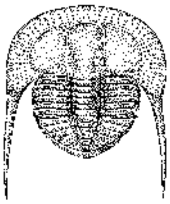

1 Introduction

- Fossils provide information on geological time, evolutionary history, and ancient environments.
- Different organisms have different likelihoods of preservation and the fossil record is generally biased towards shelly, marine organisms.
- The changing shape of the Earth's surface has had a significant impact on the evolution of living organisms, and the distribution of fossils mirrors the past distribution of continents on the planet.
- Fossil lagerstätten are deposits with exceptionally well-preserved specimens providing an unequaled view of past organisms.

Introduction

The Earth is the only planet we know to support life. Its long history shows that life and the planet it inhabits have a complicated relationship. Free oxygen in the atmosphere, the ozone shield, the movement of carbon into long-term reservoirs in the deep oceans, and the rapid weathering of rocks on the land surface are obvious examples of this relationship.

The evolutionary history of life on Earth points to the development of a series of faunas that occupied the changing surfaces of the land and sea. Through the extraordinary medium of lagerstätten, or sites of exceptional preservation, it is possible to visualize these vanished communities and to restore some of their behaviors and interactions.

In addition, the process of evolution, via Darwinian natural selection, is recorded in the fossil record. Though incomplete and tantalizing in places, fossils are the only direct information source about the nature of our ancestors, and the ancestors of any life on modern Earth.

The study of fossils offers a view of the past at all scales of space and time. From a single moment, for example the single act of making a footprint, to the study of the evolution of tetrapods, or from the study of a single locality to an analysis of the effect of the break-up of Pangea on the evolution of dinosaurs, the fossil record is the primary source of data. Paleontologists build detailed interpretations and analysis from the study of individual fossils; most are invertebrate animals, preserved in great abundance in the shallow marine record.

In this book, we provide an introduction to the methods by which fossils are studied. We discuss the biases that follow from the process of fossilization, and explain how this can be analyzed for a particular fossil locality. We provide an introduction to evolutionary theory, which is the basis for explaining the consistent changes of shape seen in fossils over time.

We describe the major groups of invertebrate fossils that form the bedrock of the discipline, and also of most introductory courses in the subject. We discuss microfossils, plants, and vertebrates, which, while less commonly encountered, are of such importance to understanding life on Earth. Finally, we briefly narrate the evolution of life on Earth as it is currently understood, including episodes of huge diversification and mass extinction. Throughout the text, we discuss the many ways in which fossils contribute to an improved understanding of the Earth's system, for example through allowing accurate relative dating of rocks, or as proxies for particular environmental settings.

By the end of this book, you should be able to identify the most common fossils, discuss their ecology and life habits based on an analysis of their detailed shape, understand how each group contributes to the wider studies of paleontology and earth systems science, and appreciate their importance at particular points in Earth's history. You should have a broad understanding of how life has both evolved on Earth and must be factored into any analysis of the evolution of the planet. You can read the book in sequence, or dip into it at will. You will find that some sections follow on from a previous chapter, but in most cases information is presented in self-contained pieces that fall on a couple of facing pages. We have used diagrams and tables wherever possible to summarize information and we have used as few technical terms as possible, to try to lay bare the ways in which fossils matter.

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Types of fossils (Fig. 1.1)

Trace fossils

Trace fossils are the preserved impressions of biological activity. They provide indirect evidence for the existence of past life. They are direct indicators of fossil behavior. As trace fossils are usually preserved where they were made, they are very good indicators of past sedimentary environments. Trace fossils made by trilobites have provided an insight into trilobite life habits, in particular walking, feeding, burrowing, and mating behavior.

Coprolites

Coprolites are fossilized animal feces. They may be considered as a form of trace fossil recording the activity of an organism. In some coprolites recognizable parts of plants and animals are preserved, providing information about feeding habits and the interaction of coexisting organisms.

Chemical fossils

When some organisms decompose they leave a characteristic chemical signature. Such chemical traces provide indirect evidence for the existence of past life. For example, when plants decompose their chlorophyll breaks down into distinctive, stable, organic molecules. Such molecules are known from rocks more than 2 billion years old and indicate the presence of very early plants.

Body fossils

Body fossils are the remains of living organisms and are direct evidence of past life. Usually only hard tissues are preserved, for example shells, bones, or carapaces. In particular environmental conditions the soft tissues may fossilize but this is generally a rare occurrence. Most body fossils are the remains of animals that have died, but death is not a prerequisite, since some body fossils represent parts of an animal that were shed during its lifetime. For example, trilobites shed their exoskeleton as they grew and these molts may be preserved in the fossil record.

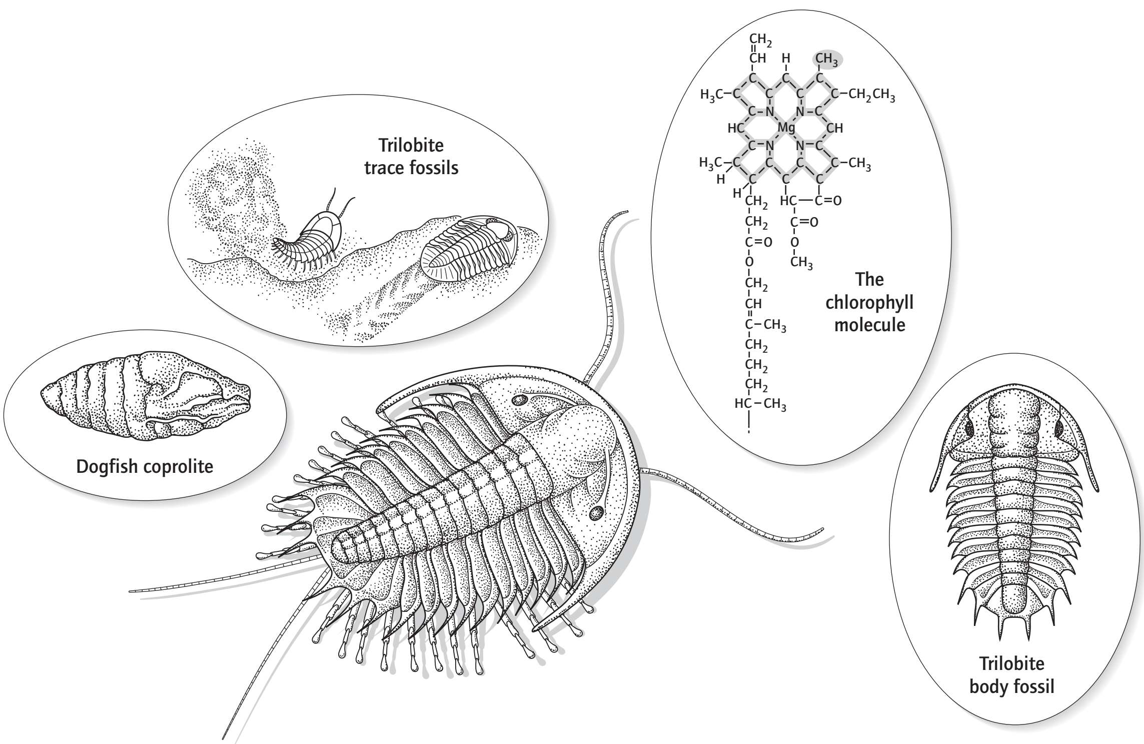

Fig. 1.1 Types of fossils.

Time and fossils

Geological time can be determined absolutely or relatively. The ages of rocks are estimated numerically using the radioactive elements that are present in minute amounts in particular rocks and minerals. Relative ages of different units of rocks are established using the sequence of rocks and zone fossils. Sediments are deposited in layers according to the principle of superposition, which simply states that in an undisturbed sequence, older rocks are overlain by younger rocks.

Zone fossils are fossils with a known relative age. In order for the zone to be applicable globally, the fossils must be abundant on a worldwide scale. Most organisms with this distribution are pelagic – that is they live in the open sea. The preservation potential of the organism must also be high – that is they should have some hard tissues, which are readily preserved.

Stratigraphy

The study of sequences of rocks is called stratigraphy. There are three main aspects to this study: chronostratigraphy, lithostratigraphy, and biostratigraphy (Fig. 1.2).

Chronostratigraphy establishes the age of rock sequences and their time relations. Type sections are often established. These are the most complete and representative sequences of rocks corresponding with a particular time interval. For example, outcrops along Wenlock Edge in Shropshire, UK, form the type section for the Wenlock Series of the Silurian.

A point in a sequence is chosen for a boundary between one geological time interval and the next. It represents an instant in geological time and also corresponds with the first appearance of distinctive zone fossils. Relative timescales can then be established with reference to this precise point. These points are called "golden spikes".

The differentiation of rocks into units, usually called formations, with similar physical characteristics is termed lithostratigraphy. Units are described with reference to a type section in a type area that can be mapped, irrespective of thickness, across a wide geographic area.

In biostratigraphy, intervals of geological time represented by layers of rock are characterized by distinct fossil taxa and fossil communities. For example, the dominant fossils in Palaeozoic rocks are brachiopods, trilobites, and graptolites.

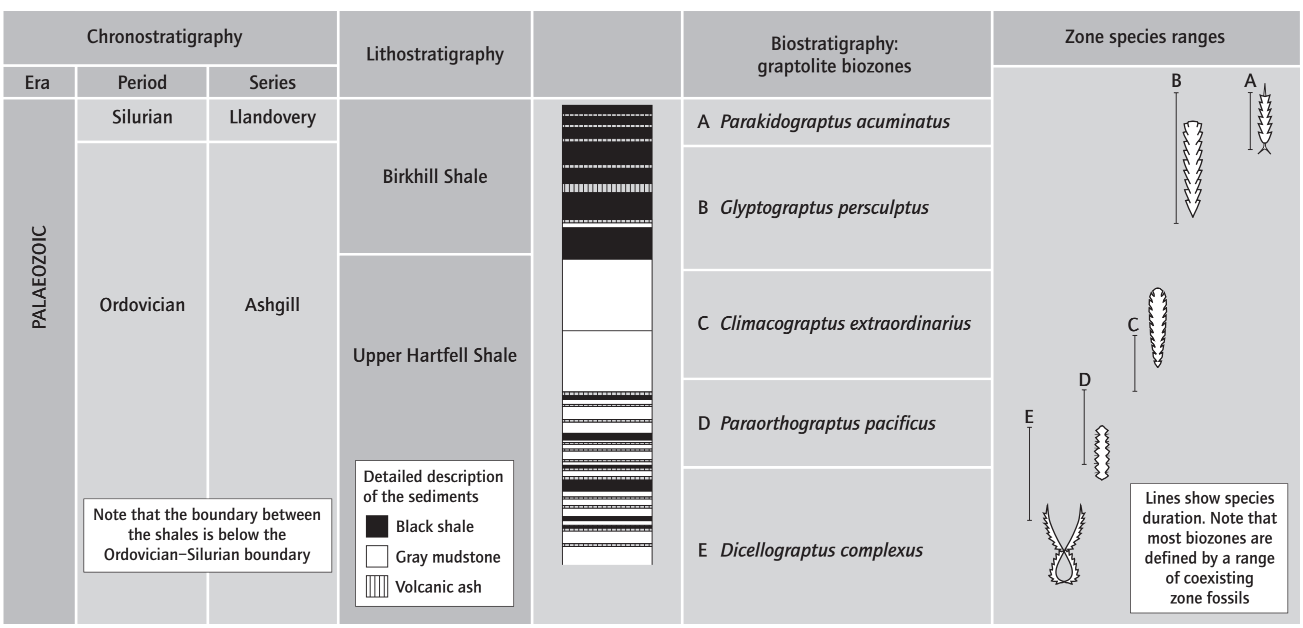

Fig. 1.2 Stratigraphic description of the sequence of rocks that crosses the Ordovician–Silurian boundary at Dobb's Linn, Southern Uplands, Scotland. Geological time is split into different zones depending on the method of analysis. Chronostratigraphy divides the section into two periods. Lithostratigraphic analysis divides the sequence into two shales. Biostratigraphy, as determined by the zone fossils, gives a more detailed division of relative age within the sequence.

Life and the evolution of continents

Life exists on a physically changing world, and these changes have both controlled the evolution of organisms and been recorded by their fossil record. Evolution operates rapidly on small populations, and so when a group of organisms becomes isolated through changes in the landscape around them, they quickly evolve to become different to their parent population. Organisms migrate across land bridges or along new seaways, as areas that were once isolated become accessible to one another. The migration of marsupial mammals such as possums into North America over the last 2 million years is a good example of this process. The analysis of the past distributions of organisms is known as paleobiogeography.

Plate tectonics drive changes to the map of the world

The continents and oceans change shape all the time, as crust is generated and modified by the forces of plate tectonics. New oceanic crust is formed at mid-ocean ridges where the mantle decompresses and melts, and as a consequence the oceans grow wider. Crust is consumed at destructive plate boundaries, where dense rock crust sinks back into the mantle. By this process oceans can become smaller or disappear altogether. Continental crust is increased in volume by the addition of island arc remnants and the sediments of the ocean floor. Continental collision joins these fragments together to form large masses, until the formation of new oceans pulls them apart.

The narrative of this evolving world map is well known for the last 200 million years, because it is recorded by the oceanic rocks of the modern sea floor. These rocks form like a conveyor belt, with the youngest rocks closest to the ridges and the oldest ones furthest away. Rock of decreasing age can be "stripped back" to reveal prior positions of the continents (Fig. 1.3). It is more difficult to reconstruct the position of oceans and continents older than 200 million years (which is only around the Triassic–Jurassic boundary), because too little oceanic crust of this age survives to produce an accurate map.

For older world maps, reconstruction is done by a variety of methods, but predominantly by tracing the latitude at which rocks cooled through the Curie point and "froze" into their minerals the direction of magnetic north. This technique, however, gives no measure of longitude, which has to be guessed from more qualitative types of data. One of the most useful of these is the distribution of the fossil remains of organisms.

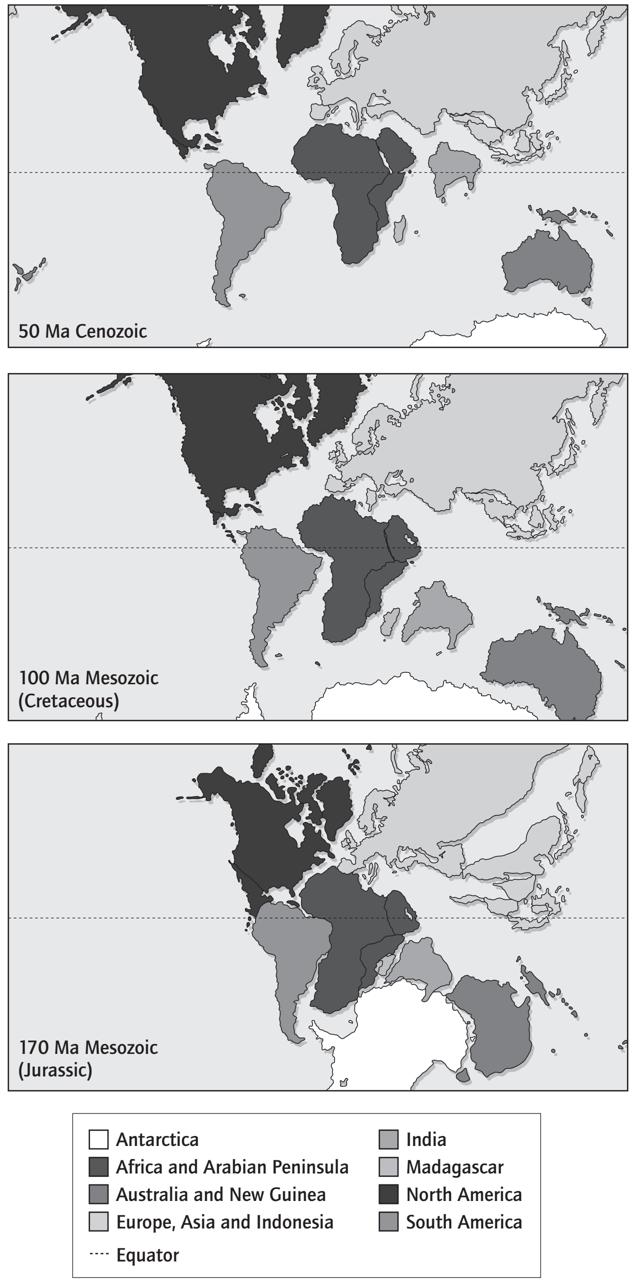

Fig. 1.3 Paleogeography: maps of the world for the last 200 million years.

Fossil evidence for ancient continental distributions

During the Lower Palaeozoic, we know from paleomagnetic data that the continents were relatively small and widely dispersed. The landmass that now forms North America and parts of Scotland was close to the equator, while the area now forming Europe, Africa, and England was far away, at around 60° south. These island continents were surrounded by deep oceans which are now long vanished, but their position is recorded by an open marine animal, a type of colonial graptolite (Chapter 10), called *Isograptus*. This species lived only in the open ocean, and colonies were fossilized in the shales of the deep sea bed. These were sometimes preserved when the oceanic crust sank back into the mantle, scraped onto the over-riding continents as deformed strips of rock. A map of the modern distribution of *Isograptus* reveals their presence in these thin collisional bands, and an ancient map can be built by "tearing up" the modern continents along these bands (Fig. 1.4).

As the Lower Palaeozoic continued, these isolated continental fragments began to collide. One of the best studied collisions is that between Scotland and England, which happened during the late Silurian period (420 Ma). The line of collision runs east–west along the present Solway Firth, and the effects of the collision can be seen in the deep marine rocks preserved in the Southern Uplands, and in the seismic structure of the mantle beneath Scotland. Organisms that lived on either side of this ocean record its progressive closure as, first, deep marine, and then progressively more shallow-dwelling organisms became common to both sides of the seaway. The mixing of freshwater fish faunas of the latest Silurian age is the final sign that the ocean had gone.

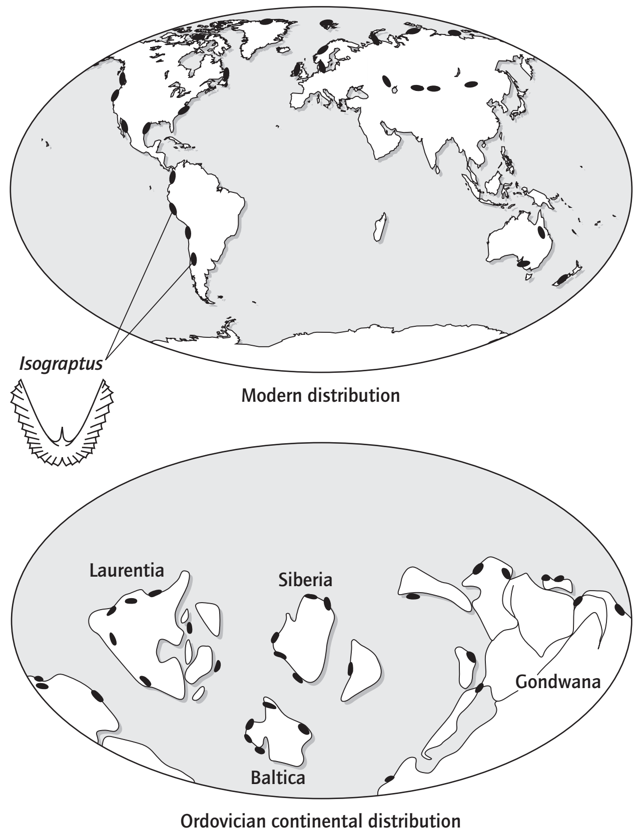

Fig. 1.4 The distribution of *Isograptus* plotted on a modern map of the world, and a reconstruction of the ancient oceans in which they lived based on this distribution.

Modern continents and mammals

The evolution of mammals coincided with, and was directly affected by, the break-up of a single giant continent, known as Pangea. The two most common groups of modern mammals – placental mammals (which gestate their young internally) and marsupial mammals (which bear tiny live young and nurture them in pouches) – are found across Pangea, and as the continent broke up they were able to migrate to all of the modern continents via land bridges. In South America, mammals have evolved independently for the last 60 million years, with little contact with the rest of the world apart from the intermittent migration of animals from North America, such as monkeys and rodents. The dominant mammals in South America were marsupials, with unusual species such as giant ground sloths and armadillos evolving. Many of these groups became extinct due to the migration of competitor placentals when the Isthmus of Panama formed, and this process of extinction was speeded up when hominids arrived a few thousand years ago.

Australia, New Zealand, and Antarctica split from the rest of Pangea during the Cretaceous period, and in turn split from one another during the early Cenozoic. The isolated faunas of Australia and New Zealand evolved independently, with both landmasses being dominated by marsupials.

Africa also became isolated from the rest of the continents late in the Cretaceous period and became a center of evolution for placental mammals, including groups that became predominantly marine, such as whales and sea cows. Elephants and other large grazers evolved here. Faunal exchanges with Asia began in the early Miocene, with cats arriving to become the dominant African predator, and apes and elephants migrating out of Africa to the north and east. The distinctive mammalian faunas of different modern continents are a product of Cenozoic continental break-ups and the consequent isolation of groups of animals.

Fossil preservation

The fossil record is incomplete. Most organisms do not fossilize and most fossils are only the partial remains of once-living organisms. Those organisms that do fossilize are usually changed in some way. Most plants and animals are not preserved in their life position and their composition is usually altered.

The study of the history of an organism from its death to its discovery within a rock or sediment is known as taphonomy (Fig. 1.5). After the death of an organism, physical and biological processes interact with the organic remains. This determines the extent to which the organism is fossilized and the nature of the fossil.

The general taphonomic history of a fossil is as follows. After death, the soft tissues of the organism decay. The remaining hard tissues are then transported resulting in disarticulation and possible fragmentation. The broken hard tissues are then buried and are physically or chemically altered. Postburial modifications are termed diagenesis. This sequence of events results in a major loss of information about the organism and its life habit.

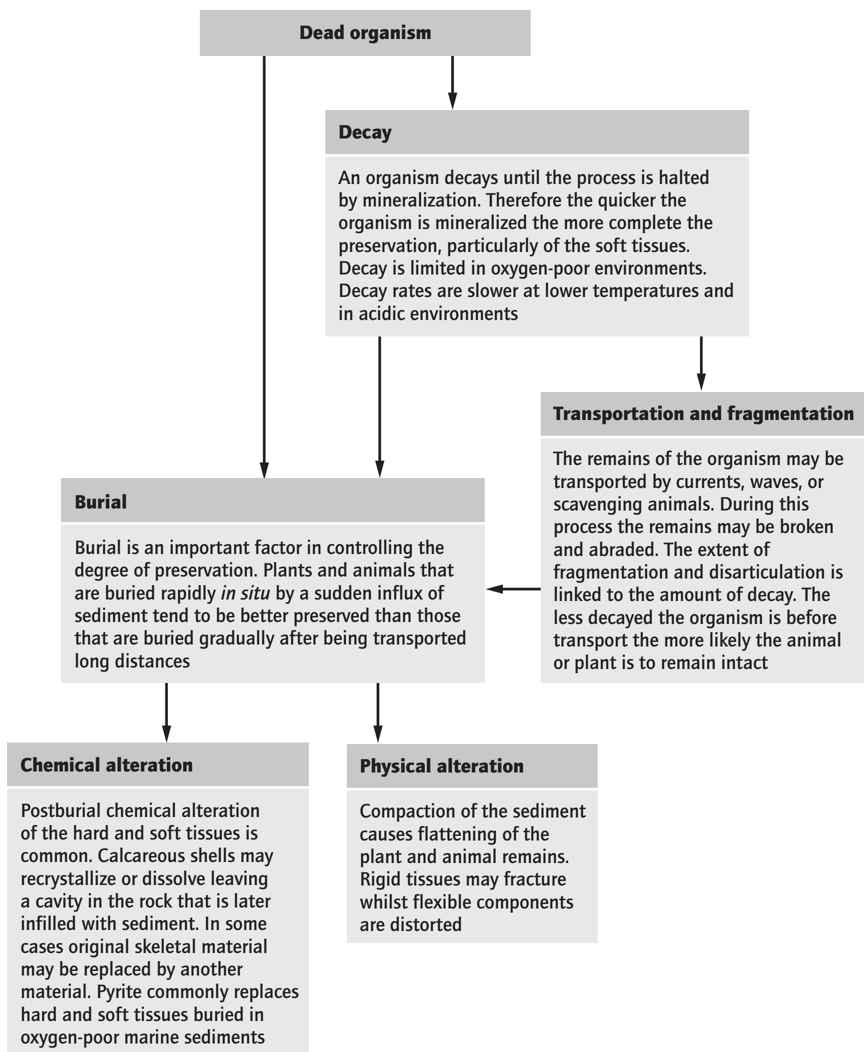

Fig. 1.5 The process of fossilization (taphonomy).

Biases in the fossil record

The fossil record is extremely selective. The term "preservation potential" is used to describe the likelihood of a living organism being fossilized. Organisms with a high preservation potential are common fossils. The nature of their morphology and the environment in which the organisms lived are important factors in determining whether they will be preserved. These inherent biases skew our view of past life. In general, the fossil record is biased towards the following:

- organisms with tissues resistant to decay;
- marine organisms;
- organisms living in low energy environments;
- more recent organisms;
- organisms that were more common.

Organisms with tissues resistant to decay

Organisms with body parts that do not decay easily are more likely to be preserved in the fossil record than soft-bodied animals. In vertebrate animals, the teeth and bones are the most commonly fossilized components. Invertebrates often have shells and carapaces that are not prone to decay. The shells of most common invertebrates are formed from calcium carbonate in the form of calcite or aragonite. Aragonite may be converted to calcite during fossil diagenesis. This can be identified by a change in the shell crystal structure from layers of needle-like crystals to large, blocky crystals. Some invertebrates have skeletons composed of silica, for example sponges, that are preserved in the fossil record. The skeleton (or rhabdosome) of graptolites was composed of collagen, a protein which is extremely durable and resistant to decay. Animals with exoskeletons molt as they grow, increasing the number of potential fossils. Plant material is particularly prone to decay, although the woody tissues that form the stem and leaves, together with spores and pollen that have a resistant waxy coating, may be preserved in the fossil record.

The skeletal structure of an organism determines the completeness of the preservation. Hard tissues that are in the form of a single component, for example gastropods, are more likely to be preserved whole in the fossil record than skeletons that are made up of many pieces, for example sea urchins.

Marine organisms

Marine organisms are more likely to be preserved than those living on land. On land there is more erosion and less deposition of sediment and consequently less opportunity for burial. Terrestrial plants and animals living close to depositional areas, for example by the side of a lake, have a greater preservation potential than those living in areas of net erosion such as uplands.

The nature of the substrate that the organism inhabits does not seem to have an effect on the preservation potential of a marine animal. However, its ecology does affect the likelihood of a marine animal being fossilized. Sedentary animals, filter feeders, and herbivores are more commonly preserved in the fossil record than carnivorous animals. Sedentary animals, like corals, tend to be heavy and robust whilst active predators have more lightly constructed skeletons. In addition, mobile animals can escape from burial by sediment.

Organisms living in low energy environments

In low energy environments the mechanical processes, such as currents, waves, and wind, that destroy plant and animal remains are less intense. Therefore organisms living in these environments are more likely to be preserved. However, this can be an oversimplistic view since organisms living in high energy environments may have more developed and more durable skeletons, thus increasing their preservation potential, or they may be buried more quickly and hence avoid postmortem damage.

Exceptionally preserved fossils

Remarkable fossil deposits are known as fossil lagerstätten. Lagerstätten is a German word that is applied to deposits of economic importance. The term fossil lagerstätten is used to describe fossiliferous formations particularly rich in paleontological information. There are two types of fossil lagerstätten: Konzentrat-Lagerstätten and Konservat-Lagerstätten (Figs 1.6 and 1.7). Occurrences where the number of fossils preserved is extraordinarily high are termed Konzentrat-Lagerstätten or concentration deposits. In Konservat-Lagerstätten the quality of preservation is exceptional, soft tissues are fossilized, and the skeletons are articulated. Konservat-Lagerstätten are a rich source of paleontological information. Preservation of the soft tissues helps explain the paleobiology of extinct organisms and the preservation of an entire community provides an insight into the structure of ancient ecosystems. Konservat-Lagerstätten can be considered as "preservation windows" that provide an exceptional view of past life.

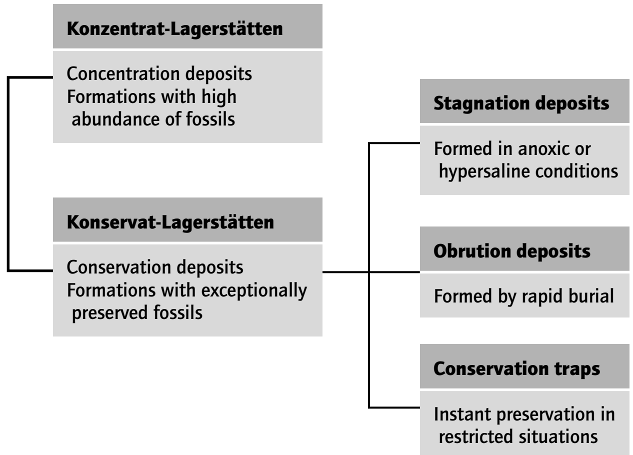

Fig. 1.6 Classification of fossil lagerstätten.

Konservat-Lagerstätten generally form in environments that are hostile to life or in environments with very high sedimentation rates. Carcasses may be transported into hypersaline or anoxic lakes that are devoid of scavengers. Such occurrences produce stagnation deposits. Rapid burial also minimizes the effect of scavengers. This can occur in deep marine environments where turbidity currents may suddenly deposit large quantities of sediment or in a delta where large volumes of material are being discharged into the sea. These deposits are called obrution deposits. Konservat-Lagerstätten are also associated with conditions that cause instant preservation. These situations are known as conservation traps and include insects preserved in amber (fossilized tree resin) and animals trapped in peat bogs.

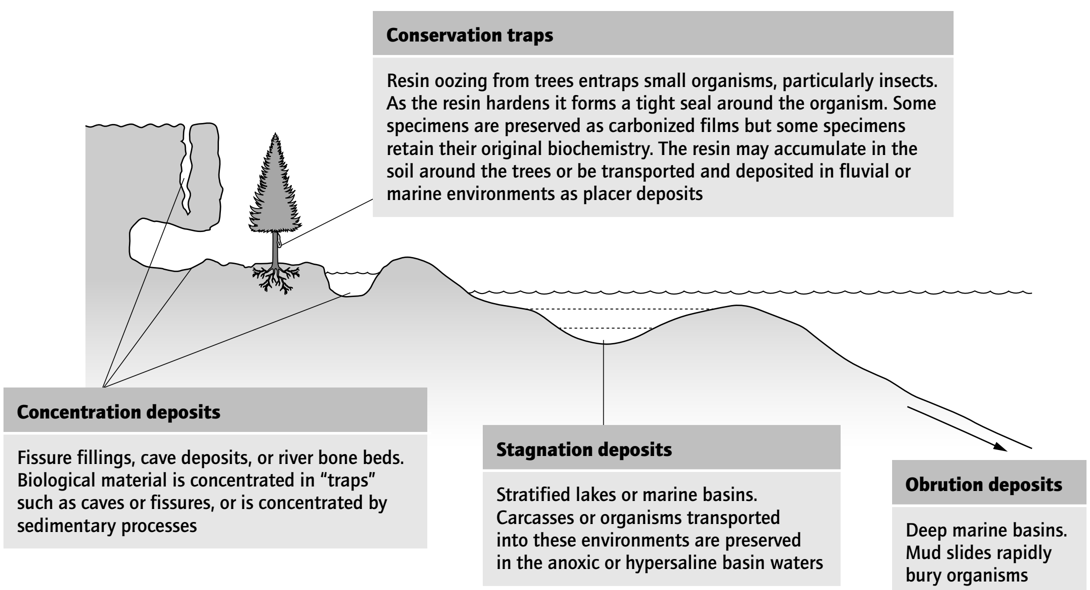

Fig. 1.7 Types of fossil lagerstätten.

The Cambrian lagerstätten

At a variety of locations around the world, exceptionally preserved organisms of Cambrian age have been found, offering an unparalleled insight into this critical point in the evolution of life on Earth (Table 1.1). The most famous site is the Burgess Shale, in Canada, which records over 125 fossil genera, dominated by arthropods. A broadly similar fauna is found at Emu Bay in Australia. The older Chengjiang site, in China, records a similar variety of life from a different paleocontinent. The Sirius Passet Formation, in Greenland, is of a similar age to the Chengjiang material, but records a more problematic, and apparently simpler fauna, dominated by soft-bodied animals. Finally the late Cambrian Orsten sites along the Baltic coast reveal in three dimensions and in outstanding clarity, the morphology and ecology of trilobites and other arthropods.

The sheer number and quality of fossil sites known from rocks of Cambrian age is partly a facet of the effort put in by paleontologists to their discovery. However, it also suggests that the Cambrian may have been ‘lagerstätten-prone’. When paleogeographic reconstructions are undertaken, they show that Cambrian lagerstätten formed in a wide variety of latitudes and across most of the continents of that time. Most of the sites were in deep water at the time of deposition, though the Emu Bay Shale represents a shallower water deposit. The Sirius Passet, Burgess Shale, and, to a lesser extent, the Chengjiang faunas were preserved through rapid burial. However, what all the sites share is evidence of anoxic conditions, and further periods when oxygen availability was reduced in the area. This prevented most types of decay, and facilitated the preservation of soft parts and of articulated animals. As overall conditions in the Cambrian indicate only perhaps 60% of current oxygen levels in the atmosphere, it is possible that exceptional preservation was generally more common than in more recent periods of Earth’s history.

The work done on Cambrian lagerstätten has generated great increases in our understanding of the evolution of ecosystems and of the phyla that currently inhabit our world.

The most significant controversy to come out of the study of Cambrian lagerstätten involves the diversity of life. It is commonly assumed that the diversity of life on Earth is higher at the present time than it has ever been before, because evolution has been at work for the longest time, facilitating the evolution of species into the widest variety of niches. There are estimated to be in excess of 2 million different species on the planet currently. The total fossil record of the last 3.5 billion years comprises around 250,000 species.

While at a species level this argument is probably a good one, and while the fossil record is clearly too poor to support any other contention, the same may not be true at higher phylogenetic levels, and especially at the level of the phylum. At this level, dealing with groups of organisms such as arthropods or mollusks, the fossil record appears to have a much higher fidelity. All modern phyla can be traced back at least as far as the Ordovician. Many of the fossils recovered from Cambrian lagerstätten fit poorly or controversially into modern phyla, leading to the suggestion that there were more phyla living in the Cambrian than exist today. In this respect, Cambrian diversity might be seen as being higher than the diversity of the modern planet, as the number of basic body plans was greater.

Table 1.1 The main characteristics of Cambrian lagerstätten.

Cambrian lagerstätten	Age	Location	Environment and preservation	Important fauna and flora
Sirius Passet	About 518 Ma	Northern Greenland	Deep water shales, with occasional episodes of rapid burial associated with slope collapse on the nearby carbonate platform	Scale-bearing animals, like *Halkieria*; rare trilobites; soft-bodied arthropods; mainly soft-bodied organisms
Changjiang	About 518 Ma	South China	Quiet, deep water shales; evidence of good oxygenation in surface waters, but possible absence of oxygen in the sediment. Episodes of rapid burial	Diverse fauna, dominated by arthropods; possible earliest chordates, or even vertebrates, *Yunnanzoon*, *Haikouella*; scale-bearing lobopods, *Microdictyon*
Emu Bay	About 510 Ma	South Australia	Fairly shallow water, low energy deposit. Preservation by phosphatization	*Anomalocaris*; trilobites, sometimes with preserved antennae; scale-bearing animals, like *Wiwaxia*
Burgess Shale	505 Ma	Canadian Rockies	Deep water shale, but with most organisms being swept in from shallower water by sudden turbidity currents. Preservation by rapid burial and the anoxic conditions of deposition	Large predator, *Anomalocaris*; many arthropods; primitive chordate, *Pikaia*; problematic scale-bearing worms like *Hallucigenia*
Orsten	About 500 Ma	Southern Sweden and elsewhere around the Baltic	Carbon-rich shales, from deep water, anoxic areas. Preservation is in limestone nodules and by phosphatization, which formed an apatite cover to the soft parts	Dominated by arthropods, including trilobites; low diversity of other organisms including algae and invertebrates

More examples of Konservat-Lagerstätten

Baltic amber, Cenozoic, Russia

Amber is fossilized plant resin. As the name implies, Baltic amber is abundant along the shores of the Baltic Sea, particularly around the Samland Promontory of Russia.

In the early Cenozoic times, forests of the extinct tree *Pinus succinifera* flourished on a landmass south of the Samland region. During the Oligocene the area was flooded and the resin from the trees was washed out and redeposited in marine sediments in the Samland area. These sediments have been reworked and the amber was subsequently redeposited in areas along the shores of the Baltic Sea. As amber has a low density it can be carried by water and is generally deposited in low energy environments such as lakes, submarine basins, and estuaries.

Around 98% of the Baltic amber biota are flying insects. Diptera, two-winged flying insects, dominate the fauna of the Baltic amber, accounting for approximately half of the organisms. Extremely rare mammal hairs, an almost complete lizard, ants (Fig. 1.8), snails, and bird feathers account for the remaining 2%.

The Baltic amber fossils are important as they show the morphology of flying insects in extremely fine detail and also provide information on the dispersal and development of these insects and the climatic conditions in which they lived.

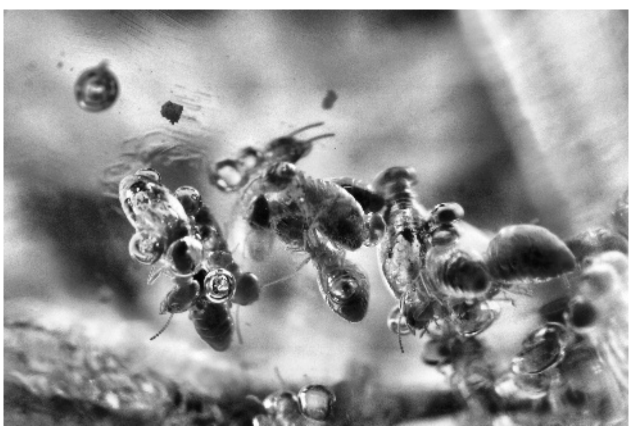

Fig. 1.8 Ants preserved in amber.

Solnhofen Lithographic Limestone, Jurassic, Bavaria

Most famous for the preservation of the feathered dinosaur *Archaeopteryx*, the Solnhofen Lithographic Limestone (Jurassic) outcrops over a wide area of Bavaria. The limestones are buff colored, fine grained, and extraordinarily regular, forming laminar beds traceable over tens of kilometers. They were deposited in a series of lagoons formed behind reefs. High evaporation rates and limited water exchange with the open sea caused the lagoon waters to stratify with the more dense saline waters forming a hostile bottom environment.

Over 600 species of animals and plants are preserved in the limestones (Fig. 1.9). Most animals were pelagic. Only a few benthic organisms are known from the area. It is believed that most of these animals were swept in from the open sea. Some were able to live in the less saline upper waters for short periods. Terrestrial animals and plants may have been washed in during rainy seasons and insects blown into the lagoons by the wind.

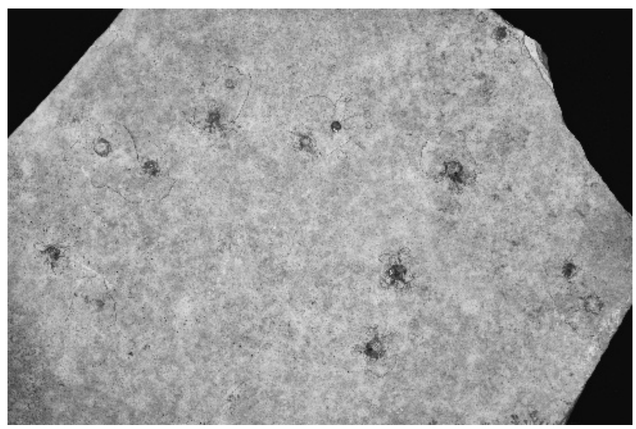

Fig. 1.9 The most common macrofossil in the Solnhofen Limestone, Bavaria: the crinoid, *Saccocoma* (diameter 5 cm).

Reconstructing the ecology of fossils

The information available to help in reconstructing a fossil and inferring its life habits come from three sources: from modern relatives, from modern analogs, or from trace fossils (Fig. 1.10).

Living relatives of a fossil are extremely useful in inferring information about that fossil's ecology. Living *Nautilus*, for example, uses a system of jet propulsion to power it through the water. Extinct ammonites share a common ancestor with this group and have a similar shell morphology. It therefore seems sensible to suggest that both groups of shelled mollusks use or used a jet propulsion system for making rapid movements.

A different example of the use of homologs comes from the discovery of what appears to be the skull modifications for whiskers in some early mammal-like reptiles. In modern mammals, whiskers are developed as highly modified hairs. If a fossil can be shown to have had whiskers, it also had fur, and fur in modern organisms is used to insulate a warm-blooded organism. Mammal-like reptiles can therefore be inferred to have been warm blooded.

Modern analogs rely on comparisons between similar environments, similar-looking organisms, or on inferences based on physics or engineering that do not change over geological time. A good example of this is the work done on the bone strength of dinosaur legs, in particular the large sauropods like *Diplodocus*. Recent work has shown that, like eggs, the bones are extremely strong in some directions and that they could easily have borne the weight of the animals as long as most of the legs were weight bearing at any one time. This has led to new reconstructions of sauropods walking on land, but not running, which would involve supporting their weight on only two legs at once.

Trace fossils preserve a moment of activity in the life of an organism, and can show that the animal did something in particular, if they can be related to the thing that made them. Trace fossils such as *Cruziana* and *Rusophycus* demonstrate that some species of trilobites walked on the sea bed, and burrowed for soft prey into the sediment, but only some trilobites can be linked directly to the traces they made.

Some information is unavailable for any fossil group, for example true color or seasonal or diurnal variations in activity. Living organisms are capable of a wide range of behaviors, and function in different manners depending on factors such as their stress levels, mating state, level of hunger, and so on.

The teeth of pterosaurs give insight into the diet of these animals, by analogy with modern organisms. Most pterosaurs had small, peg-like teeth which are like those of modern fish eaters

Reconstructing wings can be done based on exceptionally well-preserved pterosaurs, where the wing membrane can be seen. The shape of the wing can be used to infer the flight characteristics of the animal, as all wings will have predictable aerodynamic properties. Long and relatively large wings like these would have facilitated efficient gliding flight such as is seen in modern seabirds like albatrosses

Exceptionally preserved pterosaurs show that the body was covered in a mat of coarse fibers, analogous to mammalian fur. The primary use of fur is in keeping warm-blooded animals insulated against heat loss. Pterosaurs are therefore inferred to have been warm blooded. This is supported by the observation that flight is a very energy-intensive activity and that most modern fliers are endotherms

Pterosaur trackways show that the animal walked on all-fours, with the front legs held wide and the back legs making narrow tracks. They walked by moving both feet on the same side of the body, one after the other, and before the two feet on the other side, which is an unusual pattern, possibly implying that they evolved from bipedal ancestors

Fig. 1.10 An example of bringing fossils to life: pterosaurs.

Glossary

Adaptive radiation: evolutionary response to large-scale environmental change. This results in the formation of new ecological niches that can be occupied through the adaptation of previous generalists.
Amber: fossilized tree resin.
Benthic: living on or in the sea floor.
Biostratigraphy: stratigraphy based on fossil content.
Biozone: layer of rock characterized by fossil content.
Chlorophyll: green pigment found in plants.
Chronostratigraphy: stratigraphy based on geological time.
Cyanobacteria: microorganisms with chlorophyll that produce oxygen on photosynthesis.
Diagenesis: physical and chemical processes that operate on sediments after burial.
Exoskeleton: external skeleton of an animal.
Golden spike: physical point in a section equivalent to an instant in geological time marking the base of a stratigraphic unit.
Infaunal: living within the sediment.
Konservat-Lagerstätten: deposits containing exceptionally preserved fossils.
Konzentrat-Lagerstätten: deposits containing numerous fossils.
Lagerstätten: deposits containing numerous and/or exceptionally preserved fossils.
Lithostratigraphy: stratigraphy based on rock characteristics.
Pelagic: living in open water (floating or swimming).
Photosynthesis: biological process in plants that captures light energy and converts it into chemical energy.
Plate tectonics: theory that the Earth's crust is formed of moving plates.
Taphonomy: study of the process of fossilization.
Taxon (plural **taxa**): general term for any formal grouping of plants and animals.
Zone fossil: fossil species that is indicative of a particular unit of geological time.