shale-type, pointing out that anaerobic conditions were restricted to the sediment itself, or to a boundary fluctuating between the sediment and the water directly overlying it. His views were superseded by a modified stagnation model incorporating storm events (Seilacher 1982) or currents (Riegraf *et al*. 1984).

Biota

In the biotic community the autochthonous flora is represented by coccolithophorids. *Gingko*, the conifers *Pagiophyllum* and *Widdringtonites*, the cycadeans *Pterophyllum* and *Otozamites*, and the newly discovered *Pachypteris*, and the horse-tail *Equisetites* were washed in from the Vindelician continent situated about 100 km south of Holzmaden.

The microfauna, stunted in some layers, consists mainly of radiolarians and foraminiferans. Apart from benthic forms, the bivalves *Gervillia, Pseudomytiloides, Oxytoma, Exogyra, Antiquilima* and possibly *Liostrea* were fixed by their byssus to a temporarily hardened mud bottom or to floating

Fig. 2 *Passaloteuthis paxillosa*. Soft body of a belemnite (Schwarzjura ε II 1, Ohmden, near Holzmaden).

shells of mainly ammonites. The bivalves *Steinmannia*, *Meleagrinella* and *Bositra* (the earlier '*Posidonia*', which gave the Posidonienschiefer its name) were pseudoplanktic. The gastropod *Coelodiscus* is numerous in concretions and limestones; it fed on the decaying organic remains of vertebrates. The ammonites and their stratigraphic distribution are listed in Fig. 1 and by Riegraf *et al.* (1984). Coleoids are represented by vampyromorphids (e.g. *Loligosepia*, *Loliginites*, *Teudopsis*, *Phragmoteuthis*, and *Chitinobelus*), and the belemnoids *Dactyloteuthis*, *Youngibelus*, *Salpingoteuthis*, and *Passaloteuthis*. Soft

body tissues of the last are preserved (Fig. 2). The crinoids *Pentacrinites* and *Seirocrinus* lived in colonies, and are often preserved attached to the remains of floating logs. There is a rich ostracode fauna which, together with the crustaceans *Uncina*, *Proeryon*, and *Coleia*, completes the invertebrate fauna of Holzmaden.

Holzmaden is famous for its complete vertebrate skeletons. Sometimes they are preserved with the so-called 'skin' (e.g. in ε II 3–5). This decayed and transformed soft tissue marks the outline of the body as a black film and is found in the sharks *Hybodus* and *Palaeospinax*, the holocephalian *Acanthorhina*, in ganoids and holosteans, but mainly in the many species and specimens of the ichthyosaur *Stenopterygius* (Fig. 3), in the marine crocodile *Steneosaurus* (but not in *Pelagosaurus* and *Platysuchus*), and in the pterosaurs *Dorygnathus* and *Campylognathoides*. The pterosaurs and the saurischian dinosaur *Ohmdenosaurus* are allochthonous faunal elements. Fishes are represented by the ganoids *Lepidotes*, *Dapedium*, *Pholidophorus*, the subholosteans *Ptycholepis*, *Tetragonolepis*, and *Saurorhynchus*, the rare *Chondrosteus* and rare coelacanth *Trachymetopon*, and the teleosts *Leptolepis* and *Euthynotus*, all of which lived in the oxygen-rich upper water. Some, however, are believed to have been allochthonous (e.g. *Lepidotes*, *Dapedium*, *Tetragonolepis*). The plesiosaurs *Plesiosaurus* and *Rhomaleosaurus*, the ichthyosaurs *Stenopterygius* and *Leptopterygius*, and the long-snouted *Eurhinosaurus* seem to have been inhabitants of the open sea, while the crocodiles and the sphenodontid *Palaeopleurosaurus* presumably lived near the coast.

The ichthyosaur *Stenopterygius* is represented by many species and hundreds of specimens, sometimes with stomach and intestine contents (e.g. the hooks of coleoids). There are preserved females giving birth to young (Fig. 4), or containing up to thirteen embryos, or in association with an aborted foetus. The high percentage of pregnant female ichthyosaurs, and of juveniles, may be due to a 'spawning ground' to which the animals migrated periodically over a long geological time to give birth to their young.

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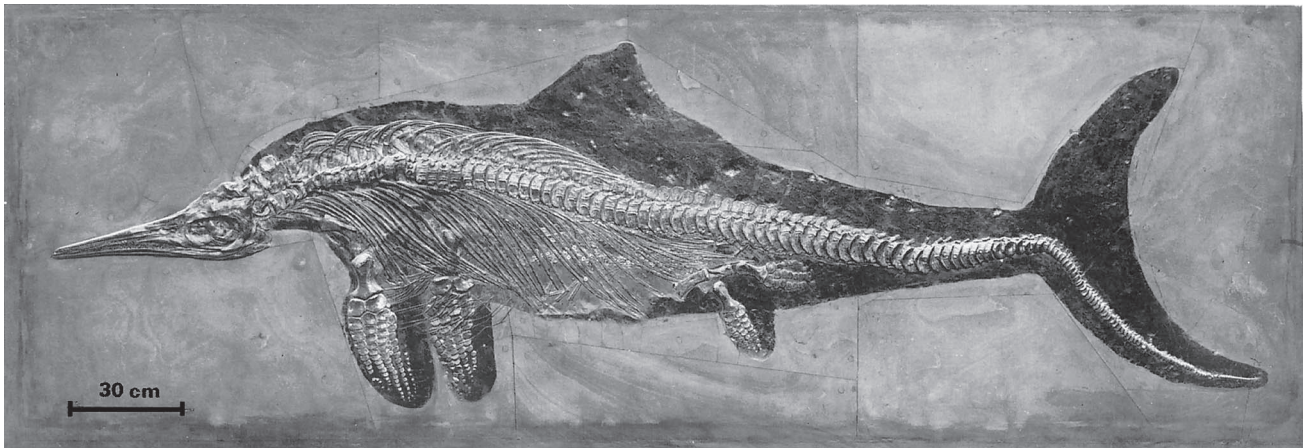
Fig. 3 *Stenopterygius macrophasma*. Soft body of an ichthyosaur with remains of three embryos in its body cavity (Schwarzjura ε II 4, Holzmaden).
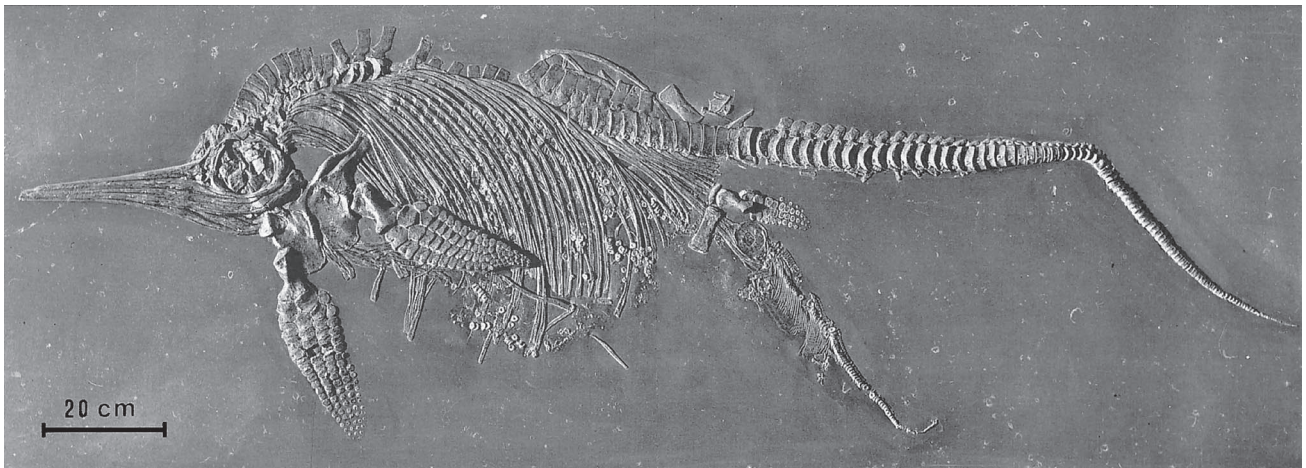

Fig. 4 *Stenopterygius quadriscissus*. Female in the process of giving birth, with the remains of three embryos in its body cavity (Schwarzjura ε II 3, Boll).

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3.11.7 Solnhofen Lithographic Limestones

G. VIOHL

Introduction

The Solnhofen Lithographic Limestones of the Southern Franconian Alb (Bavaria, West Germany) range over an area of about 70 × 30 km and display some differences in facies and preservation of fossils.

The Solnhofen Limestones comprise not more than half an ammonite zone in the lower part of the

Lower Tithonian, representing at most 0.5 myr. The lithology, best described by the German word 'plattenkalke', is characterized by micritic, even-layered limestone slabs ('Flinze') (mostly with an internal microbedding) and irregularly intercalated calcareous fine-layered marls ('Fäulen').

Sedimentary environment

The Solnhofen Limestones were deposited on a sea floor with strong relief, due to algal−sponge reefs. The limestones vary considerably in thickness (0−95 m). The depositional area was backreef in position. It was landlocked to the northwest and separated from the Tethys Ocean by discontinuous coral reefs along its eastern and southern margins.

All the evidence found in the Solnhofen Lime-stones suggests a semiarid climate (Viohl *in* Hecht *et al*. 1985). High evaporation rates and the restriction of water exchange with the open sea caused a high salinity and the development of a density stratification in the lagoonal waters. This resulted in stagnation and a hostile bottom environment. Even in the surface water layers the organic productivity must have been relatively low, as can be inferred from the scarcity of fossils and the low content of bitumen and pyrite in the sediment. Only episodically was the lagoonal water body completely mixed with waters of the Tethys Ocean.

The origin of the sediment is still controversial. Barthel (1978) regarded the marly layers (Fäulen) as the normal sediment accumulated over a long period, and the limestone layers (Flinze) as representing storm events. In this model, which seems the most probable, carbonate ooze deposited on the seaward margin of the coral reefs was periodically stirred up by storms and pushed into the lagoon as a suspension, where it settled down forming a layer of lime mud. Only the finest fraction was transported as far as the basins of Solnhofen and Eichstätt. Other models explain the limestone layers as a kind of stromatolite built up by cyanobacteria (Keupp 1977) or as the result of coccolithophorid blooms (de Buisonjé *in* Hecht *et al*. 1985).

There are no indications of strong bottom currents. Evidence of currents, such as roll marks of ammonite shells (Seilacher *et al*. 1985), orientation of fossils, and ripple marks (Janicke 1969) are confined to the eastern basins (Painten, Pfalzpaint) or to a few beds in the uppermost Solnhofen Limestones which must be interpreted as turbidites caused by earthquakes. In the area of Solnhofen and Eichstätt settling marks next to the fossils (Mayr

1967), as well as aptychi and fragments of ammonite shells lying convex side down, suggest a very calm environment (see also Section 3.4.1). Other evidence is the high percentage of articulated vertebrates, echinoderms, arthropods (Fig. 1), and ammonites with aptychi in place.

The extraordinarily good preservation, in some instances even of soft parts, also required protection by rapid burial. Swept in during storms, the fossils were buried immediately by suspension fallout, because they settled a little earlier than the micritic particles. This could also explain why most fossils lie parallel to bedding. An exception are the jellyfish found in the quarries of Gungolding−Pfalzpaint, which are embedded within the limestone slabs. Being lighter than other animals, they sank only during deposition of the lime mud.

The Solnhofen Limestones yield not only well preserved fossils but also disarticulated skeletal elements. These are due to decay processes occurring while the carcasses were floating in the water. Particularly long drift times, even after decay of the soft parts, can be inferred for belemnites with attached

Fig. 1 A characteristically complete specimen of the decapod *Eryon arctiformis*. (Scale bar = 1 cm.)

oysters. Their soft parts have never been found, only those of their relative *Acanthoteuthis*.

Some necrolytic features may be due to the hypersaline environment. Mayr (1967) described strongly bent teleostean fishes with the tail fin torn off the vertebral column. This phenomenon can best be explained by dehydration in a brine, and consequent contraction of the ligaments tying together the neural arches. The caudal fin adhered firmly to the bottom, obviously to a cyanobacterial mat; it could not follow the movement of the carcase and became detached (Fig. 2).

The dorsally bent neck, a familiar feature of *Archaeopteryx* (Fig. 3), *Pterodactylus*, and *Compsognathus*, is perhaps better explained by the drifting position in which the carcasses came to rest on the bottom (Rietschel 1976).

Seilacher *et al.* (1985) attributed the *post-mortem* contraction of the crayfish *Antrimpos*, and the coiling of the stemless crinoids *Saccocoma* and *Pterocoma*, to the dehydrating effect of hypersaline waters. The wrinkles seen in some specimens of the jellyfish *Rhizostomites* might also be due to the same cause (de Buisonjé *in* Hecht *et al.* 1985), especially those indistinctly preserved from the Eichstätt quarry area.

Diagenesis

In the Solnhofen Limestones two phases of cementation and correlated compaction must be sharply distinguished:

1 An early cementation of the superficial layer was caused by cyanobacterial mats (Keupp 1977). These were also responsible for the preservation of traces, and they prevented macrofossils from sinking into the underlying soft and mobile sediment. Syneresis phenomena on the bedding planes (Janicke 1969), formerly interpreted as mud cracks and rain-drop imprints (Mayr 1967), suggest that superficial cementation was accompanied by an early dehydration.

2 The main cementation and compaction of the sediment occurred only after the collapse of fossils, which are therefore all flattened (see also Section 3.7). Compaction could not have continued indefinitely after collapse, however, because deformational structures of adjacent bedding planes below and above the fossil have been preserved. These deformations were plastic in the case of fish, crayfish, and squids (de Buisonjé *in* Hecht *et al.* 1985) as well as the body chambers of the ammonites *Glochiceras* and *Aspidoceras*. During the collapse of shells of the ammonite *Perisphinctes*, and of the phragmocones of *Glochiceras* and *Aspidoceras*, the sediment was already stiffened and reacted by fracturing along microfaults (Seilacher *et al.* 1976).

Solnhofen fossils typically lie in a depression in the overlying bed while supported on a pedestal in the underlying bed. Depressions ('collapse calderas' of Seilacher *et al.* 1976) occur on the adjacent bedding planes above and below. Collapse of the fossil certainly plays an important role in the formation of

Fig. 2 A young *Tharsis dubius*, strongly bent by dehydration in a hypersaline environment. The vertebral column has become detached from the tail fin, itself firmly adhered to a cyanobacterial mat, × 0.65.

Fig. 3 The Eichstätt specimen of *Archaeopteryx lithographica* showing the characteristic *post-mortem* dorsally bent neck, × 0.65.

pedestals, but other processes are probably also involved (Janicke 1969; Seilacher *et al*. 1976).

Aragonite must have dissolved in the upper few metres of sediment, as the deformation of ammonites in slumped layers shows that they have been reduced to periostracal films (Seilacher *et al*. 1976).

Soft parts are often preserved, e.g. the intestines of fishes (when filled) or the ink sacs of coleoid cephalopods. The ink, consisting of very stable proteins, may survive diagenesis and, dissolved in water, can still be used for drawing (Barthel 1978). Muscles transformed into phosphate, probably as a result of bacterial activity (see also Section 3.8.4), are preserved in many fishes, coleoid cephalopods, and annelids. In some instances the wing membranes of pterosaurs are still visible as imprints with a phosphatic lining.

The soft parts of ammonites have never been found, though their presence at the time of burial is indicated by the aptychi remaining in the shell. These also prevented the body chamber filling with sediment (Seilacher *et al*. 1976).

Biota

The more than 600 fossil species preserved in the Solnhofen Limestones represent a number of different environments (open sea, coral reefs, lagoon, terrestrial habitats).

A striking feature is the scarcity of autochthonous benthos. The absence of scavengers is a prerequisite for exceptional preservation. Autochthonous epibenthos is almost exclusively represented by foraminiferans. These indicate a dilution of the lagoonal bottom waters by the influx of great quantities of normal seawater, but obviously such periods of near normal salinity were too short to allow colonization by macrobenthos. The many macrobenthic forms, such as crustaceans, echinoderms, ray-like sharks, and others, have been washed in by storms. Most of them died during transport. Only the hardiest, such as the horseshoe crab *Mesolimulus* and the crayfish *Mecochirus*, were still alive on reaching the bottom and left tracks, at the end of which the dead animal can be found (Fig. 4). The epiplankton includes oysters (*Liostrea*) (attached to seaweeds), ammonites, and belemnites.

The bulk of fossils were planktic (stemless crinoid *Saccocoma*, phyllosoma larvae, jellyfish, coccoliths) or nektic (most fishes, cephalopods). A proportion of these was also swept in, either from the open sea or from coral reefs. However, as the abundant coprolites and some evidence of predation (crushed ammonite shells, half-eaten fishes without any sign

in a storm during flight and drowning (Rietschel 1976).

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Fig. 4 The decapod *Mecochirus longimanatus* with settling mark and trail. It was washed into the hostile environment of the lagoon during a storm, sank down and died after a few steps. Only the counterpart of the fossil can be seen as a pedestal. The fossil itself is embedded in the overlying slab, × 0.25.

of decay) indicate, some of the pelagic organisms must have lived in the lagoon itself, at least for short periods.

Finally, the Solnhofen Limestones have yielded a wealth of terrestrial organisms. These were either washed-in during rainy seasons (land-plants and reptiles), blown-in by winds (many insects), or they flew actively into the lagoon (pterosaurs, *Archaeopteryx*). The only way in which complete skeletons of *Archaeopteryx* (Fig. 3) or pterosaurs could have been preserved is by becoming caught

3.11.8 Grube Messel

J. L. FRANZEN

Introduction

Grube Messel is a former opencast oil shale mine, located about 30 km southeast of Frankfurt, West Germany. The crater left after mining ceased in 1971 is 60 m deep and 700–1000 m wide. Its horizontal extent corresponds almost exactly with the occurrence of the so-called oil shale, a laminated, dark brown–olive green claystone with a petroleum content of 5–20%. In cross-section the formation is lenticular. Its maximum thickness was originally 190 m. It was covered by as much as 5 m of a black clay and by up to 33 m of multicoloured argillaceous sediments limited to three troughs in the southeast.

Underlying the oil shale are up to 25 m of coarse sediments (Weber & Hofmann 1982). Surrounded by Upper Palaeozoic sediments, diorites, and granodiorites, these Early Tertiary sediments are preserved within a tectonic graben. This was part of a large rift lake system, accompanied by early rift volcanism connected with the incipient formation of the Oberrhein Graben (Matthes 1966).

Sedimentary environment

Judging by its fossil content, the bituminous clay-stone was originally deposited on the bottom of a small lake at the beginning of the Middle Eocene (Early Lutetian, Early Geiseltalian), about 49 ± 1 Ma. Except for one restricted occurrence in the north, and some debris flows in the south, nearshore sediments have already been eroded. The lake covered only a few square kilometres and was at least some tens of metres deep. It was surrounded by a dense rainforest (Thiele-Pfeiffer *in* Ziegler 1986). With a mean annual temperature of at least 20°C, Lake Messel must have been of warm-monomictic sub-tropical type (Franzen *et al*. 1982).

The Fossil-Lagerstätte is a limnic stagnation deposit (Seilacher *et al*. *in* Whittington & Conway Morris 1985). From time to time the lake was connected with a river system and acted like a settling tank (Franzen *in* Whittington & Conway Morris 1985). All the preservable parts of organisms drifting downstream, or once living in the lake itself, were ultimately embedded in the argillaceous sediments of the lake bed. There anoxic conditions prevailed because of the low energy environment, and a high consumption of oxygen resulting from the decomposition of masses of micro-organisms (mainly algae) that flourished under a tropical−subtropical climate. Thus reducing conditions appeared
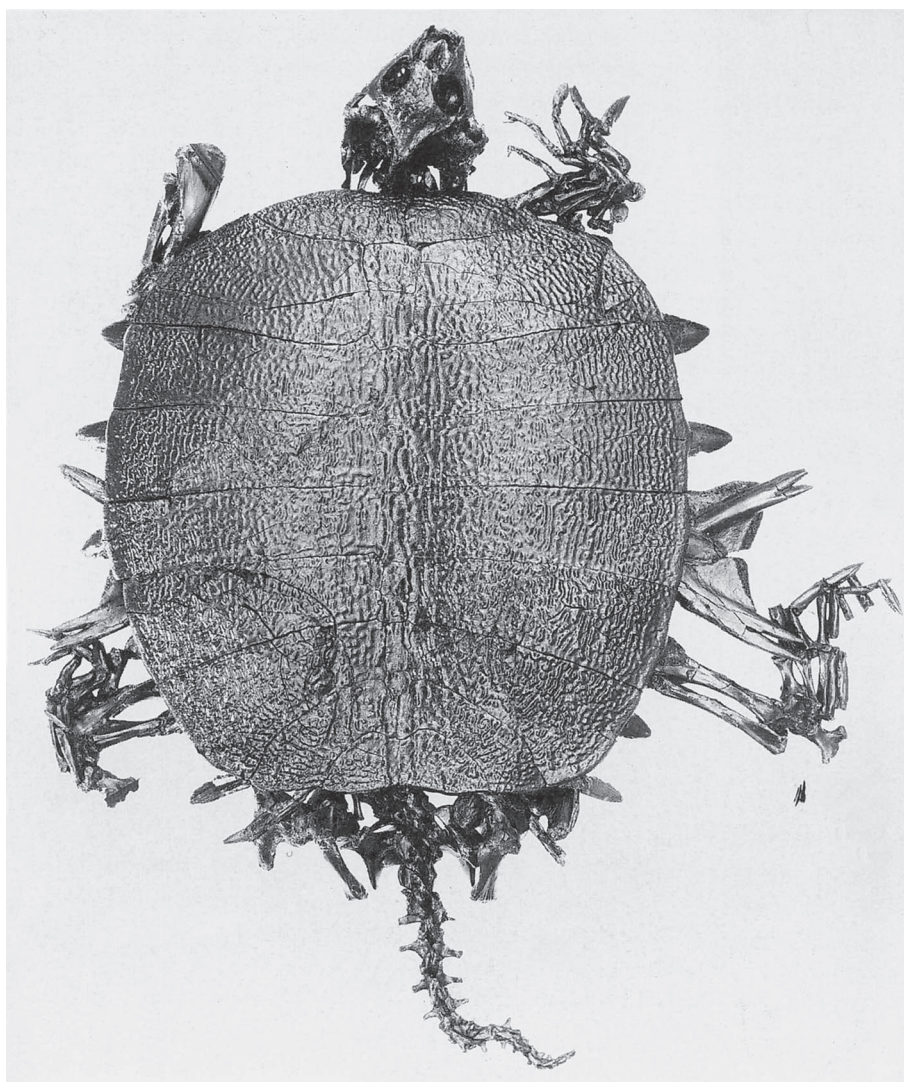

Fig. 1 Complete articulated skeleton of an Eocene turtle (*Trionyx messelianus*) from the Grube Messel, × 0.25. (Photograph courtesy of E. Haupt, Senckenberg Museum.)

which prevented the development of any benthic macro-organisms. Therefore there was no bioturbation. Vertebrate carcasses were completely buried at the bottom of the lake and were neither destroyed by scavengers nor disturbed by currents. They did not rise again to the surface because the pressure of the water column was sufficiently high to prevent inflation of their bodies by the generation of decomposition gases. Thus their carcasses were routinely preserved as complete and articulated skeletons (Fig. 1).

Reducing conditions near the bottom, or within the uppermost layers of sediment, led to the formation of typical minerals such as siderite, marcasite, pyrite, and vivianite (Matthes 1966). Within certain horizons early diagenetic phosphatic minerals such as messelite and montgomeryite also developed (Schaal *in* Schaal 1987).

The fine lamination of the claystone is due to annual climatic fluctuations. It consists of algal-rich layers caused by seasonal blooms which were superimposed on a steady background sedimentation of smectite and other clay minerals (Goth *in* Ziegler 1986). The sedimentation rate was low (about 0.1 mm per year). It was occasionally interrupted by slumps coming down the slopes. In any case it can be assumed that the Messel lake existed for hundreds of thousands of years in a lowland area.
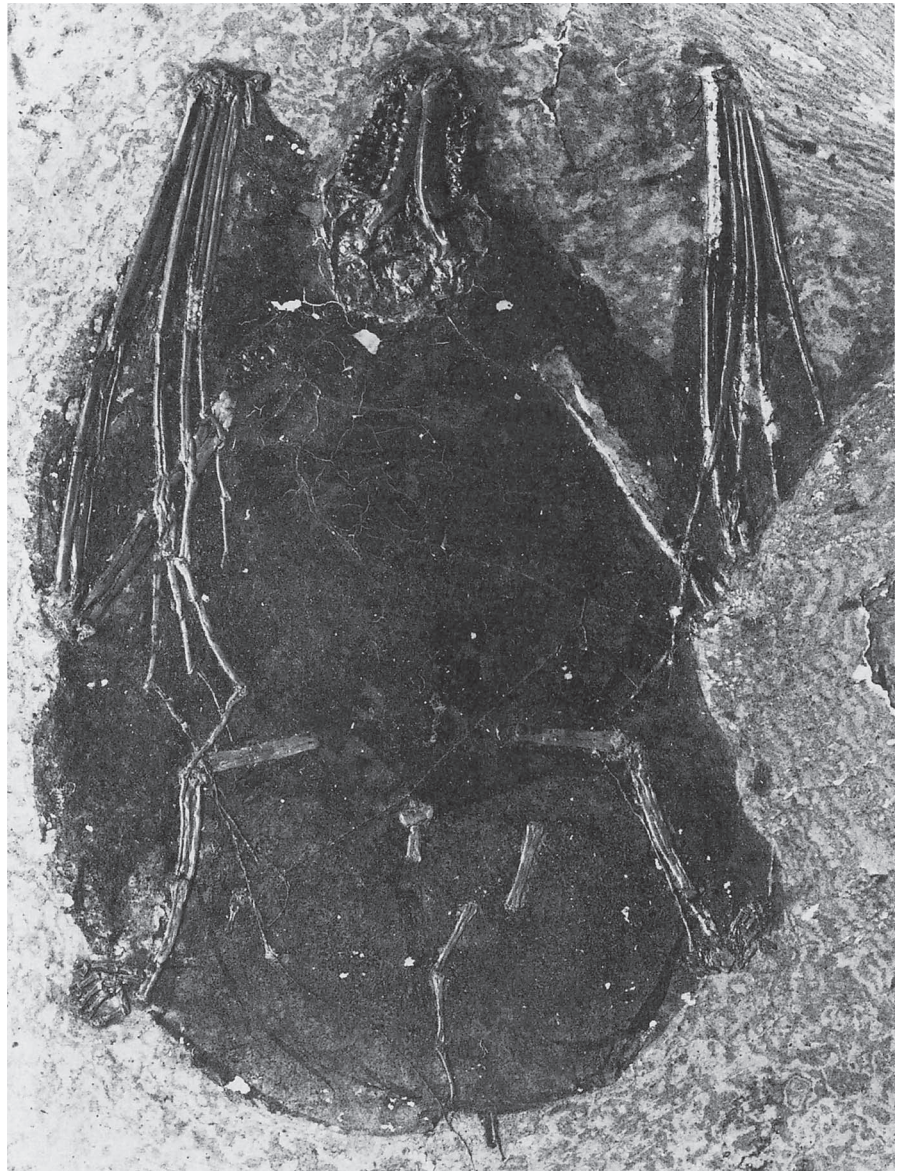

Fig. 2 Eocene bat *Palaeochiropteryx tupaiodon* from the Grube Messel, displaying its body outline together with the patagium (flying membrane) as a black silhouette, × 1.4. The bones within the body were dissolved during diagenesis. (Photograph courtesy of C. Schumacher, Senckenberg Museum.)

Biota

The fossils comprise plant remains (algae, fungi, diatoms, pollen, leaves, blossoms, fruits, seeds, and fragments of branches), spiculae and even gemmulae of freshwater sponges, gastropods, ostracodes (moulds only), thousands of insects (mainly Coleoptera, Hymenoptera, and Heteroptera; but also Odonata, Plecoptera, Blattodea, Isoptera, Saltatoria, Phasmatodea, Homoptera, Trichoptera, Lepidoptera, and Diptera), spiders, freshwater shrimps (very rare), freshwater fish (except for one eel), one salamander, frogs, turtles, lizards, snakes, crocodiles, birds, and about 35 species of mammals (Marsupialia, Proteutheria, Lipotyphla, Chiroptera, Primates, Creodonta, Carnivora, Condylarthra, Pholidota, Xenarthra, Perissodactyla, Artiodactyla, and Rodentia). Lungfishes are only represented by their coprolites. The Messel locality has also gained renown as a treasure trove of little-altered chemofossils (Franzen & Michaelis 1988; see also Section 3.2). Biomarkers among these even indicate archaebacteria.

Paradoxically, flying animals (insects, birds, and bats) are superabundant, while water-dwelling insects are lacking, except for those transported into the lake. This may be evidence of occasional pollution of the lowermost atmosphere by carbon dioxide, which could also account for the many ground-dwelling vertebrates found in relaxed positions typical for such a death (although drowning may also produce this posture) (Franzen et al. 1982). This hypothesis is supported by the fact that bats which display a wing construction especially suited for flight close to the ground (Palaeochiropterygidae) are far more abundant than those typically adapted for flight at high speed and considerable height (Hassianycterididae) (Habersetzer & Storch in Schaal 1987). Alternatively, water-dwelling insects (as well as fish) could have been affected by oxygen deficiency and/or poisoning by hydrogen sulphide and/or ammonia, both generated by the annual turnover of the lake, and/or by tanning agents produced by decomposing plant material (Lutz in Schaal 1987).

The quality of preservation is really exceptional. Plant remains often display not only delicate and soft tissues, but also feature more complete structures such as fruiting heads (Collinson in Franzen & Michaelis 1988). Collagen fibrils have been described from freshwater sponges. Insects still show colours of their original pattern. Vertebrates, in general, are not only preserved as complete skeletons, but also display various stages of ontogenetic development (including pregnant early horses with embryos; Franzen in Ziegler 1986). On occasion, vertebrate skeletons are surrounded by a black shadow tracing the former outline of the soft tissue including the detailed structure of feathers, or the tips of the hairs (Fig. 2).

Nevertheless the soft parts of the vertebrates are not directly preserved, only their silhouettes (Wuttke 1983). Scanning electron microscope studies revealed minute bodies in the form of rods or grains of siderite (see also Section 3.8.2). Evidently these originated from a dense covering of bacteria, which
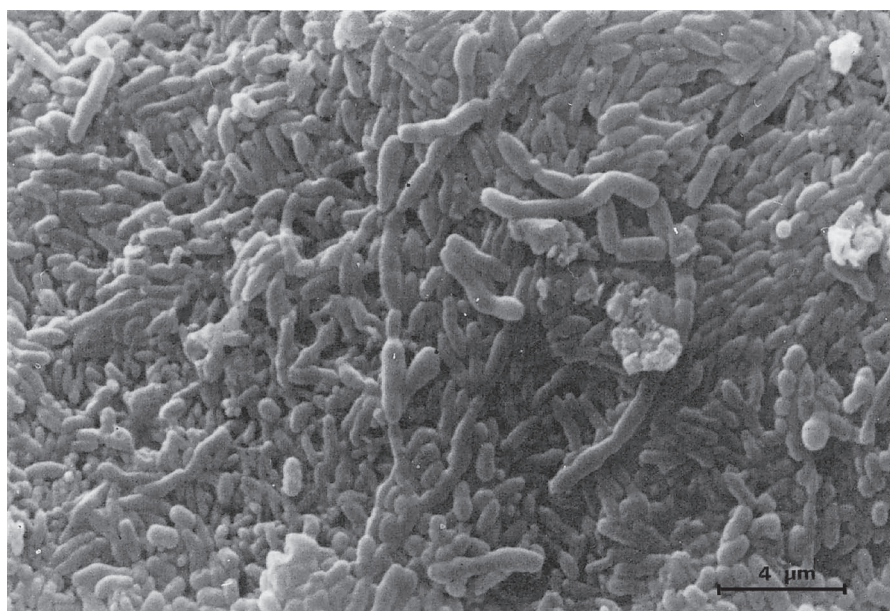

Fig. 3 Bacteria (autolithified as siderite) preserving the fur of an Eocene primate (*Europolemur koenigswaldi*) as a black shadow. Scanning electron micrograph, × 4250. (Courtesy of G. Richter, Senckenberg Museum.)

high production of micro-organisms | small freshwater lake of tectonic origin | climate tropical–sub-tropical | rivers | volcanism

occasional blooms of algae | more or less stagnant | thermal stratification | occasional floods | exhalations of CO_2

high consumption of oxygen by decay | oxygen deficit near bottom | annual turnover | death of terrestrial vertebrates | crash of insects, birds and bats

no benthos no carrion-feeding no bioturbation | reduction zone: hydrides instead of oxides | poisoning of lake-dwelling vertebrates | cadavers drifting and sinking to the bottom of the lake | drowning of insects, birds and bats

decay by micro-organisms (bacteria) only | rich production of kerogens (hydrocarbons) | infiltration of bacteria layers | preservation of articulated skeletons

metabolic production of CO_2 | autolithification of decomposing bacteria as siderite ($FeCO_3$) | preservation of soft parts as black silhouettes
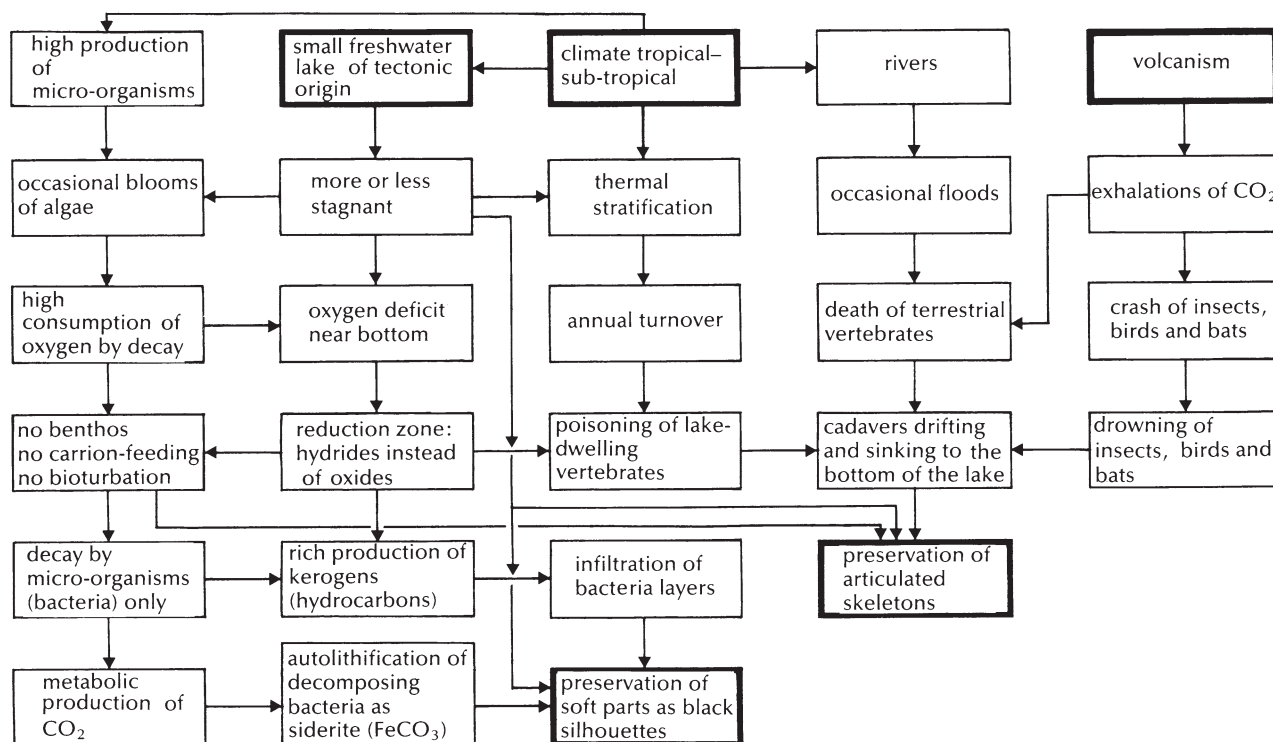
Fig. 4 Factors involved in the exceptional preservation of articulated skeletons, and so-called soft parts of Eocene vertebrates and insects from the Grube Messel (West Germany). (After Franzen *in* Whittington and Conway Morris 1985.)

had begun to decay the carcasses as soon as they were deposited on the lake bed (Fig. 3). Apparently, the bacteria then became petrified through their own metabolic production of carbon dioxide and the precipitation of iron which was present in the lake as a result of the weathering of igneous rocks and Permian red beds nearby. Only later did this thin 'lawn' of autolithified bacteria become a black silhouette, through infiltration and cementation by further organic material derived from plants. In this way, the soft part contours of the Eocene vertebrates have been handed to us not directly, but by a natural replication which could be called 'bacteriography'.

Genuine preservation of soft tissue, like cell walls of plants, hairs of mammals, or scales from the wings of moths, sometimes occurs within gut contents. They reveal remnants of the diets of omnivorous, insectivorous, carnivorous, folivorous, frugivorous, and even fungivorous mammals (Richter *in* Schaal 1987). Occasionally, even fish, snakes, and insects (pollen; Schaarschmidt *in* Ziegler 1986) preserve digestive remains.

Although the whole taphonomic context is still far from completely understood, a generalized diagram of the factors involved in the extraordinary quality of the preservation of fossils at Messel can be presented (Fig. 4).

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3.11.9 Baltic Amber

T. SCHLÜTER

Introduction

Fossil resins embedded in any type of sediment are normally called 'amber' or, in the case of stratigraphically younger examples 'copal'. Unquestionably Baltic amber is the world's most famous. Its name is derived from the fact that it is abundant along the shores of the Baltic sea, especially in the vicinity of the Samland Promontory in the U.S.S.R.

Baltic amber has been known since neolithic times and recognized as a derivative of trees since antiquity, when Aristotle, Pliny, and Tacitus described some of its physical, chemical, and biological properties. However, from medieval times up to the eighteenth century, knowledge of its origin was almost lost. Baltic amber has been commercially exploited for centuries by beach collecting, dredging, and mining. Important amber trade routes from the Samland carried raw and polished amber (the 'gold of the north') into the Mediterranean region, where amber is known from many archaeological sites. Later, most Baltic amber was used in high grade varnishes. Today, the bulk is used for making jewellery.

Sedimentary environment

Baltic amber is derived largely from the extinct tree *Pinus succinifera* (gymnospermid family Pinaceae), which flourished during Early Tertiary times (50−35 Ma) on a land mass that reached southward to the vicinity of the Samland (Fig. 1). This area became inundated in the Late Eocene or Early Oligocene and the resin left behind by the forests that grew there was washed out by the sea and/or ancient rivers. Today it is associated with an originally marine sediment called 'blue earth', from which it is continuously eroded, partly transported and sometimes redeposited at some distance (Fig. 1).

Autochthonous and allochthonous amber Lagerstätten

A model for the formation of autochthonous and allochthonous amber Lagerstätten was presented by Dietrich (1979). Generally Baltic amber now occurs only in secondary or allochthonous deposits, but originally an autochthonous preservation and concentration of this fossil resin is likely, as evidenced by the depositional environment of Recent and subfossil copal. The resin sometimes accumulates in the soil around the tree from which it falls, aided by its relatively high resistance to chemical, physical, and biological degradation. Under anaerobic or reducing conditions, resin is concentrated during the formation of peat (especially in subtropical and tropical climates), and concentration might increase during the formation of coal.

The main factor in resin concentration under aerobic or oxidizing conditions is the decomposition of the other non-bituminous substances. The likelihood of preservation of such layers increases when the resin, once concentrated, is then protected from decomposition by the onset of anaerobic conditions.

Whilst autochthonous deposits of resins are generally restricted to coal-bearing deposits, allochthonous deposits have been formed in various environments where transport mechanisms played
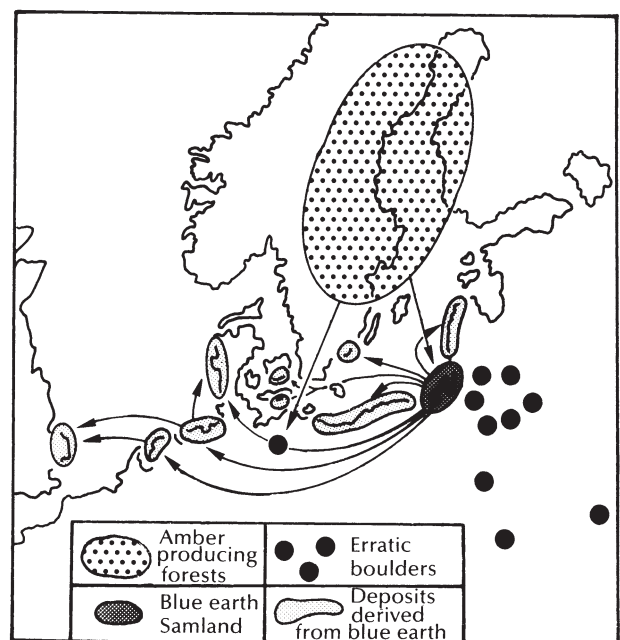

Fig. 1 Geographical setting of the Baltic amber-producing forests and their allochthonous deposits.

an important role. In allochthonous deposits the formation of amber Lagerstätten depends largely on the hydrodynamic qualities of each amber particle, which in turn depends on the density, size, and shape of the respective amber variety. Being scarcely heavier (sometimes even lighter) than water, re-worked amber can be carried in suspension even in conditions of little movement. Concentrations of amber are thus deposited where water movements slacken. The maximum diameter of amber particles which can be transported increases with water density (as a result of higher salt content). The largest Baltic amber particles have a weight of approximately 10 kg (Andrée 1951). The following amber Lagerstätten can be distinguished: continental basins (including terminal lakes), areas subjected to fluvial flooding and deltas/estuaries, limnic and marine drift lines, tranquil bays, and submarine depressions (Fig. 2).

The richest Baltic amber-bearing deposit is the bed of the upper blue earth in the Samland, which consists of glauconitic sands containing typical marine fossils. Here the index fossil *Ostrea ventilabrum*, indicating a lower Oligocene age, is very common. Approximately 15 m below lies the lower blue earth, which is comparatively poor in amber and assigned to the Upper Eocene.

Baltic amber as a trap

Generally in both Gymnospermae and Angiospermae, resin is produced by parenchyma cells that usually line rounded pockets or cysts, and elongated canals (Langenheim 1969). Two different possibilities for the development of these cell types exist: (1) the schizogenic mode involves the separation of cells which round off and increase their intercellular spaces to produce pockets or canals of which the secretory cells form an epithelial layer; and (2) the lysigenic mode results in the formation of cavities from the breakdown or disintegration of the secretory cells. Often the process of production of resin is a combinaton of both types.

In practice resin often flows from cracks which develop as a result of tension or wounds in the bark. The resin is then exuded on trunks and branches in amounts depending on the productivity of the particular species. The so-called 'schlauben', and the drops of amber, are the typical preservation mode (Fig. 3).

Schlauben arose as a result of a number of resin flows at brief intervals. Resin warmed by the sun flowed in a relatively fluid form down the tree trunk, followed by inhibition of the flow by cooling during the night, when the surface partly solidified.
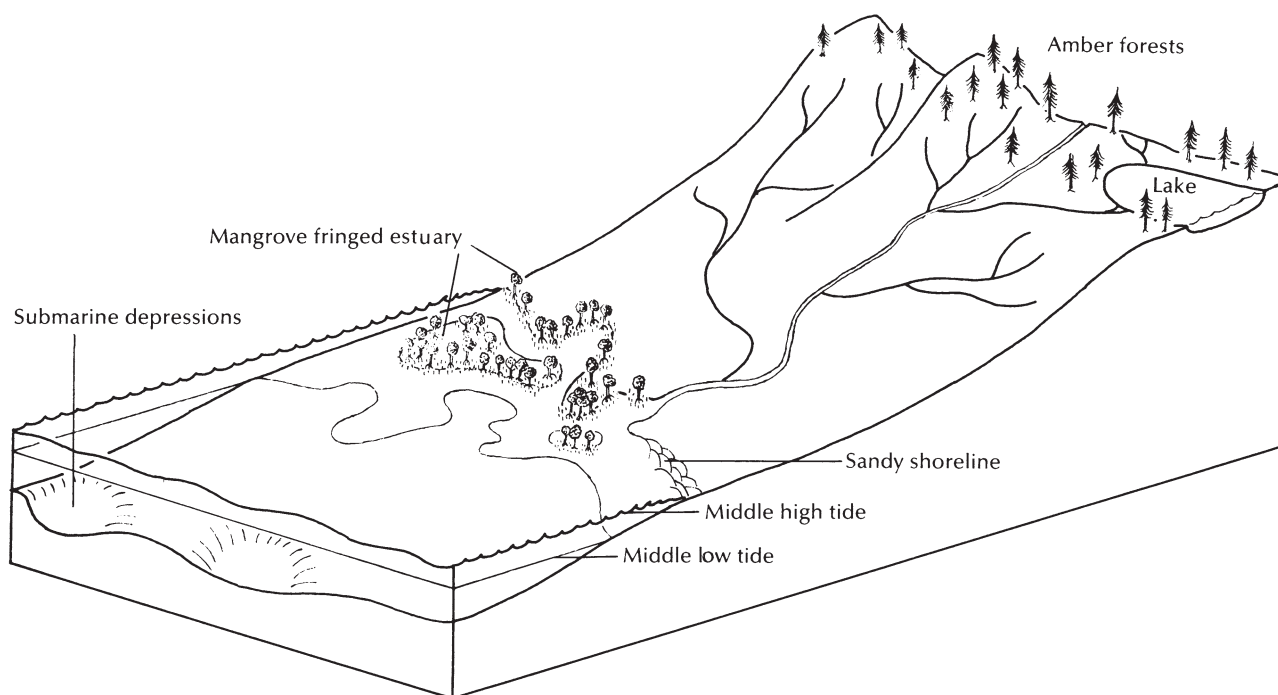

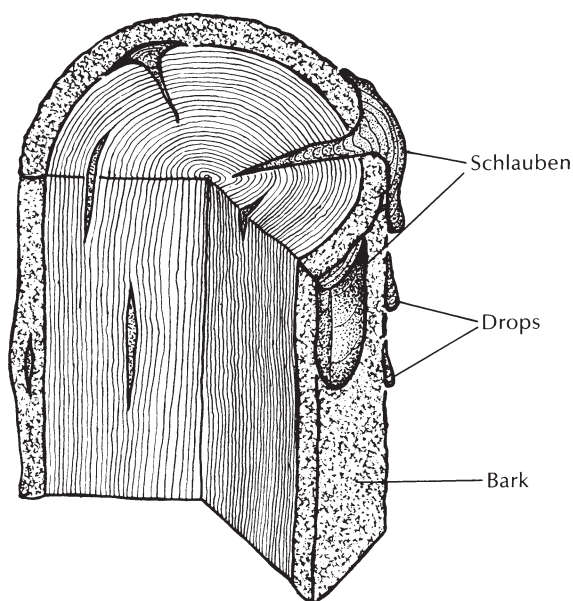**Fig. 2** Possible autochthonous and allochthonous deposits of amber.

Fig. 3 The formation of resin. The schlauben are most effective as potential traps. (After Katinas 1971.)

Then fresh resin flowed over that of the previous day. The earlier formed resin skin was a most effective trap for capturing arthropods (which often struggled to free themselves, as may be seen from the whirls created in the amber by legs, wings, etc.). Subsequent flows sealed their transparent tomb (Larsson 1978).

However, large quantities of resin are also stored inside the tree's trunk, in major lysigenous fissures in the wood and the bark. Such places do not act as potential traps for the tree's inhabitants and visitors. Resin of this type is normally empty of animal inclusions, and is represented in the Baltic amber by the so-called 'fliesen' and plates.

The fossilization potential of resin exuded and exposed is quite variable. Hence the animal inclusions of the Baltic amber represent members of several different niches in the original forests. Larsson (1978) noted that the amber tree was inhabited by a series of different animal species, only a few of which were specific, mainly phytophagous, while others were indifferent to the identity of their host plant, or were random guests. Inhabitants of the following niches were differentiated: plant-sucking insects, leaf- and seed-consumers, gall producers, nectar seekers, insects and spiders trapped while resting, the fauna of moss and bark, and the hidden fauna of tree trunks.

Biota

Generally the fauna of the Baltic amber is dominated by Diptera (Fig. 4) (approximately 50% of all animal inclusions and represented by both Nematocera and Brachycera), whilst in other fossiliferous resins — especially those formed under tropical conditions — Hymenoptera and Diptera account for almost equal percentages (Fig. 5) (Schlüter 1978).
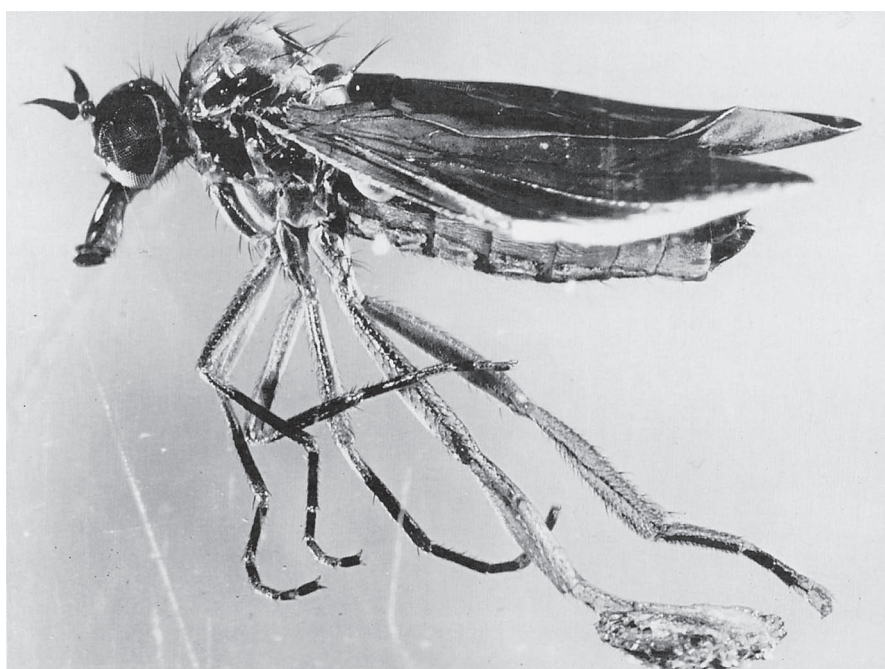

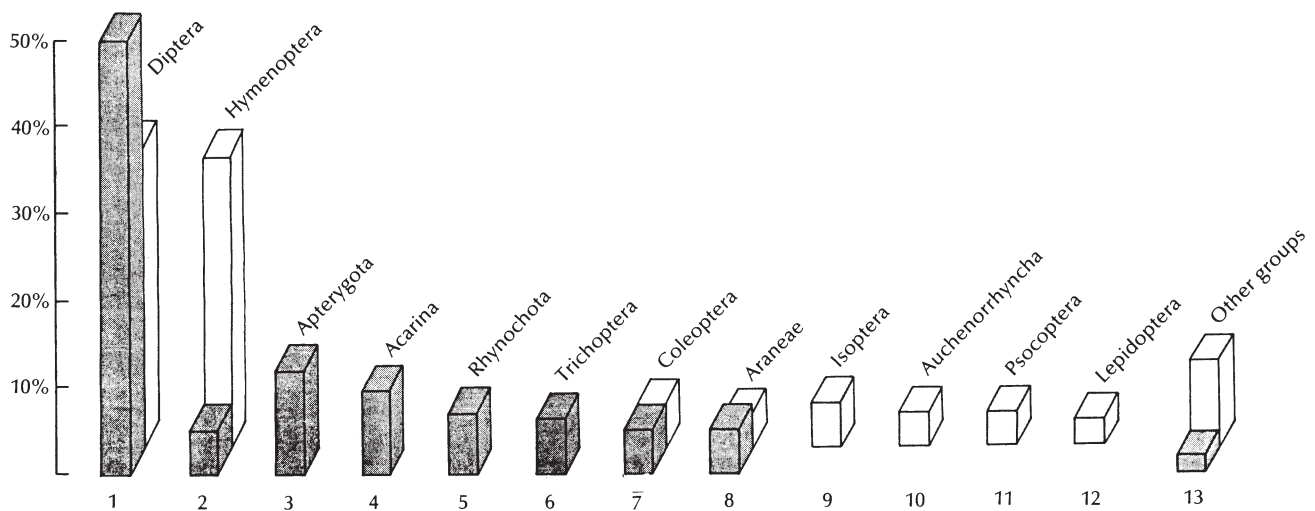**Fig. 4** A species of Diptera: Empididae from the Baltic amber.

Fig. 5 Relative frequency of different higher systematic groups of animals in Baltic amber (anterior darker columns) and in amber of the Dominican Republic (Oligocene) (posterior lighter columns).

In Baltic amber the percentage of Hymenoptera (only 5%) is exceeded by that of Apterygota (11%), Acarina (9%), Rhynchota (7%), and Trichoptera (6%). Coleoptera and Araneae account for approximately 5% each, and all the other higher systematic groups together for less than 2% (including myriapods, snails, and the very rare hairs of mammals, feathers of birds, and at least one almost complete lizard).

Fossiliferous amber-bearing deposits range stratigraphically down to the Lower Cretaceous, although fossil resins are recorded as early as the Carboniferous. Baltic amber has provided by far the most inclusions. However, a higher frequency of fossils per quantity of resin occurs in tropical regions (e.g. amber of the Dominican Republic, and different types of copal).

Since the inclusions of almost all fossiliferous ambers are extraordinarily well preserved, microscopic details of the specimens can sometimes be enlarged by approximately 1000 times. These fossils are interesting not only in themselves, but also because they provide evidence of the development and dispersal of the taxonomic groups they represent. Such information is basic to a proper under-

standing of the phylogeny and biogeography of present-day forms, and it allows conclusions to be drawn about the ecological and climatic characteristics of the area in which they lived.

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3.12 Completeness of the Fossil Record

C. R. C. PAUL

Introduction

Completeness may be defined or estimated in several ways. The completeness of the sedimentary record limits that of the fossil record (and not all sediments are fossiliferous). It is usually expressed as the proportion of time actually represented by sediments. Equally, completeness of the fossil record may be defined in terms of the proportion of all the species that have ever lived which are known as fossils, or in terms of how accurately we know relative abundances, geographical or stratigraphic ranges, etc. In short, degree of completeness is relative to some predetermined objective, which also defines the type of information required. To construct a faunal list requires a single identifiable fragment of a fossil; to describe that fossil requires a complete, well preserved individual; to establish its relative abundance requires a large sample of fossils, whereas to determine its geographical or stratigraphic range requires samples from many localities and horizons. Thus the same data may be complete for one purpose, but incomplete for another. The related, but separate, concept of adequacy is also defined by the initial objectives, and the completeness of the fossil record may be quite irrelevant to its adequacy. Too often incompleteness has been equated with inadequacy. If that were true generally, all science would be inadequate since no science is based on complete knowledge.

Completeness of the sedimentary record

Here the objective is to estimate in a given section the proportion of time actually represented by sediment, and it has often been asserted that bedding planes represent more time than the beds they bound. Estimates are made by determining median short-term sedimentation rates in different modern environments, using a very large sample of published values, and then comparing them with median long-term sedimentation rates for that particular section (e.g. Retallack 1984). Long-term sedimentation rates are calculated from observed thickness and estimates of total duration taken from published radiometric time-scales. Completeness is

the ratio of short-term to long-term sedimentation rates, usually expressed as a percentage. Since median short-term sedimentation rates vary very widely in different environments, only the rates for the appropriate environments can be used to calculate this ratio. Even so, completeness has been defined as the proportion of intervals of a given duration (e.g. 10 000 years) represented within a measurable thickness of sediment, and this proportion varies with the time interval chosen. The same section may be complete at a resolution of one million years, but very incomplete on a time-scale of millenia or centuries. This follows from the definition of completeness. When an interval is represented by a measurable thickness of sediment, it does not mean that the sediment accumulated continuously throughout that interval (Fig. 1). Thus a 1 million year interval may be represented by 1 m of sediment, all of which was deposited in a thousand years. Under the definition given above, the section
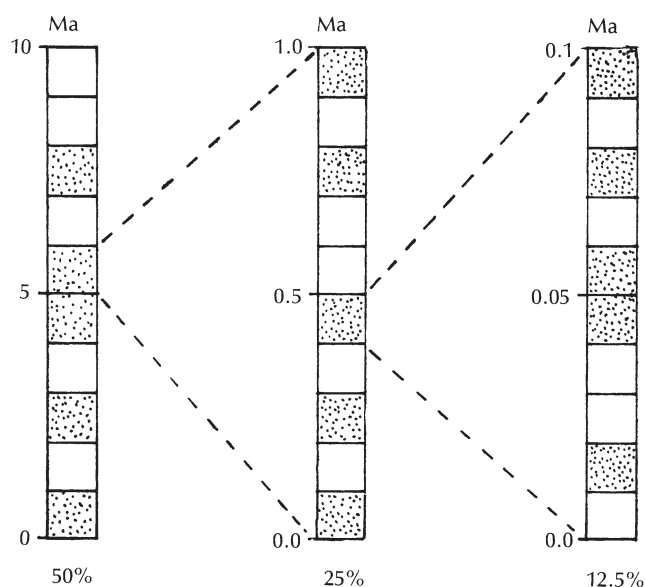

Fig. 1 Diagram to show how the completeness of the sedimentary record, defined by the number of intervals represented by measurable sediment (stippled), decreases with increasingly fine time-scale. At each level of analysis 50% of the time intervals are represented by sediment. Figures at the foot of each column represent total completeness.

would be complete at a resolution of 1 million years, but only 0.1% complete at a resolution of millenia since 999 of the 1000-year intervals would not be represented by any measurable thickness of sediment.

Estimates of completeness of a wide range of sedimentary successions determined by this method are very low at a resolution of 1000 or even 10 000 years (Schindel 1982), and it was originally concluded that most sedimentary successions are far too incomplete to determine, for example, whether speciation events were gradual or punctuational (Schindel 1980). However, there is a flaw in the calculation of short-term rates of sedimentation which tends to maximize them. Where thickness of accumulated sediment is too small to measure (including all zero values), no one in fact records this. Thus published values of short term sedimentation rates are biased and, furthermore, the greater the variance of the sedimentation rates, the greater the effect of this bias on calculated median short-term rates. Anders *et al.* (1987) presented a method of overcoming this bias. For pelagic sediments they suggested that short-term and long-term sedimentation rates are almost identical and therefore that many pelagic sections are nearly complete.

Even in other environments where the sedimentary record is genuinely more incomplete, different sections are unlikely to have precisely the same time intervals represented by sediment or by gaps. Thus analysis of the time intervals actually represented by sediment, combined with improved quantitative methods of correlation between sections, offers the possibility of more refined stratigraphy and improved levels of resolution of palaeontological events.

Completeness of the ultimate fossil list

In this case the aim is to estimate the proportion of all species that have ever existed which are known as fossils. Consequently only the presence/absence of data is under consideration. To test this we need a situation where it is known that an organism existed but has not been found. Gaps in the stratigraphic record of fossils provide just such a situation. A gap occurs where a fossil is known from below and above, but not actually within, a given horizon. Such fossils have been called 'Lazarus taxa'. Provided any Lazarus taxon is correctly identified at its known horizons, it must have existed during any intervals between them. Thus, analysis of gaps

provides a crude quantitative estimate of completeness, but again precise values depend on both the taxonomic and stratigraphic levels of the analysis.

Analysis of gaps provides a minimum estimate of incompleteness because gaps may exist beyond the known ranges of Lazarus taxa, in addition to the detectable ones between their first and last known occurrences. Equally, fossils found in a single stratigraphic interval cannot have gaps in their ranges and are best omitted from such analyses. A cladistic or phylogenetic analysis of taxa can detect gaps beyond known ranges, but only for those taxa that left descendants. There is always the possibility that real ranges extended beyond the apparent point of extinction of a clade. Despite this drawback, analysis of gaps is very instructive in providing estimates of completeness. Fig. 2 represents data for 18 cystoid families at series–stage level to illustrate the principles of the method. Total range is 107 stratigraphic intervals, total gaps 26; hence the cystoid fossil record is at least 25% incomplete at the family–series level of analysis. Analysis of gaps at the ultimate level of species in samples provides the highest values for incompleteness. Even here, values are around 40% for Cretaceous ostracodes, implying that as much as 60% of the record might be known.

Analysis of gaps has additional spin-offs. The largest gap so far encountered in the echinoderm fossil record proved to be an artifact of taxonomic misinterpretation. The edrioasteroid family Cyathocystidae used to contain two Lower Ordovician and two Middle–Upper Devonian genera with nothing known between. Redescription of the Ordovician genera showed them to be morphologically unique and not at all closely related to the Devonian forms. Hence this large gap disappeared. Analysis of gaps directs attention to such taxonomic errors. Equally, cystoids have an exceptionally poor fossil record in the Llandovery. Whatever the reason for this, it inevitably accentuates the apparent major extinction of cystoids at the end of the Ordovician. Of 14 Upper Ordovician cystoid families, eight are known to have survived into the Lower Silurian but only one is actually represented by fossils in the Llandovery. The exceptionally poor fossil record of cystoids in the Lower Silurian casts doubt on whether all the other six families really did become extinct at the end of the Ordovician. Again analysis of gaps directs attention to stratigraphic anomalies.

Growth of knowledge of the fossil record is also a crude estimator of completeness. If only a small proportion of all organisms is known, then new fossiliferous localities would yield fossils most

	ORDOVICIAN						SILURIAN				DEVONIAN						G	T
	Tr	Ar	Lv	Ld	Ca	As	Ll	We	Lu	Pr	Ge	Si	Em	Ei	Gi	Fr		
1																	1	4
2																	0	6
3																	6	13
4																	0	2
5																	0	2
6																	3	11
7																	1	5
8																	0	5
9																	2	7
10																	0	5
11																	0	5
12																	1	5
13																	1	3
14																	1	3
15																	3	6
16																	5	14
17																	1	3
18																	1	8
G	0	1	1	3	0	1	7	2	2	3	1	2	2	1	0	0	Totals	
T	5	10	12	13	14	14	8	8	4	4	4	3	3	3	1	1	26	107

Fig. 2 Ranges of cystoid families known from more than one series, to show gaps (G) as well as total range (T). Known occurrences indicated by solid lines, gaps by dots. Rows give proportion of gaps for each family; columns for each stratigraphic interval. In both cases G/T yields the proportion of gaps. (After Paul 1982.)

of which would be new to science. Alternatively, if we already knew most of the organisms that ever existed, discovering new ones would become a relatively and increasingly rare event. This type of analysis cannot be done simply by examining the rate at which new taxa are being described. Many new taxa, particularly those above specific rank, simply result from taxonomic refinement. If two formerly congeneric species are reassigned to two separate genera, one genus may be new but still based on a species first described last century, and the total number of species known has not increased at all. The way around this problem is to assign all taxa in the sample to one classification, preferably the most recent or thorough, and then to determine when the first representative of each constituent taxon was originally described (irrespective of the taxon to which it was assigned at the time). For example, when the first two species of cystoids were described in 1772 they were thought to be related to the modern sea urchin *Echinus*. They are now placed in separate classes, and *Echinus* in a third. Nevertheless those cystoids represent the first examples of the two classes ever described, even if the classes themselves were not recognized until much later. Using such techniques curves describing the rate at which genuinely new taxa have been discovered can be drawn up (Fig. 3B). These curves show that for cystoid families the pace of discovery has slowed (only three new families since 1900 and one of those based on specimens discovered last century but left undescribed for over 75 years). The numbers of genuinely new genera and species have risen significantly since 1900, by over 50%, and 100%, respectively. These curves imply that the majority of cystoid families are already known, but there are probably many more genera and certainly more species to be discovered. Hence rare fossils may be rare not because the fossil record is incomplete, but because they were originally
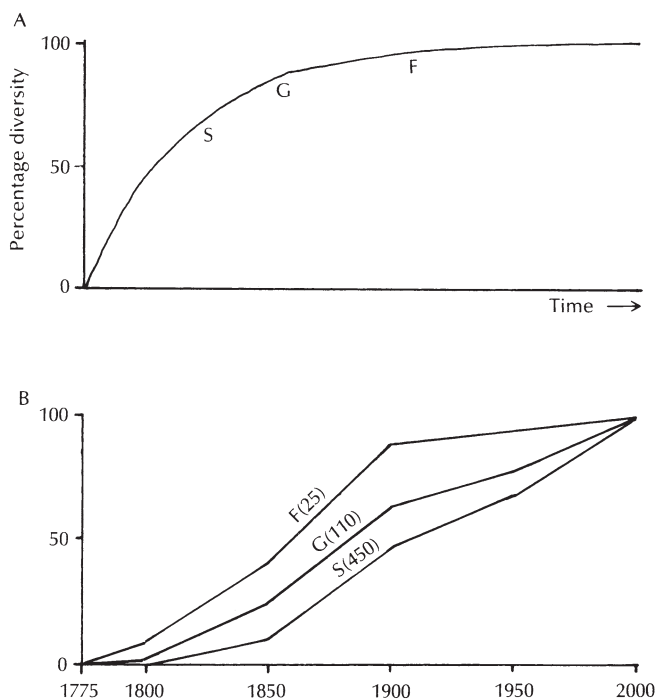
Fig. 3 A, Theoretical growth of knowledge curve. The longer fossils are collected, the greater the proportion of total diversity that will be discovered. Average slopes from 1900 to date (Fig. 3B) suggest that the proportion of cystoid families (F), genera (G), and species (S) already known are as indicated. B, Actual plots of the growth of knowledge of cystoid taxa to date. All three curves normalized to present day diversity (shown in parentheses). (After Paul 1982.)

rare animals. Analysis of gaps for several major echinoderm groups showed that the rarest forms, the cyclocystoids, had the most complete record, whereas the blastoids (the most diverse group treated by the analysis) had the most incomplete record.

Completeness of stratigraphic ranges

Here the objective is to estimate how accurately the stratigraphic range of a fossil is known. (The arguments may be applied to other relative information from the fossil record such as geographical range or specific abundance.) Shaw (1964) approached the problem from the point of view of sample size. In a section fossil x is present up to sample L, but absent in the next sample ($L + 1$). Shaw asked how one could test whether fossil x was in fact present, but had been overlooked. He argued that in any sample all taxa fall into two groups; they are either species x or they are something else. If we suppose that species x is present but rare (say 1% of the preserved

fauna), then when a fossil from sample $L + 1$ is identified the probability (p) that it will be species x is 0.01 (or 1%), and the probability that it will be something else (q) is 0.99 (or 99%). ($p + q = 1$ because there are only two possible outcomes.) As more fossils are identified the total probability (Q) of species x being overlooked declines as follows:

$$Q = q^n = (1 - p)^n,$$

where n = number of fossils identified.

Thus sample size and the proportion of the total fauna that a given taxon constitutes (i.e. n and p) determine the probability of overlooking that particular fossil. Hay (1972) published an extensive graph of values for n, p, and Q. Note that we can never be certain that a species has not been overlooked. As long as one fossil remains in the rock it might be a specimen of the species sought. However, sample size does enable us to estimate the chances that we have overlooked a fossil and hence not determined its range accurately. It follows that the required sample size should be determined by the degree of confidence with which stratigraphic ranges need to be established. Furthermore, bulk sampling is more likely to detect all species present, than picking from exposed surfaces. Where the latter is unavoidable, stereological techniques should be used to assess relative abundances (McKinney 1986). The chances of a random section, such as a quarry face, cutting through a fossil not only depend on its abundance but on the size and shape of the fossil as well. Small species are less likely to be encountered than large ones, whereas spherical fossils are more likely to be cut than disc- or rod-shaped ones.

Paul (1982) approached the problem from a different standpoint. To determine any range requires at least two specimens from different horizons. A range based on just two fossils is unlikely to be even approximately complete, whereas one based on a very large number of examples is unlikely to be significantly incomplete, unless some special circumstances prevail. Paul argued that if, throughout a section, the chances of a specimen being preserved were equal and the sedimentation rate was more or less uniform, then the frequency distribution of intervals between specimens of the same taxon should follow an exponentially declining curve identical to the radiometric decay curve. In this case the median interval would be an estimate of the 'half interval' (i, equivalent to the half-life of radiometric decay) and could be used to put confidence intervals on known ranges (Fig. 4). Thus 95 and
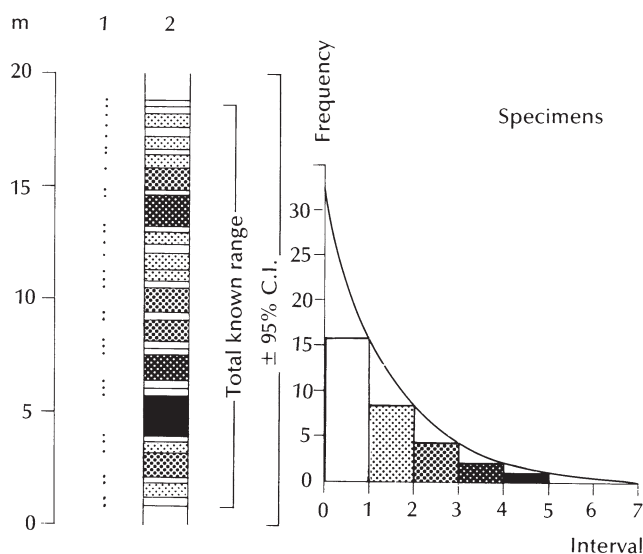
Fig. 4 Derivation of frequency curves from intervals in a measured section. The actual occurrences of specimens are plotted in column 1. The intervals between them are shaded according to size (column 2), in classes that are multiples of the median interval (i). The frequency histogram is derived from these intervals. Confidence limits (95%) are $\pm 4i$ above and below known range. (After Paul 1982.)

99% confidence intervals are approximately $\pm 4i$ and $\pm 7i$, respectively (the exact figures are 93.75 and 99.22%).

Comparisons of real distributions with the ideal curve showed that some did satisfy the initial assumptions. In other cases it is usually possible to determine which of the two assumptions is invalid, because significant changes in sedimentation rate should affect all fossils which range through that part of the section. One case was particularly instructive. The trilobite *Grandagnostus falanensis* had a single enormous gap in its range. The brachiopod *Lingulella* showed the expected frequency distribution throughout the section, implying that sedimentation rates were uniform. Another agnostid trilobite ranged through the gap, which was therefore unlikely to be due to diagenesis destroying *G. falanensis*, or to this trilobite being overlooked. Paul concluded that *G. falanensis* was not preserved through this interval because it was originally absent from the area. Thus in a single section gaps may reflect faithfully what actually happened. One would not expect a marine species to be present through an interval of non-marine sediments. Local gaps are not necessarily due to the incompleteness of the fossil record.

Reliability of sequence

This is one case where the completeness of the fossil record is largely irrelevant. Despite the claims of some evolutionary scientists that relative stratigraphic position cannot be used to determine ancestor–descendant relationships, it is extremely rare for fossils to be preserved in the wrong sequence with respect to the order in which they evolved. This can only happen when two species coexisted. If one became extinct long before the other evolved, there is no way in which they can be preserved in the wrong stratigraphic order (Fig. 5). So to estimate the adequacy of the fossil record it is only necessary to determine what proportion of all species that ever lived coexisted at any one time. The precise value depends on the distribution of relative survivorship of fossil species, as well as changes in diversity throughout the Phanerozoic. Nevertheless, if it is assumed that, on average, species existed for 6 million years, and the Phanerozoic was 600 million years long, published estimates of Phanerozoic diversity patterns indicate that approximately 3% of all Phanerozoic species coexisted at any one time (Paul 1985). Thus in 97% of possible comparisons there is no possibility whatsoever of species being preserved in the wrong order. Furthermore, the probability is always greater that the correct, as opposed to incorrect, sequence will be obtained even in the 3% of cases where it is possible the order might be wrong. These percentages are not affected at all by the completeness of the fossil record. Indeed if it consisted of just two
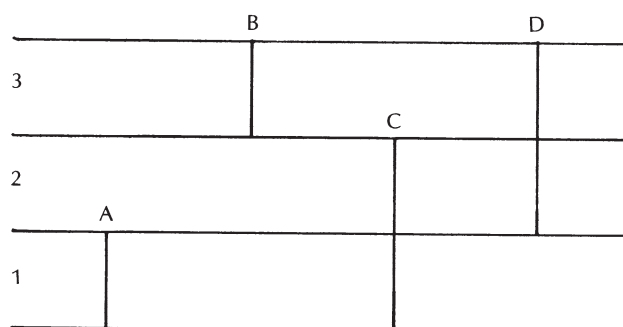

Fig. 5 Total original ranges over three time intervals (1–3) for two pairs of species. As the ranges of A and B do not overlap there is no chance whatsoever that they could be preserved in the wrong stratigraphic order. C and D did coexist (at time 2) and so could possibly be preserved in the wrong sequence. However, note that the probability of this occurring is low and that as soon as a single example of species C is found from time 1, the possibility ceases to exist. (From Paul 1985.)

fossils, the probability is overwhelming that they would be preserved in the correct sequence.

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