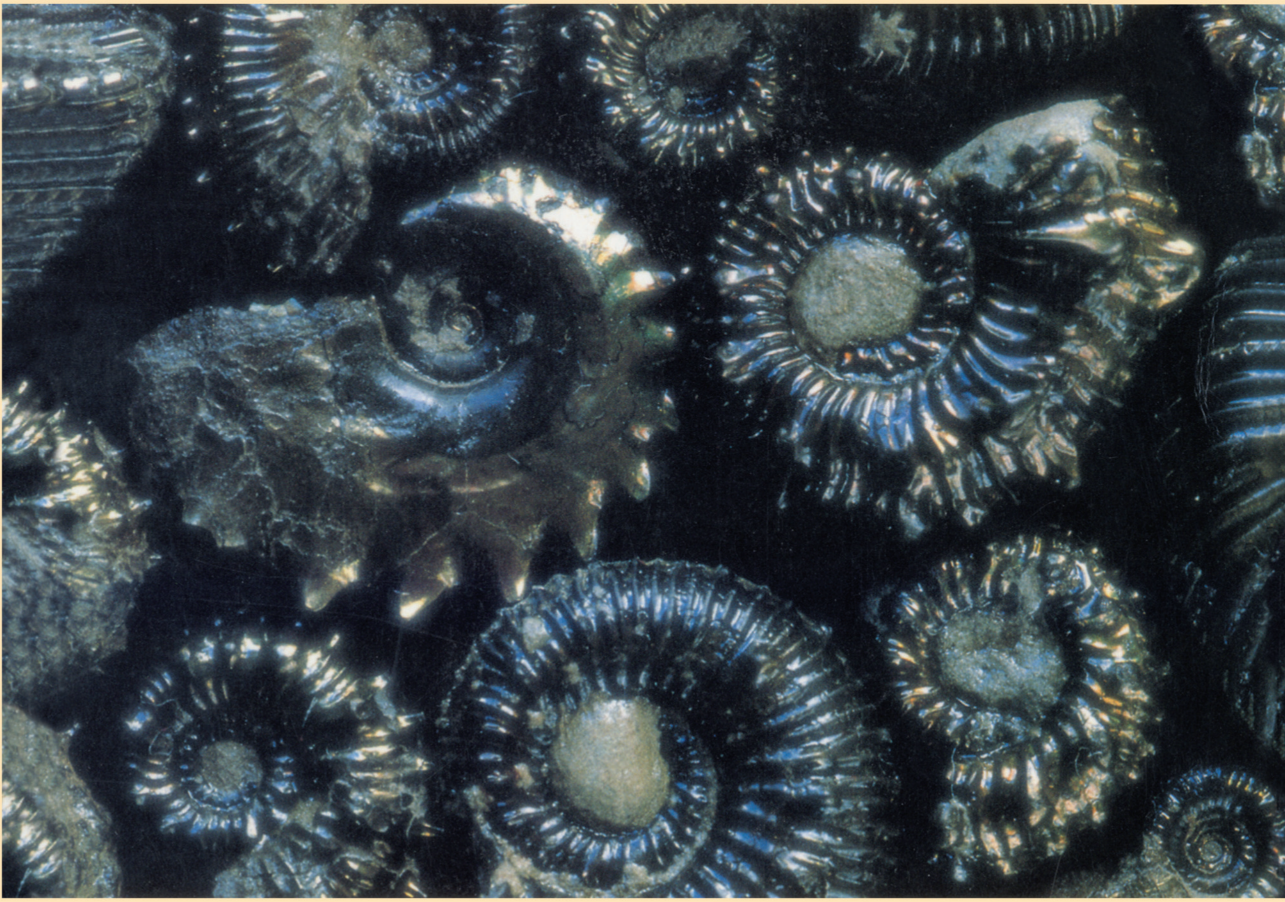
Understanding Fossils

An Introduction to Invertebrate Palaeontology



Peter Doyle

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An Introduction to Invertebrate Palaeontology

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with contributions by
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Preface

Fossils are among the most highly prized natural objects in the world. They figure in our everyday lives as decorative objects in our homes, and as the dinosaur products which fill the toy and book shops and which periodically appear in the cereal packets at our breakfast tables. Collecting fossils is an absorbing pastime which grades into a passion for weekend geologists, and many students enter higher education through their interest, reading for degrees in the earth sciences which have a direct benefit for the national economy.

Despite this, palaeontology is often one of the most neglected, misunderstood and poorly promoted subjects on the geological curriculum. It suffers from two preconceived ideas: that it is a subject steeped in Latin names, and that learning lists of species and genera is at the core of any teaching strategy. The names are important, of course; they are part of a truly international scientific language, but learning them parrot-fashion should be a task undertaken by only the most dedicated specialist. Palaeontology is much more than this. The reality is that each fossil has a tale to tell, as each one is a fragment of an ancient ecosystem, a frozen frame in an evolutionary lineage or a chronometer of geological time. Putting aside the long names and the stupefying detail of their component parts, it is the value of fossils in applied studies which determines that they should be included within the text of any geology course.

This book is intended for first-level students. It is an overview and introduction, and is not the last word on the subject. It is meant to demonstrate the geological applications of fossils. Each of the main fossil groups is deliberately dealt with in brief so that the tedium of unnecessary detail is pared down. Undoubtedly this treatment may dissatisfy, even annoy, specialists, but this book is intended for undergraduates, from those who will go on in palaeontology to those who may never study palaeontology beyond the first level of their degree. It is a book written out of a love for a subject born when I was a young boy collecting fossils in North Wales and North Yorkshire. If it goes some small way in inspiring interest in one of the cornerstones of geology, I shall have succeeded in my aim.

Peter Doyle
London, 1995

Acknowledgements

This book is in part the product of several years of feedback from undergraduates on palaeontology. I am grateful for their interest. When asked to provide a title for this book, my students came up with various ideas, most of them unprintable. I particularly liked the suggestion 'Why are dead things so ugly?'. There are several other people whom I would like to thank. For supplying photographs and illustrations, often at short notice, I am grateful to Mike Barker, Denis Bates, Martin Brasier, Des Collins, Jane Francis, Neville Hollingworth, Dave Horne, Florence Lowry, Dave Martill, Clare Milsom, Dave Norman, Adrian Rushton, Tom Sharpe, Peter Sheldon, David Siveter and the editors of *The Stereo-Atlas of Ostracod Shells*, Paul Smith and Ian Slipper. Many friends and colleagues read and commented on drafts of all or parts of this book, or helped with advice and wise words. They are numerous: my students Adie Meredith, Jon Roberts, Clare Youdan and Steve Tracey; my postgraduates Kez Baggley and Jason Wood; and my colleagues Alistair Baxter and Andy Bussell. The manuscript has particularly benefited from critical readings by Matthew Bennett, Florence Lowry, Angela Holder, Tony Hallam, Duncan Pirrie, Alistair Crame, Bob Owens, Colin Prosser, Jonathan Larwood and Paul Bown. Martin Gay, Hillary Foxwell, Pat Brown and Nick Dobson provided technical and library support, and worked hard to meet my (at times) almost impossible demands. Amanda Hewes and Nicky Christopher at John Wiley helped guide me through this book from its early days.

Finally, this book owes a lot to four allies: my wife Julie for her support through the long hours needed to complete the text; my close friend Matthew Bennett for his constant guidance; my friend and colleague Florence Lowry who helped me in the planning of the book and who contributed materially to its text by writing Chapters 16 and 17 and cowriting Chapters 4 and 15 with me; and my research assistant Angela Holder who read, criticised and returned text almost as soon as it was produced, and who helped in its production in many other ways.

Illustrations

Many of the illustrations in this book were drawn by Hillary Foxwell and Angela Holder, for the most part from actual specimens held in the collections of the University of Greenwich. In other cases, illustrations have been substantially modified from published figures. These are denoted in the text by the words 'modified from . . .', together with the the full reference to the original source. Some diagrams have been reproduced in their entirety from published sources. Permission to reproduce these has been sought from the original publishers. I am grateful to the following organisations for permission to reproduce original figures or photographs: John Wiley and Sons, Chichester (Boxes 1.1, 3.7, 5.4; Figures 4.9, 4.10, 5.1, 5.3–5.6, 10.12, 13.6, 21.6, 22.2); The Palaeontological Association, London (Box 2.4; Figure 3.1); Cambridge University Press (Figure 11.10); Dudley Museum and Art Gallery (Box 1.2); Leicestershire Museums (Figure 2.10); Royal Ontario Museum, Toronto (Figure 2.9); and British Geological Survey (Figure 2.7), reproduced by permission of the Director: NERC copyright preserved.

1
What is Palaeontology?

1.1 PALAEONTOLOGY: THE STUDY OF ANCIENT LIFE

The Earth is 4600 million years old. Life has existed on Earth for at least 3550 million years, and since its first appearance it has adapted and changed the planet. The early atmosphere, almost devoid of oxygen, was adapted by the first organisms which produced this gas as a by-product of photosynthesis. The bodies of countless millions of organisms, microscopic and macroscopic, form whole rocks; the invaders of the land, plants and animals, have helped shape the landscape by both accelerating and reducing erosion. Life on Earth, in every form, has contributed to the story of our planet. The story of the development of life on Earth, of the biosphere, forms the subject of palaeontology: the study of ancient life.

Palaeontology has its roots in two subjects: geology and biology. Geology and palaeontology are intimately linked. The birth of both subjects can be arguably traced to the work of one man, the Danish physician Niels Stensen, often known as Steno (1638–1686). Stensen discovered that the fossil shark's teeth enclosed in the rocks of Tuscany were in fact identical with those of modern sharks, and from this he concluded that the layered rocks forming the land surface had themselves been formed in the sea. Significantly, he concluded that the fossils within them were not the result of mysterious vapours pervading the Earth, as many thought at the time, but that they were actually the remains of once living animals. Drawing both upon geology and the biology of living organisms, Stensen explained the origin and occurrence of fossils, and laid the foundations of palaeontology.

Since Stensen's day, palaeontology has provided important tools for geologists and biologists alike. In geology, fossils are important in piecing together rock successions from the same time interval across the globe, and in interpreting the nature of ancient sedimentary environments. In biology, fossils are a legacy of the diversity of life in the geological past, and the most direct evidence of evolution of life on Earth. This book is primarily concerned with understanding fossils so that they can be widely used in these subjects.

1.2 THE SCOPE OF PALAEONTOLOGY

Palaeontology is fundamental to geology. From the study of the environmental tolerances of their living relatives, fossils provide the clearest insight into the nature and development of ancient Earth environments. Fossils are also unrivalled as stratigraphical tools. The process of evolution acts as an irreversible clock in which the appearance of successive species through time can be used to match and correlate rock successions. Every day, microfossils are used in industry as routine stratigraphical ciphers, unlocking the relative age of successions of oil-bearing rocks. Palaeontology also has a pivotal role in biology, in providing proof of the evolution and diversification of life on Earth. Despite this, palaeontology is not popular with students. Dinosaurs have universal appeal, but simple invertebrate fossils appear insignificant and dull. In many undergraduate courses, palaeontology is seen by students as a necessary – or, even worse, unnecessary – hurdle which has to be negotiated in order to pass through the course. The most common accusation is the 'plethora of long names' pervading the subject. In reality, palaeontology is more than a catalogue of fusty-sounding names: it is a living subject of fundamental importance to both geology and evolutionary biology.

The basis for any science is the accumulation and ordering of data in order to develop and test hypotheses. The scientific approach demands a rigorous data set. In palaeontology, this data set is based on the fossils themselves, and in particular, their occurrence and diversity. It is encompassed in **taxonomy**, the scientific ordering and naming of fossil groups. Taxonomy provides the solid foundation of the science of palaeontology, and geologists and biologists alike can apply the information it provides in three fields: **palaeobiology**, **palaeoenvironmental reconstruction** and **stratigraphy** (Figure 1.1). It is in these fields that the value of palaeontology lies, and these three subject areas provide the broad themes of this book.

Examining these themes, Palaeobiology is the study of fossils as once living animals and plants. It involves the interpretation of the function or mode of life (the functional morphology) of fossil organisms, and the study of the pattern, process and timing of evolution. Palaeoenvironmental reconstruction is possible because fossils are an important part of sedimentary rocks, and, when living, were an integral component of their environment. Through the interpretation of their ancient ecologies, fossils serve as indicators of past climate, oxygen levels, salinity, and a range of other environmental factors. The determination of ancient geographies and the unravelling of complex tectonic terranes are possible using the ancient distribution patterns of fossil organisms. Finally, fossils are important in stratigraphy as indicators of specific time periods, and as tools by which rock successions can be correlated.

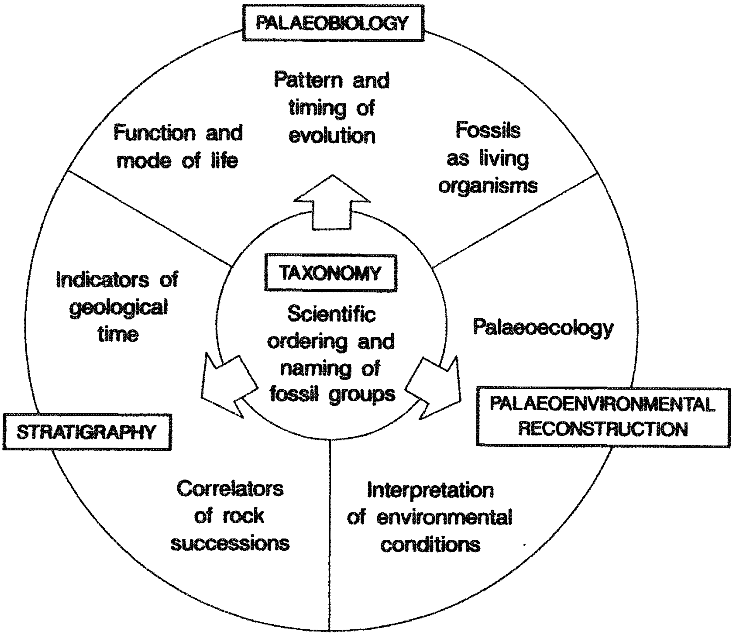


Figure 1.1 *Taxonomy as the basis for the three main fields of applied palaeontology: palaeobiology, palaeoenvironmental reconstruction and stratigraphy [Modified from: Clarkson (1993)* Invertebrate Palaeontology and Evolution *(Third edition), Chapman & Hall, Fig. 1.3, p. 6]*

1.3 THE AIM AND STRUCTURE OF THIS BOOK

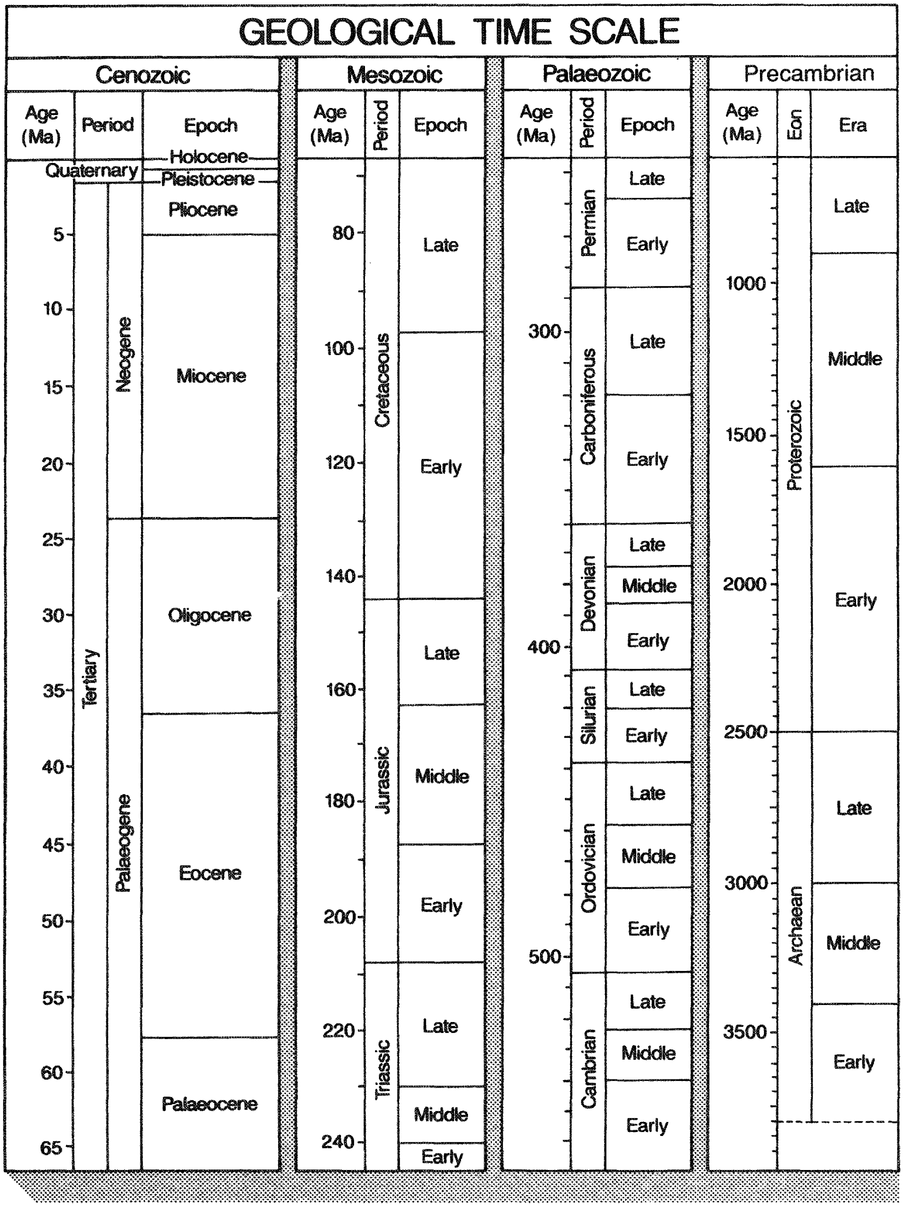
This book is primarily intended for geologists, but will also be of interest to biologists. It assumes some basic knowledge of geology and biology. It is an attempt to illustrate the use of fossils in geological studies; in palaeobiology, stratigraphy and palaeoenvironmental analysis. It has three parts. In **Part I** the key concepts in palaeontology are examined: the processes of fossilisation, the principles of palaeoecology, the role of fossils in evolutionary studies, and the use of fossils in stratigraphy. In **Part II** are introduced the most important invertebrate fossil groups. These provide the basis for understanding the most useful fossil groups, and serve as an introduction to further study. In **Part III** specific case studies of the use of fossils in the three areas of applied palaeontology are discussed.

BOX 1.1: THE GEOLOGICAL TIME-SCALE

Palaeontologists are concerned with both great tracts of time, studying the large-scale changes in life on Earth over the past 3500 million years, and infinitely smaller intervals, examining with some precision the evolution of individual groups over thousands of years. The geological time scale is a standard frame of reference for geologists and evolutionary biologists. It has been developed over the last 150 years by the work of numerous scientists, and is seen as a crowning achievement in science. The time scale is based upon the dating of rock successions called **chronostratigraphical units**, calibrated by measuring the amounts of specific radioactive elements known to decay at a set rate. The boundaries of chronostratigraphical units are time-significant, as they are denoted by global events in the geological record. As an example, for much of the Phanerozoic (the Palaeozoic, Mesozoic and Cenozoic eras), the larger chronostratigraphical units have boundaries which are indicated by global mass extinctions or evolutionary radiations, such as the boundary between the Mesozoic and Cenozoic or Precambrian and Cambrian. The boundary of each unit is defined by international agreement at specific localities on the Earth's crust called **stratotypes**, providing a standard with which geologists from across the world can match in time or correlate their own rock successions. For much of the chronostratigraphical record it is the relative order of the evolutionary changes of the fossils which is of greatest importance in correlating rock successions with the stratotype.

Sources: Berry, W.B.N. (1986) *Growth of the prehistoric timescale based on organic evolution*. Blackwell, Oxford; Doyle, P., Bennett, M.R. & Baxter, A.N. (1994) *The key to earth history*. Wiley, Chichester [Figure reproduced from: Doyle *et al.* (1994, Fig. 4.8, p. 52)]

BOX 1.1: (*cont.*)

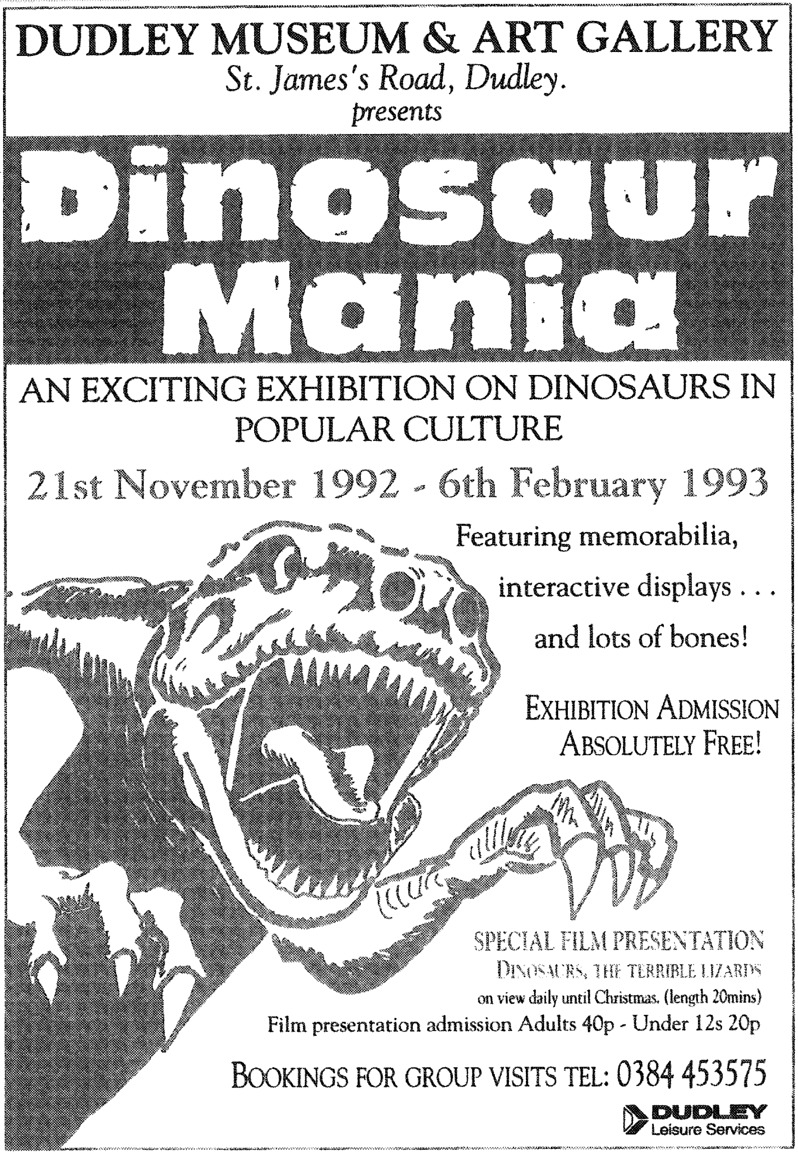

GEOLOGICAL TIME SCALE
Cenozoic
Age (Ma)
Period
Epoch
Quaternary
Holocene
Pleistocene
Pliocene
Tertiary
Neogene
Palaeogene
Miocene
Oligocene
Eocene
Palaeocene
5
10
15
20
25
30
35
40
45
50
55
60
65
Mesozoic
Age (Ma)
Period
Epoch
Cretaceous
Jurassic
Triassic
Late
Early
Late
Middle
Early
Late
Middle
Early
80
100
120
140
160
180
200
220
240
Palaeozoic
Age (Ma)
Period
Epoch
Permian
Carboniferous
Devonian
Silurian
Ordovician
Cambrian
Late
Early
Late
Early
Late
Middle
Early
Late
Early
Late
Middle
Early
Late
Middle
Early
300
400
500
Precambrian
Age (Ma)
Eon
Era
Proterozoic
Archaean
Late
Middle
Early
Late
Middle
Early
1000
1500
2000
2500
3000
3500

BOX 1.2: FOSSILS IN SOCIETY

Fossils have figured in human culture since prehistory, and have a broader appeal than is widely appreciated. They figure as objects of the natural world in our everyday lives, in at least six areas:

- **As folklore objects**: many fossils have been part of folklore and mythology for centuries. Some fossils are known from early human burial sites; others, such as snakestones (ammonites) and devil's toenails (the oyster *Gryphaea*) are associated with specific myths; and some are considered to have healing powers ('thunderbolts', otherwise known as belemnites).
- **As objects of aesthetic beauty**: many fossils are prized as aesthetically pleasing, natural art objects, and in many cases utilised as part of interior design.
- **As objects of a recreational pursuit**: many people collect fossils either casually while visiting an appropriate locality, or as a hobby, grading into a semi-professional pursuit.
- **As objects of economic value**: a thriving fossil trade has existed in many parts of the world since at least the late eighteenth century. While some fossils are considered to be 'priceless' (e.g. the first bird, *Archaeopteryx*), others are offered at pocket-money prices. In some locations, such as Lyme Regis in Britain, the fossil trade is an important part of the local economy.
- **As objects worthy of scientific study**: stored in collections and museums, worthy of serious scientific attention, and subject to sensationalist journalism in the wake of exciting finds.
- **As an extension of dinomania**: the twentieth century has seen several dinosaur booms; each one, bigger and better than the last, focuses attention on the life of the geological past, and brings fossils to the public as toys, on cereal packets, and in the cinema.

BOX 1.2: (*cont.*)



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BOX 1.3: FOSSILS IN SCIENCE

Fossils are one of the most important sources of information from the geological record. At least ten broad categories of scientific information can be recognised:

- **Taxonomic**: fossils contain morphological information which allows them to be recognised and named, and their relationships to other taxa recognised.
- **Ethological**: fossils provide information which can lead to a direct understanding of the mode of life of once living, and now extinct, organisms.
- **Evolutionary**: fossils provide direct evidence of the evolution of life on Earth.
- **Ecological**: fossils and fossil assemblages provide insight into the nature and development of ecosystems, and of the interaction of plants and animals with each other and their ancient environment.
- **Environmental**: living organisms are limited in distribution and diversity by environmental factors. The nature of ancient environments, and the specifics of depth, temperature, salinity and oxygen levels, may be determined through the comparison of living and fossil assemblages.
- **Chemical**: fossil shells and other hard parts often contain vestiges of the biochemistry of the original organism, or have isotopic signatures which help in the determination of ancient temperatures or salinities, among others.
- **Sedimentological**: 'bones as stones'; fossils act as sedimentary particles and can provide important information on the nature of the hydraulic regime of flowing water, with some fossils commonly aligned parallel to current flow direction, for example, as well as determining the rate of sedimentary accumulation.
- **Diagenetic**: fossils provide information about the processes which occur in sedimentary sequences following death and burial through to their discovery.
- **Way up**: *in situ* fossils can prove valuable in the determination of the original 'right way up' of rock successions subjected to overturning in mountain building episodes.
- **Stratigraphical**: fossils are the most important guides in subdividing the stratigraphical column into units denoted by time boundaries.

Sources: Goldring, R. (1991) *Fossils in the field*. Longman, Harlow; Briggs, D.E.G. and Crowther, P.R. (eds) (1990) *Palaeobiology – a synthesis*. Blackwell, Oxford

Part I

KEY CONCEPTS

2

Fossils and Fossilisation

In this chapter the term 'fossil' is explained and the processes which lead to the preservation of fossils in the sedimentary rocks of the geological record are described.

2.1 WHAT ARE FOSSILS?

Fossils are the remains of once living plants and animals. Put simply, they are the visible evidence of life on Earth during the 3550 million years or so that geologists now know have sustained life. The name 'fossil' is derived from the Latin word, *fossilis*, which refers to any object which has been dug from the ground. The term was first applied in geology in the sixteenth century; at that time, and until the late eighteenth century, a fossil could also refer to any mineral object, archaeological artefact or curiosity dug from the ground. This is no longer the case. Since the birth of the science of **palaeontology** (the study of ancient life) in the late eighteenth century, the term 'fossil' refers to the remains of any ancient organism. Effectively, these remains are the physical evidence of past life found in rocks and sediments. There are two basic types: **body fossils** and **trace fossils**.

Body fossils preserve elements of the original body of an organism, and have undergone the process of **fossilisation**. This usually means that the organism has died and been buried, and is therefore **preserved**, but does not imply great age, or even the process of 'turning to stone'. Effectively, therefore, a shell buried on a modern beach, a man or woman interred at a funeral, or an organism incorporated in sediments formed millions of years ago is encompassed within the definition. Other fossils include 'mummies' – organisms that have been preserved because of desiccation, without the necessity of burial. However, in practice, many scientists would exclude recently dead and buried organisms from the definition as a convenience, choosing as an arbitrary cut-off point the base of the

Holocene, the most recent geological time interval (Box 1.1). The nature of the preservation of body fossils is extremely important to palaeontologists: the better the preservation state, the greater the information available about the nature of ancient life and its changes through time. In essence, body fossils can be preserved intact or fragmented; they can be found complete with the most delicate soft body parts and their ancient biomolecules preserved, or as fragments, eroded and broken down.

Trace fossils are the physical evidence of the existence of plants and animals through their traces: tracks, burrows and borings which disturb the bedding surfaces and fabric of sedimentary rocks. Traces are defined on the interpretation of the action of the organisms that created them: feeding, moving, resting and so on. These traces are mostly ephemeral, created as disturbances in or on sediments. Hence, burial is important in the preservation of surface traces, but most traces are created *in situ* within the sediment. Both are effectively preserved through rapid sedimentation. A few other traces, notably **coprolites**, the fossil faeces of a variety of organisms, undergo a similar process of fossilisation to body fossils.

Together body and trace fossils furnish scientists with the information to interpret mode of life: the body fossil (e.g. a dinosaur bone) illustrates the form of the animal, the trace fossil (e.g. a dinosaur footprint) the way in which it interacted with its environment.

2.2 TAPHONOMY: THE PROCESS OF FOSSILISATION

The process of fossilisation through which fossils are created is complex, and the outcome is determined by a variety of interrelated physical, chemical and biological factors. As such the subject of fossilisation is almost a science in its own right, usually referred to as **taphonomy**. However, three broad stages can effectively be identified in the fossilisation of an organism. These are: **death**, **pre-burial**, and **post-burial** (Figure 2.1).

2.2.1 Death of the Organism

Death is the first process that has to occur before fossilisation can take place. Death and illness can be caused by old age, infection, parasitic infestation, predators, and through physical, chemical and biological conditions of the environment, such as changes in climate or exclusion of oxygen from the water column. However, few of these factors can ever be identified as the cause of death. It is often the case, when we find a fossil, that we are at the scene of the crime – the death of the organism in the geological past – but usually we have only circumstantial evidence of the cause of death, and very little idea of the motive. In some cases, we can identify illness, infection and parasites. Dinosaurs commonly give indications of medical conditions through their bone architecture; arthritis of joints, for instance, is fairly common. Parasites are also fairly common in invertebrate animals, and crinoids (Chapter 11) appear to be particularly prone to

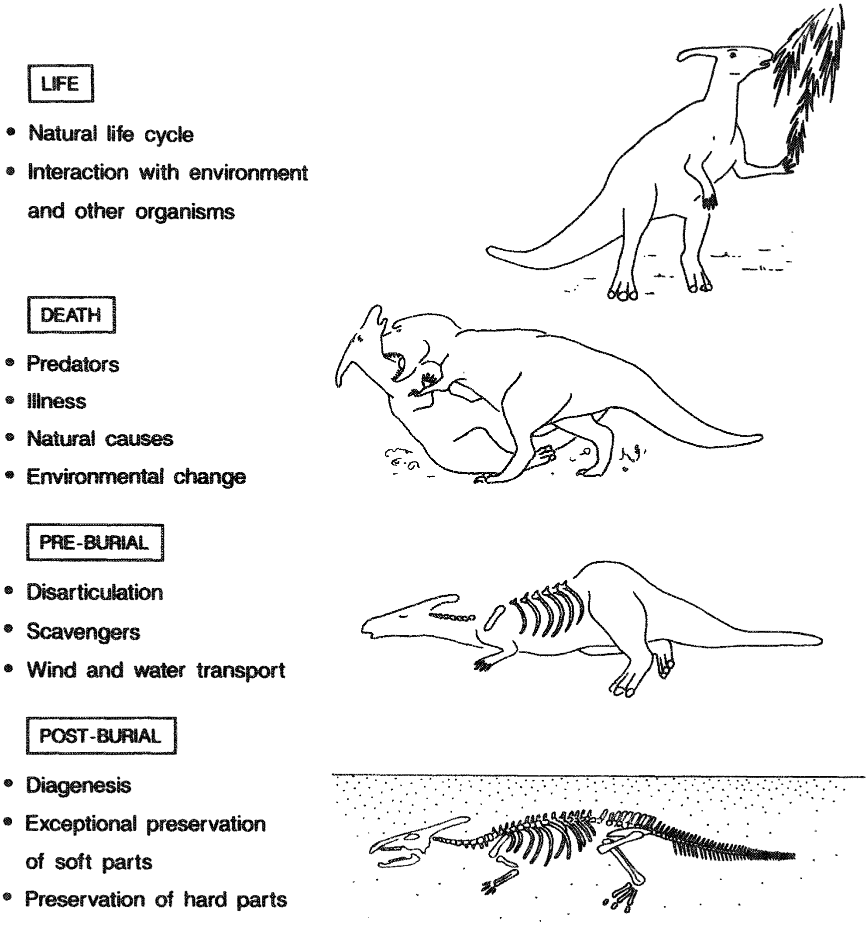


Figure 2.1 *The four phases of the fossilisation process, from life, through death and on to burial. Death can occur through a variety of factors, and the processes which act upon an organism before and after burial determine whether it is to be preserved as a fossil in the sedimentary record*

infestation by worm-like organisms, often with swellings and pits illustrating the parasitism. Other natural causes of death, such as old age, may be deduced from fossil remains. For example, mammoth 'graveyards' can be interpreted through the study of modern elephant bone sites in Africa caused by die-offs associated with drought or other environmental hardships, or just the sum of deaths from disease or old age over a long period of time. Accumulations of mammoth bones may be interpreted as a result of similar processes (Box 2.1). Mass death in communal organisms as a part of the natural life cycle, particularly after mating, has been recognised in other organisms, paralleling the behaviour of modern-day squid. However, the actual cause of death can be clearly determined in only very few instances. Predators are sometimes found with stomach contents containing the remains of other fossil organisms. In the Jurassic shales of Holzmaden in southern Germany, for example, a shark has been recovered with the remains of 250 belemnites in its stomach (Figure 2.2). This certainly illustrated the cause of death of the squid-like belemnites, but may also have lead to the death of the shark from some form of indigestion. Other instances of gluttony are also recognised and are clear indicators of the cause of death (Box 2.2). Similarly, fossils preserved within coprolites are also good pointers to mode of death – demonstrating the preferred diet of an ancient predator.

BOX 2.1: ACTUALISM AND ELEPHANTS

Much research has been carried out since the mid-1980s in the study of the remains and causes of death of elephants in Zimbabwe. This research was intended to establish the main causes of death and particularly mass death in elephant populations, in order that the same processes can be determined for mammoth and other fossil proboscidean remains. Seven causes of death were determined: bone fracture; accidental death through falls, becoming stuck in mud or drowning; injury, accidental or through fighting; disease; old age; drought-related stress; and human activity, particularly hunting. The main cause of catastrophic mass death in Zimbabwe was drought-related, from heat, dehydration and starvation. Similar studies in Zambia have recorded the death of 31 elephants around a water hole in a single drought event. Bones were characteristically fractured from scavengers, trampling or the effects of weathering.

Mammoth and other fossil proboscidean bones are commonly found in clustered assemblages in Eurasia and North America, and have often been interpreted in a context of human hunting. Many such sites lack the artefacts of human activity, such as stone tools. Bones displaying fractures have commonly been interpreted as the results of butchering by humans; yet similar fractures in modern elephant bone sites can be attributed to trampling or scavenging. Studies of late Pleistocene bone sites have shown that the ages of the animals that are found within them are similar to that of the non-mass kill sites in Africa. Here, hunting profiles show selective killing of males or young, while mass deaths from environmental causes affect all ages. Many of the end-Pleistocene bone assemblages previously thought to be the result of human activity have similar characteristics. Age profiles do not show selective mortality. It is probable that, like the modern elephants, these were mass die-offs associated with environmental stress, in this case probably rapid climatic change. 'Evidence' of butchering either reflects human or hyena scavenging, or trampling by mammoths and other large animals.

Source: Haynes, G. (1991) *Mammoths, Mastodonts and Elephants. Biology, Behaviour and the Fossil Record.* Cambridge University Press, Cambridge.

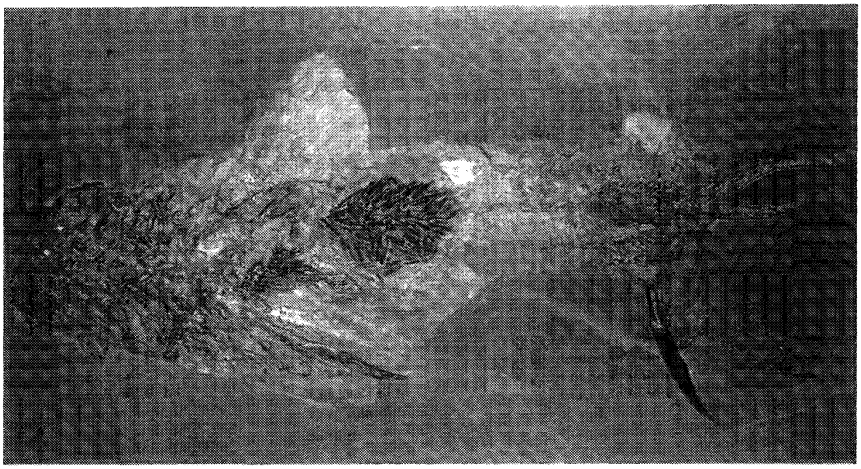


Figure 2.2 *A* Hybodus *shark from the Lower Jurassic of Holzmaden in southern Germany. The shark has eaten over 250 belemnites, the hard parts of which have accumulated in its stomach. The belemnites were obviously killed by the shark – but the build-up of belemnite skeletal remains may have ultimately lead to the death of the shark itself [Photograph: J.E. Pollard]*

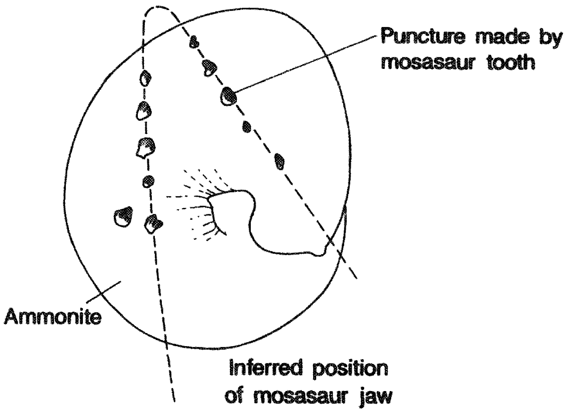
Physical and chemical causes of death are, if substantiated, useful clues for the geologist in determining the nature of ancient environments. The clearest examples of physical death are organisms trapped in the sticky resin produced by trees as sap, or entombed in tar pits. Amber is fossil tree sap, and is common in some river deposits close to the site of ancient forests. Occasionally, amber contains the remains of fossil insects intact, preserved from the moment of entrapment by the tree resin. Tar pits enclosing the remains of larger animals trapped by upwelling asphalt represent another instance of entrapment and preservation. The pit at Rancho La Brea, in Los Angeles, California, USA, is a gruesome example. Here, during the Pleistocene, a variety of vertebrates came to drink from a water hole and were trapped, sucked in and drowned in the asphalt welling beneath its surface. In rare instances like this, geologists have an exceptionally clear illustration of the direct cause of death.

Changes in the physical or chemical environment can promote death on a large scale. Rapid **mass mortalities** are difficult to substantiate but may be represented by great accumulations of fossils under volcanic ash, as in the case of the human tragedy of the Roman cities of Pompeii and Herculaneum, in southern Italy, or associated with black shales in the sea indicating asphyxiation through low-oxygen conditions. Over a longer time scale, the death of coral reefs through drowning in deep water or exposure to the elements, or the inundation of forests by the sea, is recorded by the physical remains of the dead reef or forest surrounded by rocks indicating the environmental change. Even individual tragedy may be recorded. In the Jurassic limestones of southern Germany, *Eulimulus*, the king crab, is sometimes encountered at the end of a series of meandering trails, a record of the death throes of an organism in the harsh environment of the Solnhofen lagoon (Figure 2.3).

BOX 2.2: THE DEATH OF AN AMMONITE

Fossils rarely provide evidence of the nature of their death. In some exceptional cases, however, it is possible to determine the cause of death from the physical evidence presented by the fossil itself. Such evidence is useful as it provides an insight into a detailed aspect of the nature of the geological past.

One such example was documented by Kauffman and Kesling (1960). They described a large fossil ammonite shell (*Placenticeras*) in the Upper Cretaceous rocks of South Dakota which exhibited several sets of regularly spaced puncture marks. The puncture marks were of the same size as the teeth of the marine reptile *Mosasaurus*. Could this ammonite have been the victim of an attack by a mosasaur? Ammonites are related to the present-day *Nautilus*; like them, they had buoyancy chambers maintained as a kind of pressure vessel. A bite from a mosasaur inflicting the punctures could have created a loss in buoyancy, disabling the ammonite and leading to its death. Comparison of the puncture marks with the jaws of coexisting marine reptiles demonstrated a clear relationship between the size and tooth spacing of the jaws and the tooth marks on the ammonite. Clearly, the mosasaur punctured the ammonite shell while attempting to eat it. The multiple bite marks show that this was a difficult task, although it is probable that the ammonite died in the attack. However, a similar *Placenticeras* with punctures, from the Upper Cretaceous of Canada, has been interpreted as an animal attacked *after* death, but while drifting before sinking to the sea bed (Hewitt and Westermann, 1989).



Sources: Kauffman, E.G. and Kesling, R.V. (1960) An Upper Cretaceous ammonite bitten by a mosasaur. *Contributions from the Museum of Paleontology, The University of Michigan*, **15**, 193–243. Hewitt, R.A. and Westermann, G.E.G. (1989) Mosasaur tooth marks on the ammonite *Placenticeras* from the Upper Cretaceous of Alberta, Canada. *Canadian Journal of Earth Sciences*, **27**, 469–472. [Figure modified from: Pollard (1990) *In* Briggs & Crowther (eds) *Palaeobiology – a synthesis*, Blackwell, Fig. 1A, p. 369]