The Ecology of Fossils

an illustrated guide

edited by W. S. McKerrow

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Contents

Introduction

Palaeontology is the study of fossils, the remains of past life preserved in old sediments. Throughout geological time, there have been marked changes in the dominant animal and plant groups, while the total range of physical environments has changed very little.

In some instances, the changes in the fauna and flora are the result of progressive evolutionary changes in particular fossil lineages, but much more commonly the 'fossil record' shows that many organisms become widespread soon after they first appear; they may then flourish for a while before they become extinct and are replaced by another form. This changing pattern of forms of life in similar habitats is the basis for this book.

In a small village in western Newfoundland, I used to play cards with the schoolmaster's father in the evenings. I am sure he was the most intelligent man in the village. After I had been there for some time, he plucked up enough courage to ask me why I was not looking at the rocks up on the ridge where the old gold mines were. I told him I was not looking for gold, but (reaching into my bag and pulling out a slab of rock containing brachiopods) "I was looking for these". He studied the slab carefully and said, "Are these sea shells?" He had never seen a fossil before, nor even heard of fossils. This question reminded me of the best of the early eighteenth century palaeontologists. But my friend went on: "Does that mean the sea was once up here?" When I had replied "Yes", he then asked: "How long ago would that be then?" He clearly had all the makings of a first-class scientist. I replied, with a perfectly straight face, "About 450 million years ago", but I was not at all prepared for his final remark, "You'll be an atheist then".

This conversation demonstrates the type of questions asked by contemporary palaeontologists: Are these fossils marine? When and how did these animals live? What factors controlled where they lived?, and, though not really within the scope of this book, Why do they each have characteristic structures and shapes?

Plenty of books have been written on fossils, but in this book fossil assemblages, rather than individual genera or species, are the units of study. Only a selection of these is illustrated. Many fossils are not mentioned, for this book is not a treatise. Its main purpose is to educate and stimulate, rather than to describe every known fossil. We hope it will make the reader think about fossils in new ways, and lead to a better understanding of past life. Nowadays, most major fossil groups have been described (see, for example, the *Treatise on Invertebrate Paleontology,* (Ed.) R.C. Moore and C. Teichert, and *Vertebrate Paleontology* by A. S. Romer) and the most exciting and significant advances in palaeontology are being made by considering fossils as animals, and not just as formed stones. The study of palaeoecology includes attempts at reconstructing the relationships between organisms and sediments and the interactions between organisms, including those with no close relatives now living. This has direct implications for palaeogeography, stratigraphy, and certain aspects of structural geology (like the development and evolution of sedimentary basins, and the recognition of old oceans). In addition, the knowledge of past environments and their inhabitants has important contributions to make to evolutionary biology and to the whole history of the Earth.

The selection of communities illustrated in this book has been largely based on those found in the British Isles, but the range is such that most marine fossil communities throughout the world have some close parallel with a community illustrated here.

COMMUNITIES

A community is a group of organisms living together. The term is sometimes applied to organisms which depend on each other in some way (such as for food, or for protection), but in palaeontology it is normally only applied to organisms living in the same habitat.

At any one time there are different communities of animals living in different environments. The study of animals in relation to each other and to their habitats is known as ecology. Modern communities can be examined to determine not only where animals and plants live, but how they interact, especially in providing food and protection for each other. In looking at fossil associations, the palaeoecologist can describe those forms which occur together, but he can only speculate as to their interactions. Biologists argue as to whether a community should be defined according to the animals' habitat or according to their interactions. There is no doubt that, in the study of fossils, only the habitat definition can be used. The definition of "Community" used throughout this book is thus: a group of animals living in the same habitat.

The communities in this book are all known to be recurring assemblages; they are not just random collections of fossils. Some of the faunas illustrated have been analysed statistically in great detail, but many others have only been qualitatively assessed. To some extent the diagrams must be considered as cartoons in that they emphasize those elements which are most easily preserved as fossils (by having hard parts or recognizable burrows). The soft parts of extinct organisms are, of course, conjectural. The reconstructions presented here are based on the best information available, but they are deduced largely from similar organisms alive today, so there is a considerable element of informed guesswork in many of the illustrations.

It may well be that further work will indicate the presence of other animals and plants in these communities. On the other hand, it may eventually be seen that some of the communities described in this book in fact have members which occupied slightly different habitats. In the geological record, it is not always easy to separate fossils which occur together in a deposit, but which lived at slightly different times. Most fossil collections include those animals which have lived in one area over a period of several years, or possibly several centuries. So, even if the shells have not been transported after death, there may be a greater variety of animals on a square metre of a bedding plane than could have existed at any one time while that bedding plane was exposed on the sea floor.

It should also be stressed that the communities illustrated have been selected either because they are the most commonly occurring or because they are of particular interest. The vast majority of ancient communities still await description, and other palaeontologists would certainly make a different selection.

Modern aquatic organisms can be classified according to where they live (Figure a). Those which float or drift are known as plankton and are dominantly pelagic, that is, they live mostly on or near the surface of the sea. Actively swimming animals, like many fish and cephalopods, are called nekton. Bottom-dwelling organisms (benthos) can be placed in one of two categories: epifauna which live on the substrate, which may be soft sediment, rock or vegetation, and infauna which live within the substrate (burrowers or borers).

Plankton can be subdivided according to size (microplankton are those organisms which can only be studied under a microscope); they can also be classified according to their methods of obtaining energy: whether they manufacture their foodstuffs by photosynthesis (like most plants) or whether they feed on organisms or organic debris (like most animals). In many simple small organisms, the difference between the animal and plant kingdoms becomes blurred. In groups of apparently closely related organisms, some may employ photosynthesis and some not, and

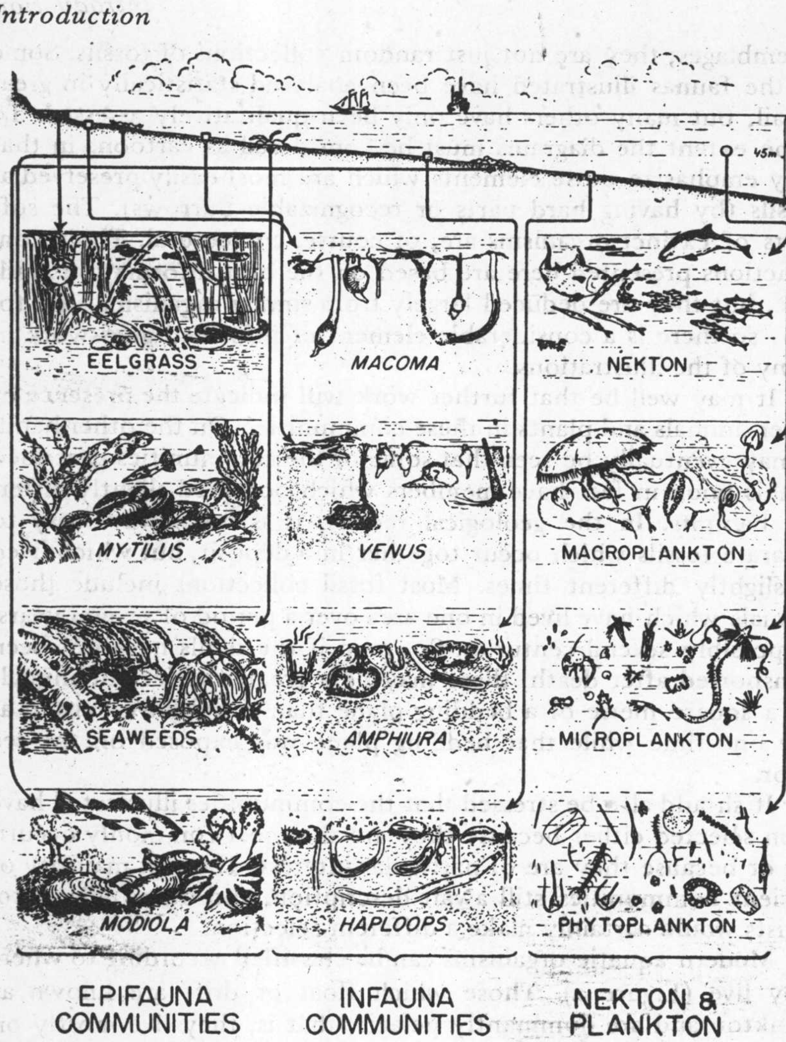

Fig. a. ***Modern animal communities between Denmark and Sweden (from Hedgpeth, 1957, p. 31 with permission).***

in common with other recent publications (e.g. *Treatise on Invertebrate Paleontology*) we refer these simple organisms to a third kingdom: Protista.

There are some problems in our definition of a community. For example, are the animals living above (or below) the sea floor to be included in the same habitat as those on the sediment surface? It is quite reasonable to argue that they are not, but for the purpose of this book, we frequently show free-swimming animals in the same diagram as the benthos on the floor below. However, in Figure a (above) the epifaunal and infaunal organisms are shown as separate communities.

Within a single habitat there can be many niches. For example, on a particular patch of sea floor there may exist, side by side, epifaunal suspension-feeding bivalves attached by byssal threads to shell fragments on the sea floor, infaunal burrowing deposit-feeding crustaceans, epifaunal suspension-feeding serpulid worms encrusting some of the bivalves, and an epifaunal carnivorous gastropod boring the bivalves with its rasp-like radula. Each of these animals is in a distinct niche within the same habitat.

In many fossil assemblages, the niche occupied by a particular organism can often be determined by a comparison with present day animal and plant communities, but further back in time we see fewer and fewer close relatives of living organisms, and other criteria (like the type of sediments or geographical distributions) have to be used to determine the ecology of these ancient assemblages. In some cases geologists have produced very convincing evidence for accurate interpretations of ancient environments, but in other instances there is still much uncertainty.

Many modern marine communities have sharp boundaries. At the margin of a rock outcrop in the sea, the mussels, limpets and winkles (*Mytilus, Patella* and *Littorina*) living on the rock will suddenly give way to sand-dwelling cockles and heart urchins (*Cardium* and *Echinocardium*). There is no difficulty in recognizing a different bottom-dwelling community in a case like this. A change from clean sand to muddy sand will allow a great increase in deposit feeders and a marked reduction in sessile epifauna. Here again, though the change may be more gradual, there is a reasonable boundary between the two distinct habitat communities.

Many fossil collections from Palaeozoic rocks consist largely of suspension-feeding brachiopods, and thus contain very few fossils which were not suspension feeders. Some beds show burrows (perhaps made by annelid worms or arthropods) and there must have been carnivores or scavengers around, but their fossil record is very poor by comparison with that of the brachiopods. Five Silurian communities have been described (Ziegler, 1965) living on the sea floor between the coast and the deep sea. A single sample from each community is very distinctive, but when a large number of samples are made gradations between most of the communities become evident, and some arbitrary decisions, depending on the proportions present of certain selected species, have to be made to define the community boundaries. We still do not yet know in many cases which fossil communities are gradational and which are not, but it must be borne in mind that those communities described here (especially those with a high proportion of suspension feeders) may be arbitrary points on an ecological gradient.

ECOLOGICAL CONTROLS

In the sea, the factors controlling the distribution of organisms can be classified as:

1. Biological: food supply, competition from other organisms, and sometimes protection by or dependence on other organisms.
2. Physical: the sedimentary environment, turbulence, currents, temperature, light intensity.
3. Chemical: salinity, water and substrate chemistry.

Some of these controls are related to depth (light, turbulence, temperature fluctuations and suspended organic matter all show a general decrease with depth), but hydrostatic pressure only has marked effects in the deepest environments, so depth alone is not a significant control.

Latitude is closely related to temperature, but temperature can vary according to the distribution of oceanic currents. Many marine organisms are restricted by temperature and other factors which may change with latitude, but latitude by itself is not a primary control.

Every animal needs to feed, and different methods of feeding can restrict animals to certain habitats. Marine animals (and it is these we are chiefly concerned with in this book) can be classified into four types of feeders (Raup and Stanley, 1971):

1. Grazers, which remove algal and other encrusting organic material from rocks and other hard surfaces.
2. Deposit feeders, which ingest sediment and feed on the organic matter coating the grains or mixed with the grains.
3. Suspension feeders, which select organic matter suspended in water.
4. Carnivores and scavengers, which eat other animals alive or dead.

Grazers normally inhabit rocky areas which are coated by organic films, they are thus generally confined to shallow water areas where bare rock is exposed, but they can occur in deeper water if suitable substrates are present.

Deposit feeders are often burrowers in muddy sediments, especially if the mud is mixed with a little sand or silt so that stable burrow systems can be developed. Organic matter in sediments normally occurs as a thin coating on individual grains of sediment. With decreasing grain size, the proportion of surface area in a given volume will increase. Thus fine grained sediments contain more organic matter and can support greater densities of deposit feeders. Fine grained sediments can occur in all depths of water.

The infauna are protected by their burrows; many of them have no external hard parts, and those that do often have thinner shells (or other external covering) than the epifauna exposed above the substrate. Many burrowing animals (especially worms and some decapod crustaceans) are thus rare as fossils although their burrow systems may be quite common. Deposit feeders often have characteristic complex burrow systems, which are developed as they search for food (these are in marked contrast to the simple burrows produced by infaunal suspension feeders).

Suspension feeders may be epifaunal, infaunal or pelagic. They include sedentary animals like corals, bryozoans, brachiopods, many bivalves and the crinoids, all of which have well-developed hard parts and are thus common as fossils. Their main food supply is probably diatoms and other protists which rely on photosynthesis, and which can thus only develop in abundance very near the surface of the sea (Ryther, 1963). The pelagic larval stages of many marine invertebrates also feed on these protists and live with them near the surface of the oceans. These larvae are also an important part of the marine food chain. Much more of this (protist and larval) food supply is thus available on the sea floor in shallow water areas; these are the areas, both today and in the Palaeozoic, where the majority of suspension feeders live.

Although well endowed with food supplies, the shallow water faunas have to contend with high environmental stresses, including much variation in sedimentary deposition rates, the unsettling effects of storms, and (except in low latitudes) fluctuations in temperature. So the only places for a quiet life (in a stable environment) are those where food is scarce. In the deep sea, there are sparse, but diverse, populations of specialized benthos. It is possible that some epifauna (e.g. spiriferide brachiopods) developed especially efficient feeding systems to cope with a limited food supply in these deep bottom environments.

Suspension-feeding epifauna usually require a stable anchorage, and are thus more common (at least since the Mesozoic) on stable sands and silts rather than on muds. Moreover, a large mud supply would tend to choke the filter-feeding structures of many bivalves. It has recently been suggested (Steele-Petrovic, 1975) that some brachiopods can tolerate a high mud flow through their feeding structures. This may account for the fact that in the Palaeozoic, when brachiopods were a major part of these epifaunal communities, there appears to have been a much lower correlation between an epifaunal community and the sediment on which it rested than there is at present time (Ziegler, 1965).

Rocky bottom communities consist mainly of suspension feeders and grazers; they are a mixture of epifauna and of infaunal boring animals. In the geological record they are restricted to beds immediately above depositional breaks and to hardgrounds. As far as we understand them at present, the animals inhabiting rocky bottoms have always formed quite distinct communities from those on areas of unconsolidated sediments.

Carnivores and scavengers feed on other animals. They can thus never be as abundant as suspension feeders and deposit feeders. Today, certain worms, echinoderms, gastropods and fish are the most important carnivores on the sea floor; similar forms are also present as far back as the Mesozoic. The direct evidence for early carnivores is very meagre; before fish became common in the sea and before gastropods developed radulae, soft-bodied worms, arthropods, medusoids and sea-anemones appear to have been the most probable carnivores and scavengers. If a carnivore species becomes specialized in its choice of food, it will naturally become a member of the animal community in the habitat where its food is situated. Unspecialized carnivores may, on the other hand, feed on members of several communities and thus extend over broader areas than any one species of the suspension feeders or deposit feeders on which they prey.

It can be concluded from the above discussion that Mesozoic, Tertiary and modern bottom-dwelling communities are more intimately linked with sediment type than those in the Palaeozoic (except for some early Palaeozoic communities which were dominated by the deposit-feeding trilobites). All communities appear to be influenced to some extent by depth of water, but this influence has nothing to do with hydrostatic pressure. There is no question of depth control, but depth is correlated with greater food supply in shallow environments, and with uniform conditions on deeper sea floors. It will be observed that in this book the community names reflect this change with time. Those from the Ordovician to the Carboniferous are often named after a characteristic genus or species, while those in the Cambrian and from the Jurassic onwards are normally named after the habitat in which they occur.

Plankton and nekton may occur in all depths of water. The chief controls which govern their distribution are temperature, salinity and water currents. Their abundance can vary greatly with the distribution of dissolved nutrients in the water. Many migrate long distances during their life span, and seasonal changes in distribution are common in many groups. From the palaeontological point of view, plankton and nekton are not always very reliable indicators of the environment in which they are found fossil; many may drift for long distances after death. For example, *Nautilus* shells have been recovered from Madagascar and Japan, though living forms are only known between Australia, the Philippines and the Fiji Islands.

Salinity is largely independent of water depth or sediment. In most open seas the salinity is nearly constant at about 35 parts of dissolved salts to a thousand parts of water. But in isolated or semi-isolated seas and lagoons this may change a great deal: much of the Baltic Sea, for example, has a salinity of less than 10 parts per thousand, while in areas subject to high evaporation rates the salinity may increase to over 40 parts per thousand or much more.

When there is a change in salinity (either upwards or downwards) only the more tolerant (euryhaline) species survive. Most marine species are not very tolerant of changes in salinity (they are stenohaline), so that the effect of any marked change is reflected by a reduction in the number of species present. But this does not necessarily mean that there are fewer animals; many brackish water regions contain an abundance of individuals of a very few species. It is often possible to determine salinity tolerance in extinct species. If a sedimentary formation changes from normal marine deposits into brackish water deposits, a series of fossil collections may then show a progressive reduction in the number of species present. In the Middle Jurassic of England, for instance, it is possible to deduce that ammonites are among the most stenohaline animals, and that certain oysters are among the most euryhaline.

In addition to the marine faunas, there are some aquatic organisms which have become adapted exclusively to fresh water. These are usually stenohaline, that is, they are restricted to fresh water; but some species are euryhaline and can extend their range into brackish environments, where they may occur with euryhaline marine species.

STRATIGRAPHIC NOMENCLATURE

With the development of stratigraphy, it has been found useful to develop a standard method of nomenclature. The Cambrian **System** consists of rocks deposited during the Cambrian **Period**. The system consists of rocks; while the period is the time during which these rocks were formed. Both terms have an age connotation.

Systems are recognized and defined by the fossils they contain. If the fossils within a system can be shown to change regularly with time, systems can be subdivided into series, stages and zones, each of which represent the rocks laid down during shorter intervals of time respectively (as recognized by the fossils).

The systems are grouped together into eras. After the Precambrian, there are three eras: Palaeozoic, Mesozoic and Cenozoic (Table 1). The Cenozoic Era can be divided into the Tertiary (Palaeocene to Pliocene) and the Quaternary.