



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

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 dif-

ferent 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





**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,  $\times 0.25$ .

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

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

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### 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.



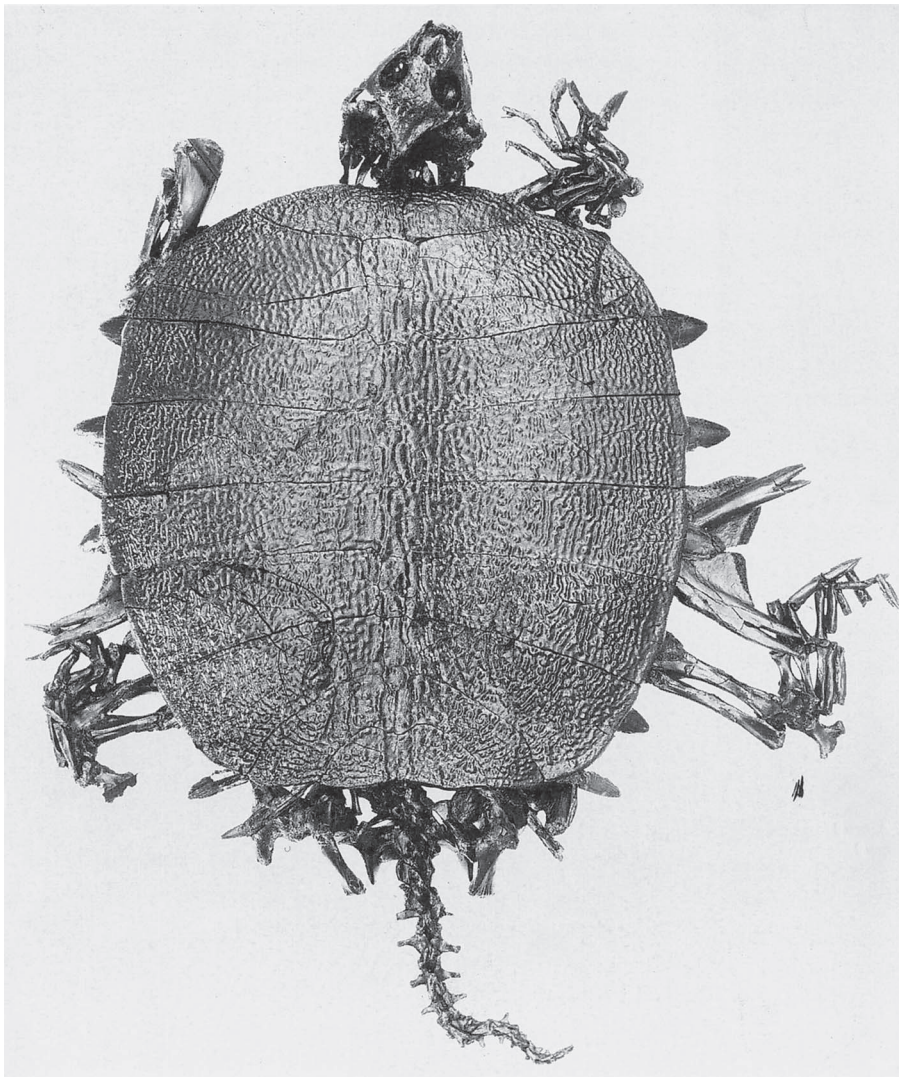
Underlying the oil shale are up to 25 m of coarse sediments (Weber & Hofmann 1982). Surrounded by Upper Palaeozoic sediments, diorites, and granodiorites, these Early Tertiary sediments are preserved within a tectonic graben. This was part of a large rift lake system, accompanied by early rift volcanism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

### Sedimentary environment

Judging by its fossil content, the bituminous claystone was originally deposited on the bottom of a small lake at the beginning of the Middle Eocene (Early Lutetian, Early Geiseltalian), about  $49 \pm 1$  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 subtropical 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,  $\times 0.25$ . (Photograph courtesy of E. Haupt, Senckenberg Museum.)

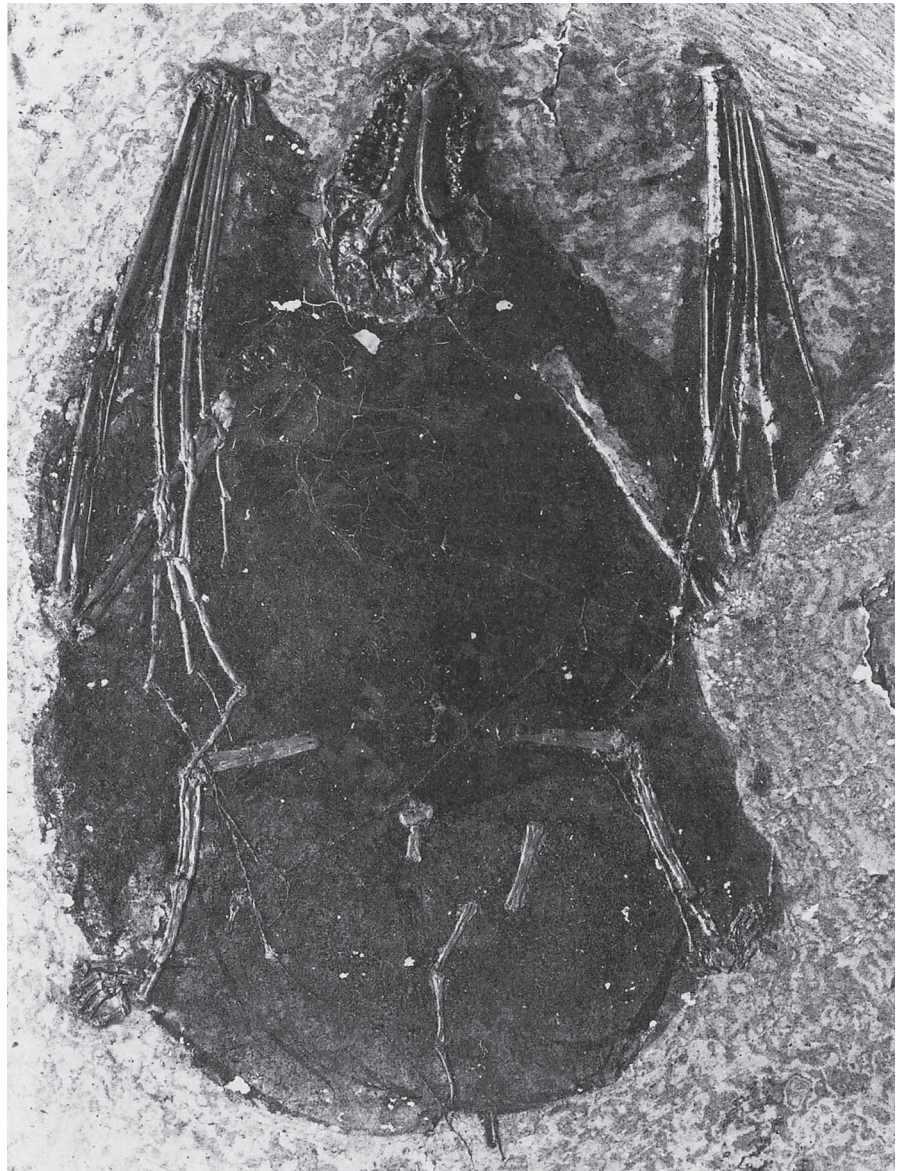


which prevented the development of any benthic macro-organisms. Therefore there was no bioturbation. Vertebrate carcasses were completely buried at the bottom of the lake and were neither destroyed by scavengers nor disturbed by currents. They did not rise again to the surface because the pressure of 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,  $\times 1.4$ . The bones within the body were dissolved during diagenesis. (Photograph courtesy of C. Schumacher, Senckenberg Museum.)



## Biota

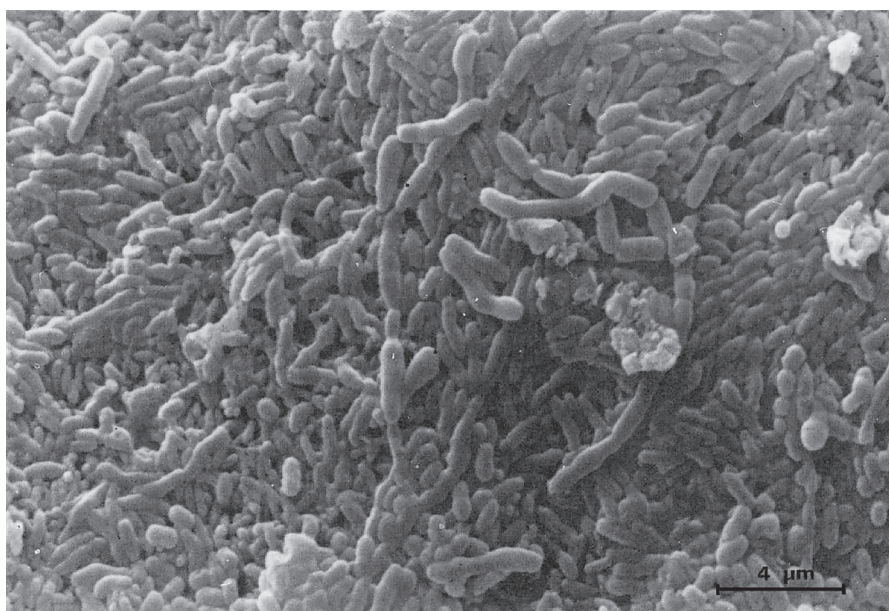
The fossils comprise plant remains (algae, fungi, diatoms, pollen, leaves, blossoms, fruits, seeds, and fragments of branches), spiculae and even gemulae of freshwater sponges, gastropods, ostracodes (moulds only), thousands of insects (mainly Coleoptera, Hymenoptera, and Heteroptera; but also Odonata, 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 archaeobacteria.

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,  $\times 4250$ . (Courtesy of G. Richter, Senckenberg Museum.)

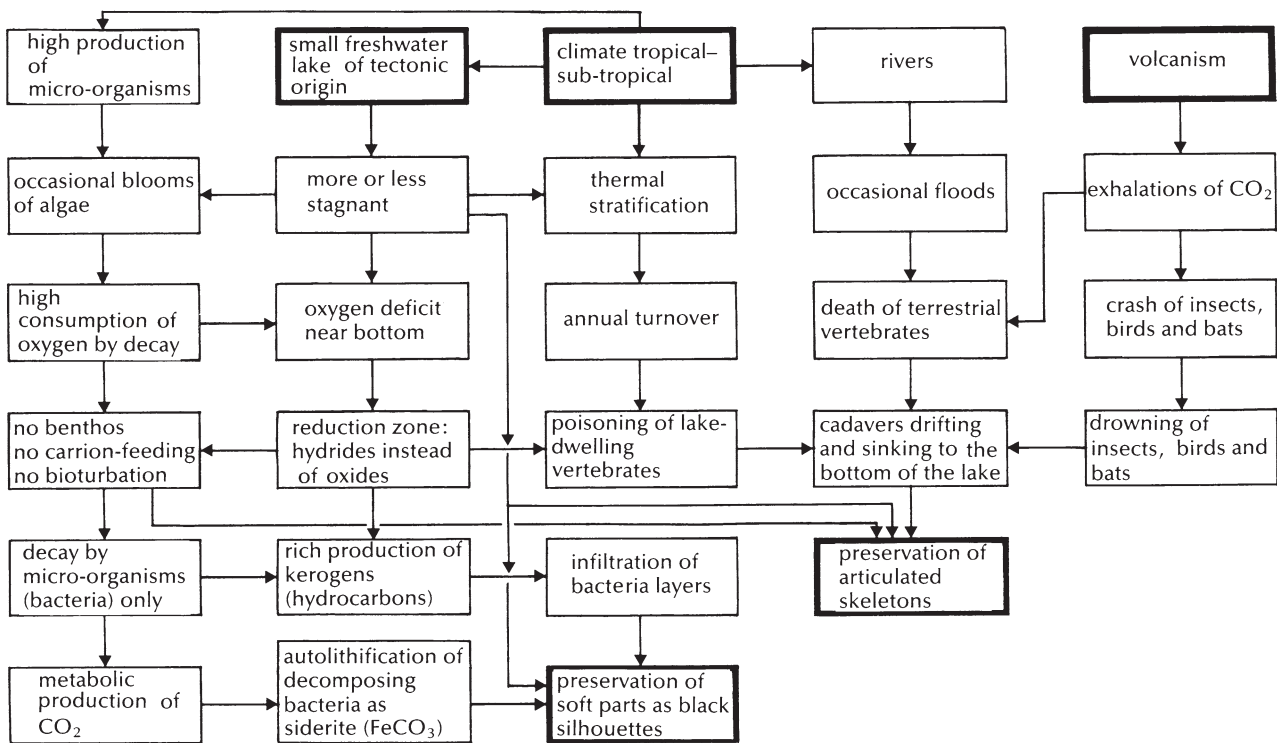


Fig. 4 Factors involved in the exceptional preservation of articulated skeletons, and so-called soft parts of Eocene vertebrates and insects from the Grube Messel (West Germany). (After Franzen in Whittington and Conway Morris 1985.)

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

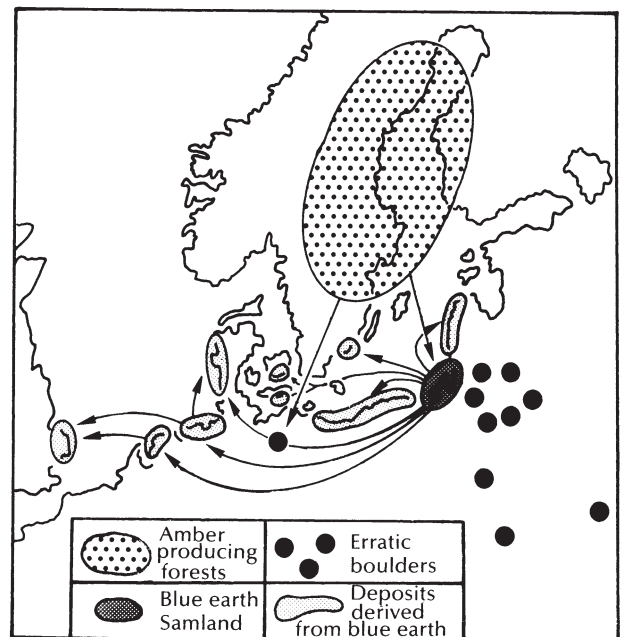


Fig. 1 Geographical setting of the Baltic amber-producing forests and their allochthonous deposits.



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 ventralabrum*, 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 combination 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.

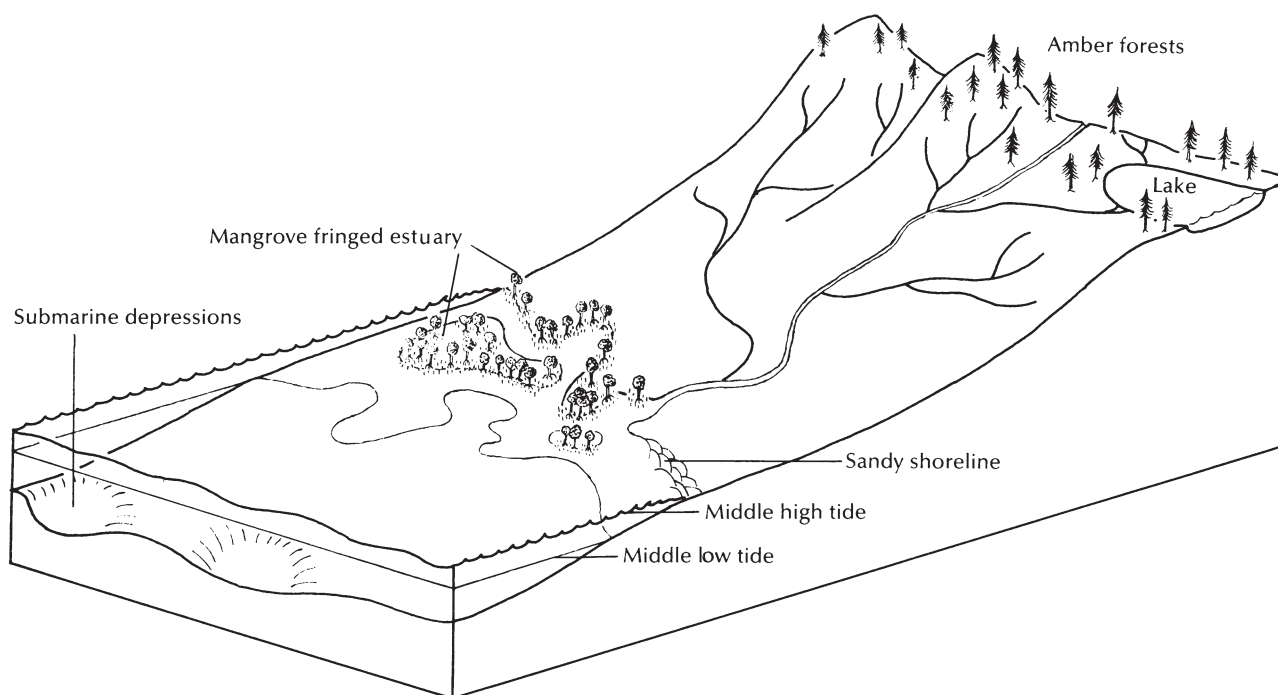


Fig. 2 Possible autochthonous and allochthonous deposits of amber.



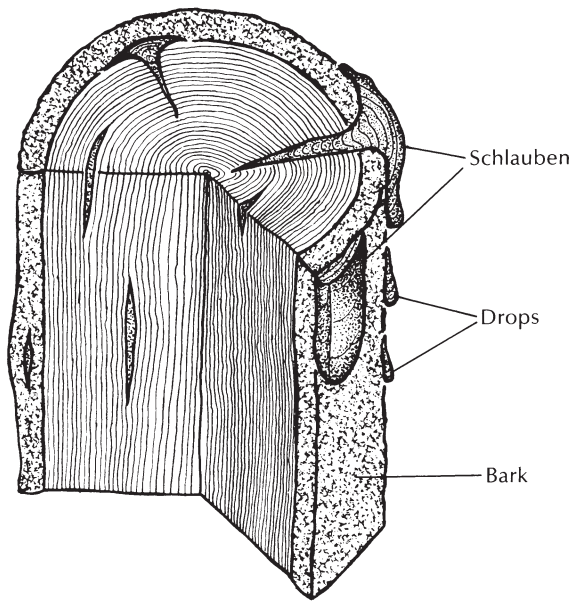


Fig. 3 The formation of resin. The schlauben are most effective as potential traps. (After Katinas 1971.)

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).

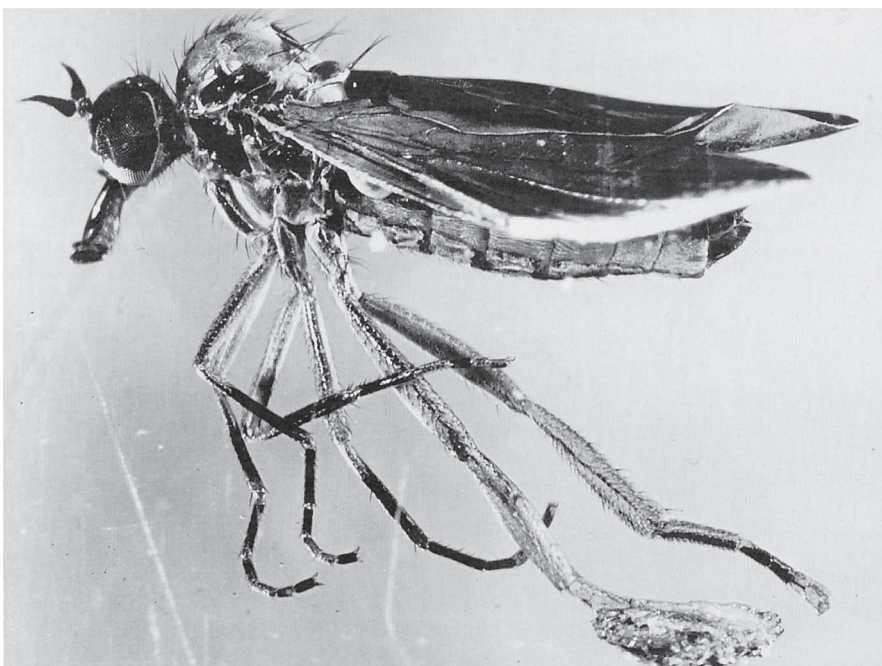


Fig. 4 A species of Diptera: Empididae from the Baltic amber.

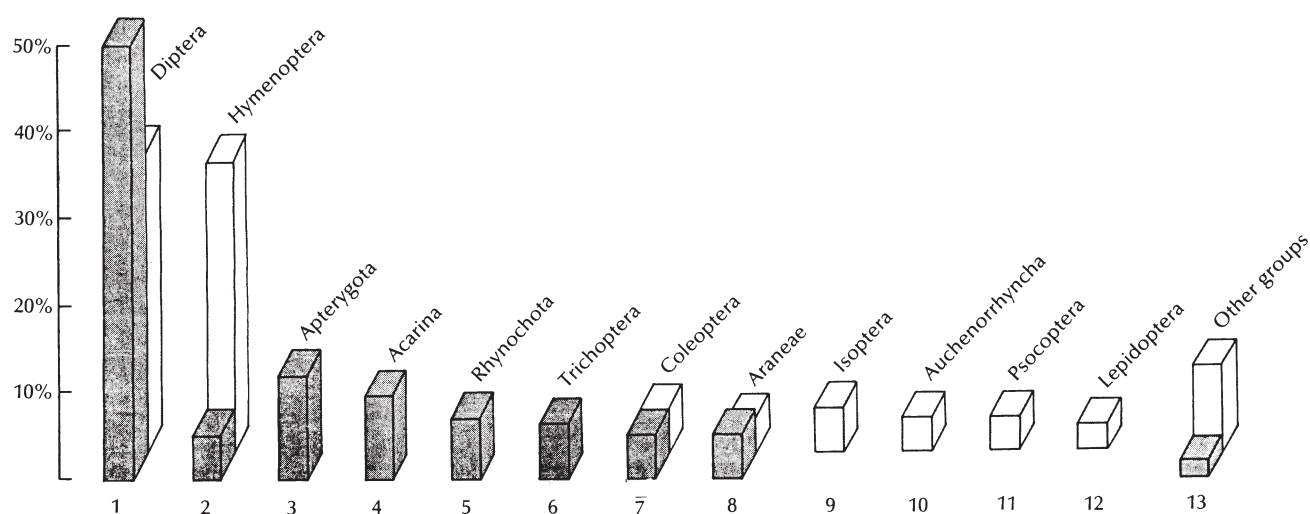


Fig. 5 Relative frequency of different higher systematic groups of animals in Baltic amber (anterior darker columns) and in amber of the Dominican Republic (Oligocene) (posterior lighter columns).

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

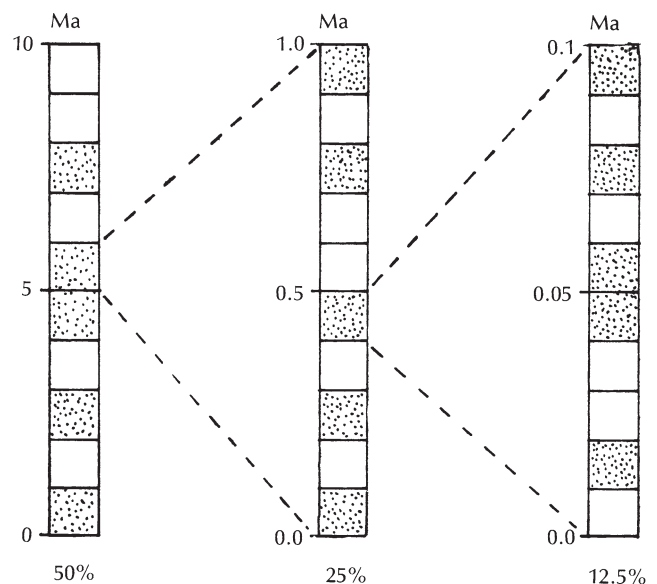
### Introduction

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 10000 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



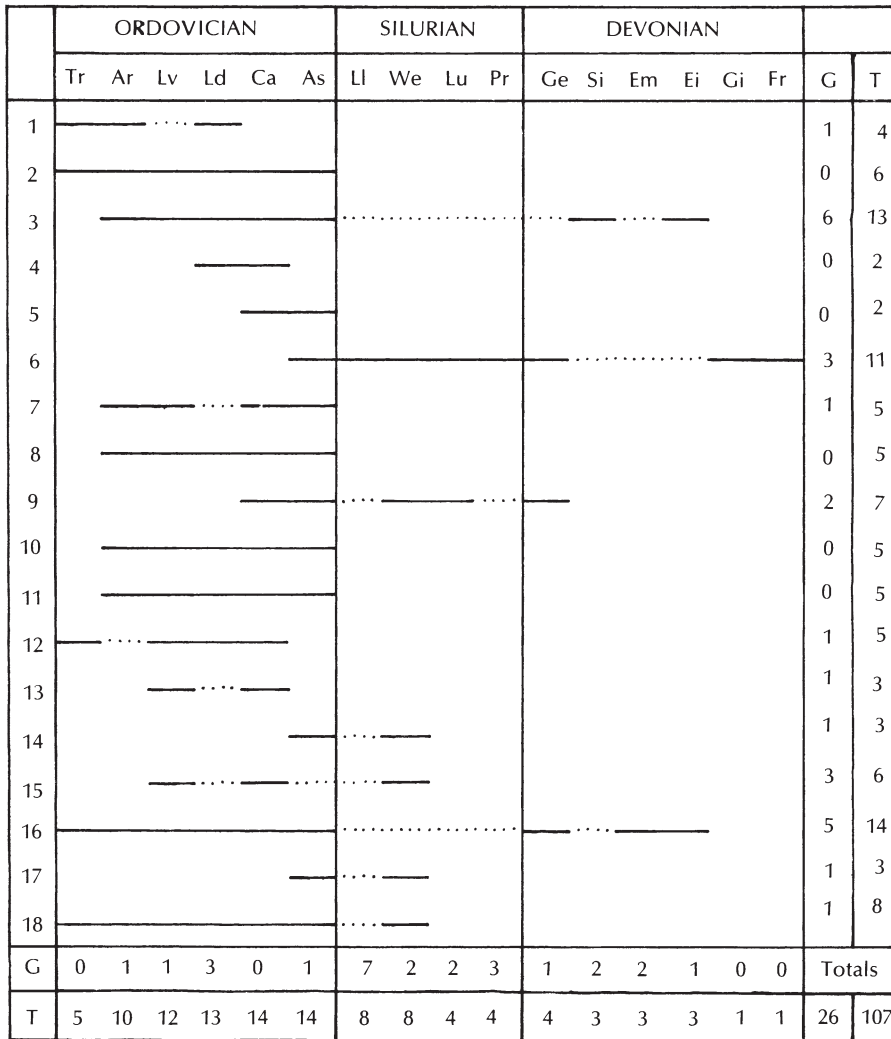
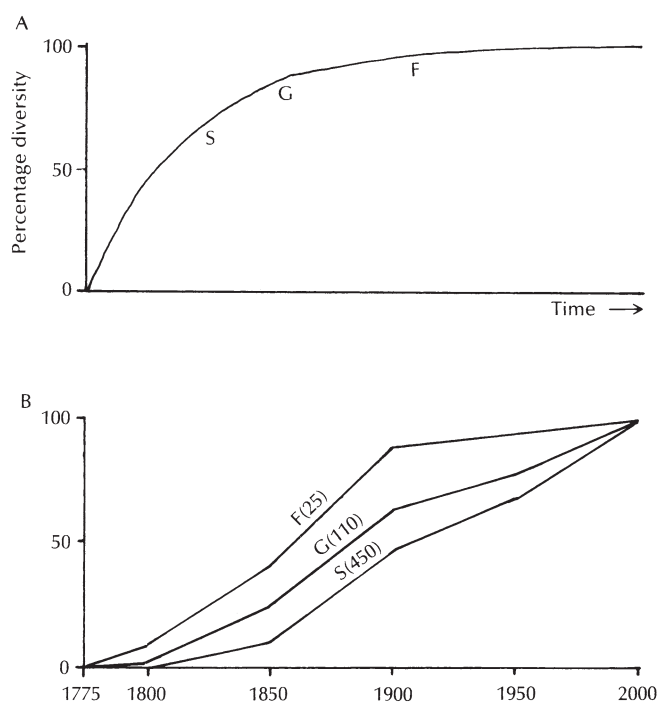


Fig. 2 Ranges of cystoid families known from more than one series, to show gaps (G) as well as total range (T). Known occurrences indicated by solid lines, gaps by dots. Rows give proportion of gaps for each family; columns for each stratigraphic interval. In both cases G/T yields the proportion of gaps.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



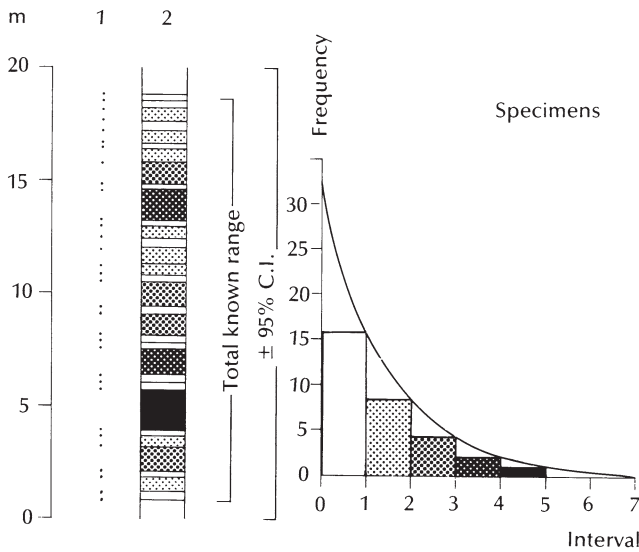


Fig. 4 Derivation of frequency curves from intervals in a measured section. The actual occurrences of specimens are plotted in column 1. The intervals between them are shaded according to size (column 2), in classes that are multiples of the median interval ( $i$ ). The frequency histogram is derived 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

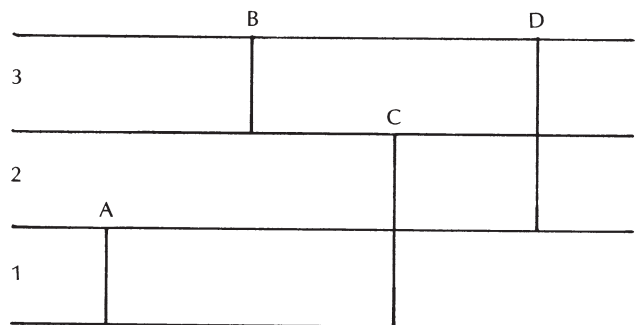


Fig. 5 Total original ranges over three time intervals (1–3) for two pairs of species. As the ranges of A and B do not overlap there is no chance whatsoever that they could be preserved in the wrong stratigraphic order. C and D did coexist (at time 2) and so could possibly be preserved in the wrong sequence. 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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