PART 1

Applied micropalaeontology

CHAPTER 1

Introduction

Microfossils – what are they?

A thin blanket of soft white to buff-coloured ooze covers one-sixth of the Earth's surface. Seen under the microscope this sediment can be a truly impressive sight. It contains countless numbers of tiny shells variously resembling miniature flügelhorns, shuttlecocks, water wheels, hip flasks, footballs, garden sieves, space ships and chinese lanterns. Some of these gleam with a hard glassy lustre, others are sugary white or strawberry coloured. This aesthetically pleasing world of microscopic fossils or microfossils is a very ancient one and, at the biological level, a very important one.

Any dead organism that is vulnerable to the natural processes of sedimentation and erosion may be called a **fossil**, irrespective of the way it is preserved or of how recently it died. It is common to divide this fossil world into larger **macrofossils** and smaller **microfossils**, each kind with its own methods of collection, preparation and study. This distinction is, in practice, rather arbitrary and we shall largely confine the term 'microfossil' to those discrete remains whose study requires the use of a microscope throughout. Hence bivalve shells or dinosaur bones seen down a microscope do not constitute microfossils. The study of microfossils usually requires bulk collecting and processing to concentrate remains prior to study.

The study of microfossils is properly called **micropalaeontology**. There has, however, been a tendency to restrict this term to studies of mineral-walled microfossils (such as foraminifera and ostracods), as distinct from **palynology** the study of organic-walled microfossils (such as pollen grains, dinoflagellates and acritarchs). This division, which arises largely from differences in bulk processing techniques, is again rather arbitrary. It must be emphasized that macropalaeontology, micropalaeontology and palynology share identical aims: to unravel the history of life and the external surface of the planet. These are achieved more speedily and with greater reward when they proceed together.

Why study microfossils?

Most sediments contain microfossils, the kind depending largely on the original age, environment of deposition and burial history of the sediment. At their most abundant, as for example in back-reef sands, 10 cm^3 of sediment can yield over 10,000 individual specimens and over 300 species. By implication, the number of ecological niches and biological generations represented can extend into the hundreds and the sample may represent thousands if not hundreds of thousands of years of accumulation of specimens. By contrast, macrofossils from such a small sample are unlikely to exceed a few tens of specimens or generations. Because microfossils are so small and abundant (mostly less then 1 mm) they can be recovered from small samples. Hence when a geologist wishes to know the age of a rock or the salinity and depth of water under which it was laid down, it is to microfossils that they will turn for a quick and reliable answer. Geological surveys, deep sea drilling programmes, oil and mining companies working with the small samples available from borehole cores and drill cuttings have all therefore employed micropalaeontologists to learn more about the rocks they are handling. This commercial side to micropalaeontology has undoubtedly been a major stimulus to its growth. There are some

philosophical and sociological sides to the subject, however. Our understanding of the development and stability of the present global ecosystem has much to learn from the microfossil record, especially since many microfossil groups have occupied a place at or near to the base of the food web. Studies into the nature of evolution cannot afford to overlook the microfossil record either, for it contains a wealth of examples. The importance of understanding micro-fossils is further augmented by discoveries in Pre-cambrian rocks; microfossils now provide the main evidence for organic evolution through more than three-quarters of the history of life on Earth. It is also to microfossils that science will turn in the search for life on other planets such as Mars.

The cell

A great many microfossils are the product of single-celled (**unicellular**) organisms. A little knowledge of these cells can therefore help us to understand their way of life and, from this, their potential value to Earth scientists. Unicells are usually provided with a rel-atively elastic outer **cell membrane** (Fig. 1.1) that binds and protects the softer cell material within, called the
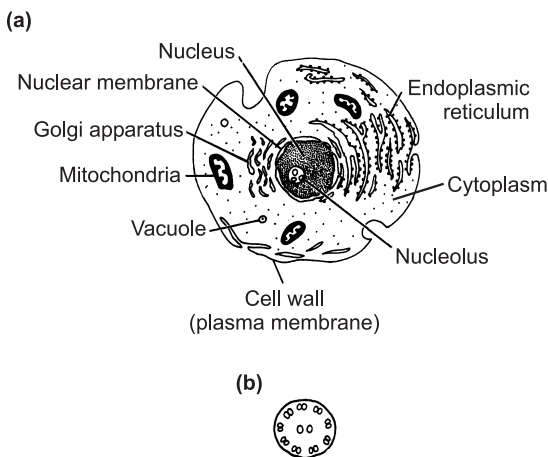
(a)

(b)

Fig. 1.1   The living cell. (a) Eukaryotic cell structure showing organelles. (b) Cross-section through a flagellum showing paired 9+2 structure of the microfibrils. (Reproduced with permission from Clarkson 2000.)

cytoplasm (or **protoplasm**). Small 'bubbles' within the cytoplasm, called **vacuoles**, are filled with food, excret-ory products or water and serve to nourish the cell or to regulate the salt and water balance. A darker, membrane-bound body, termed the **nucleus**, helps to control both vegetative and sexual division of the cell and the manufacture of proteins. Other small bodies concerned with vital functions within the cell are known as **organelles**. The whip-like thread that protrudes from some cells, called a **flagellum**, is a locomotory organelle. Some unicells bear many short flagella, col-lectively called **cilia**, whilst others get about by means of foot-like extensions of the cell wall and cytoplasm, known as **pseudopodia**. Other organelles that can occur in abundance are the **chromoplasts** (or chloroplasts). These small structures contain chlorophyll or similar pigments for the process of photosynthesis.

Nutrition

There are two basic ways by which an organism can build up its body: by heterotrophy or by autotrophy. In **heterotrophy**, the creature captures and consumes living or dead organic matter, as we do ourselves. In **autotrophy**, the organism synthesizes organic matter from inorganic CO_2, for example, by utilizing the effect of sunlight in the presence of chlorophyll-like pigments, a process known as **photosynthesis**. Quite a number of microfossil groups employ these two strategies together and are therefore known as **mixotrophic**.

Reproduction

Asexual (or vegetative) and **sexual** reproduction are the two basic modes of cellular increase. The simple division of the cell found in asexual reproduction results in the production of two or more daughter cells with nuclear contents similar in proportion to those of the parent. In sexual reproduction, the aim is to halve these normal nuclear proportions so that sexual fusion with another 'halved' cell can eventually take place. Information contained in each cell can then be passed around to the advantage of the species. This halving

process is achieved by a fourfold division of the cell, called **meiosis**, which results in four daughter cells rather than two.

The empires of life

Living individuals all belong to naturally isolated units called **species**. Ideally, these species are freely interbreeding populations that share a common ecological niche. Even those lowly organisms that disdain sexual reproduction (such as the silicoflagellates) or do not have the organization for it (such as the cyanobacteria), occur in discrete morphological and ecological species. Obviously it is impossible to prove that a population of microfossils was freely interbreeding but, if specimens are sufficiently plentiful, it is possible to recognize both morphological and ecological discontinuities. These can serve as the basis for distinguishing one fossil species from another.

Whereas the species is a functioning unit, the higher taxonomic categories in the hierarchical system of classification are mere abstractions, implying varying degrees of shared ancestry. All species are placed within a **genus** that contains one or more closely related species. These will differ from other species in neighbouring genera by a distinct morphological, ecological or biochemical gap. **Genera** (plural of genus) tend to be more widely distributed in time and space than do species, so they are not greatly valued for stratigraphical correlation. They are, however, of considerable value in palaeoecological and palaeogeographical studies. The successively higher categories of **family**, **order** and **class** (often with intervening sub- or super-categories) should each contain clusters of taxa with similar grades of body organization and a common ancestor. They are of relatively little value in biostratigraphy and palaeoenvironmental studies. In 'animals' the **phylum** taxon is defined on the basis of major structural differences, whereas in 'plants' the corresponding **division** has been defined largely on structure, life history and photosynthetic pigments.

An even higher category is the **kingdom**. In the nineteenth century it was usual to recognize only the two kingdoms: Plantae and Animalia. Plants were considered to be mainly non-motile, feeding by photosynthesis. Animals were considered to be motile, feeding by ingestion of pre-formed organic matter. Although these distinctions are evident amongst macroscopic organisms living on land, the largely aqueous world of microscopic life abounds with organisms that appear to straddle the plant–animal boundary. The classification shown in Box 1.1 overcomes these anomalies by recognizing seven kingdoms: the Eubacteria, Archaebacteria, Protozoa, Plantae, Animalia, Fungi and Chromista.

The highest category is the **empire**. The classification of the empire Bacteria will be considered further in Chapter 8. The Bacteria are single celled but they lack a nucleus, cell vacuoles and organelles. This primitive **prokaryotic** condition, in which proper sexual reproduction is unknown, is characteristic of such forms as cyanobacteria. The empire is currently divided into two kingdoms, the Archaebacteria and the Eubacteria. The other five kingdoms are **eukaryotic**. That is their cells have a nucleus, vacuoles and other organelles and are capable of properly coordinated cell division and sexual reproduction. Attempts to divide unicellular eukaryotic organisms, often called **protists**, into plants or animals based on feeding style were abandoned when it was recognized that dinoflagellates, euglenoids and heterokonts have members that are both photosynthetic and heterotrophic, feeding by engulfing. Since the 1970s both ultrastructural analysis under the scanning electron microscope and molecular sequences have been used to elucidate protistan phylogenies and develop a large-scale classification. The new classification of Cavalier-Smith (1981, 1987a, 1987b, 2002) has put forward two new categories: the predominantly photosynthetic kingdom **Chromista** (brown algae, diatoms and their various relatives) and the primitive superkingdom **Archezoa** (which lack mitochondria (**amitochondrial**)). He has also proposed an ultrastructurally based redefinition of the kingdom **Plantae** which requires the exclusion of many aerobic protists that feed by ingestion (**phagotropy**). The kingdom **Protozoa** is now considered to contain as many as 18 phlya (Cavalier-Smith 1993, 2002) and their classification and phylogenetic relationships, which is in a state of flux, is largely based upon cell ultrastructure and increasingly sophisticated analyses of new molecular sequences. The kingdom

Empire	Superkingdom	Kingdom	Subkingdom(s)
BACTERIA		EUBACTERIA	NEGIBACTERIA
			POSIBACTERIA
		ARCHAEBACTERIA	
EUKARYOTA	ARCHEZOA		
	METAKARYOTA	PROTOZOA	GYMNOMYXA
			CORTICATA
		PLANTAE	VIRIPLANTAE (green plants)
			BILIPHYTA (red algae and glaucophytes)
		ANIMALIA	RADIATA
			BILATERATIA
		FUNGI	
		CHROMISTA	CHLORARACHINA
			EUCHROMISTA (cryptomonads, *Goniomonas*, heterokonts, haptophytes)

Fig. 1.2 The empires of life. (Modified from Cavalier-Smith 1993.)

Protozoa includes two subkingdoms, the Gymnomyxa and Corticata. Members of the Gymnomyxa have a 'soft' cell wall often with pseudopodia or axopodia (e.g. foraminifera). The Corticata are ancestorally biciliate (e.g. dinoflagellates).

Members of the superkingdom Archezoa differ from most Protozoa in having ribosomes, the RNA-protein structures on which messenger RNA is 'read' during protein synthesis, found in all other eukaryotes, and they also lack certain other organelles (e.g. mitochondria, Golgi bodies). The Archezoa comprise three phyla: the Archamoebae, Metamonada and Microsporidia. There is reasonable rDNA phylogenetic evidence to suggest that the latter two represent surviving relics of a very early stage in eukaryote evolution. The evolution of the eukayotes can thus be divided into two major phases. The origin of the eukaryote cell (the first archezoan) is marked by the appearance of the membrane-bounded organelles, cytoskeleton, a three-dimensional network of fibrous proteins that give order and structure in the cytoplasm, nucleus and cilia with a 9+2 structure (Fig. 1.1). This was apparently followed by the symbiotic origin of mitochondria and peroxisomes (Margulis 1981; Cavalier-Smith 1987c) to produce the first aerobically respiring protozoan. The change in their ribosomes may have occurred somewhat later in their evolution.

The kingdom Chromista is a predominantly photosynthetic category in which the chromoplasts are located in the endoplasmic reticulum but separated by a unique smooth membrane, thought to be a relic of the cell membrane of the photosynthetic eukaryotic symbiont that was 'engulfed' by the protozoan host, leading to the emergence of the Chromista (Cavalier-Smith 1981, 1987c). The Chromista contains a number of important microfossil groups such as the silicoflagellates, diatoms and calcareous nannoplankton.

The kingdon Plantae is taken to comprise two subkingdoms. The subkingdom Viriplantae includes the

green plants including the green algae (Chlorophyta), the Charophyta and the 'land plants' or the Embryophyta. The subkingdom Biliphyta includes the red algae (Rhodophyta) and the Glaucophyta. It is not yet clear whether these two subkingdoms are correctly placed together in a single kingdom or should be separate kingdoms. The Viriplantae have starch-containing chloroplasts and contain chlorophylls *a* and *b*. The Biliphyta have similar chloroplasts but there is a total absence of phagotrophy in this group.

The kingdom Fungi comprises heterotrophic eukaryotes that feed by the adsorption of pre-formed organic matter. They are rarely preserved in the fossil record and have received little study as fossils and are not considered further in this book.

The kingdom Animalia comprises multicellular invertebrate and vertebrate animals that feed by the ingestion of pre-formed organic matter, either alive or dead. Invertebrates that are microscopic when fully grown, for example the ostracods, are considered as microfossils, but we are obliged to leave aside the microscopic remains of larger animals (such as sponge spicules, echinoderm ossicles and juvenile individuals). For more information on the macro-invertebrate fossil record the reader is referred to our companion volume written by Clarkson (2000).

Microfossils that cannot easily be placed within the existing hierarchical classification, for example acritarchs, chitinozoa and scolecodonts, are accorded the informal and temporary status of a **group** in this book.

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