004118.a0001 # Fossil Record

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Fossils are the remains of plants and animals that once lived. Quality of preservation ranges from complete to traces of hard parts only, and it is important to consider how this incompleteness affects understanding of past life.

Introductory article

Article Contents

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004118.s0001 ## Introduction

004118.p0001 Fossils are the remains of plants and animals that once lived. The common image of a fossil is an ancient shell or bone that has been turned to rock, or petrified. However, fossils can include a wide of remains, including delicate impressions of leaves and flowers of ancient plants, traces of soft tissues of animals, tracks and burrows, mammoth flesh preserved in icy soil and complete insects in amber.

004118.p0002 Fossils were first recorded by scholars in the times of the ancient Greeks. These writers recognized that the specimens they extracted from the rocks were evidences of former life. In medieval times, there was a certain amount of debate about the meaning of fossils. Many people regarded them as simply unusually shaped rocks that mimicked modern shells, bones and leaves, but which meant nothing more. Even in the seventeenth and eighteenth centuries, many people regarded fossils as ‘sports of nature’, strangely shaped objects that had been created by some unknown ‘plastic force’ in the Earth’s crust which made them look like real artefacts. Some people even believed they were the work of the Devil, created somehow to test the faith of God-fearing Christians who might be tempted to believe when they proved the former existence of extinct forms of life.

004118.p0003 In these early times, scholars had a clearer, more logical interpretation. Leonardo da Vinci found fossil shells in limestones far inland in Italy, some of them from mountain tops. He reasoned that these fossils looked like shells because they were the remains of ancient shells. Not only that they were clearly sea shells, but they were present in such abundance that they could not be explained away as the remains of the lunch of a Roman army that had passed by. Therefore, he concluded: the sea had once covered these ancient mountain tops, and that proved that the Earth’s crust had not always been the same.

004118.p0004 In 1676, Robert Plot, Professor at the University of Oxford, described a large fossil bone fragment in his book *The Natural History of Oxfordshire*. He reasoned in a similar way: the massive object looked like the end of a bone in general shape, and also the fine detail of its internal structure looked just like modern bone. Hence it was a bone. He identified it as the knee end of a giant thigh bone. He concluded that was too big to have come from an elephant, and so must have come from one of the giant men or women who are mentioned in the Bible. Though this conclusion does not appropriate, now the basic reasoning was correct. We are now aware of this fact that Plot’s bone was part of the thigh bone of the dinosaur *Megalosaurus*, but Plot could not have possibly known anything about dinosaurs, a species that was not named until 1842. **See also**: Dinosauria (dinosaurs).

As more and more fossils were found, it became clear 004118.p0005
that they truly did represent evidence of former life, and that there had been a long history of life on the Earth. Modern interpretations developed from 1750 onwards. Around 1750, bones of fossil elephants – mastodonts and mammoths – were found in Ohio, and they were sent back to London and Paris for study. Some anatomists claimed that these huge elephants would soon be found by explorers in the remote parts of North America. Others accepted that these bones were evidence of the extinct elephants. Over the next decades, as European explorers pushed westwards, and failed to find any living elephants, it became more and more obvious that extinction, the complete disappearance of species, was a possibility. The idea of extinction was resisted at first, since it might be interpreted by the devout as evidence that God had made a mistake in His Creation, but as more and more bizarre fossil creatures were found, it became impossible to deny. The case was clinched by Georges Cuvier, the great French palaeontologist, in a series of papers and books published from 1790 to 1820, in which he described the complete fossil skeletons of dozens of remarkable ancient reptiles, birds and mammals around the world, many of which had no obvious living relatives. **See also**: Cuvier, Georges Léopold Chrétien Frédéric Dagobert Baron de; Extinction.

Fossils 004118.s0002

There are two kinds of fossils: body fossils and trace fossils. 004118.p0006
Body fossils are remnants of the bodies of ancient plants and animals, preserved either completely or in part. Examples are a complete external skeleton of a trilobite, a dinosaur bone, a leaf of an ancient fern or a complete insect in amber. Trace fossils are evidences of the activity of ancient animals or plants. They usually indicate movements

or other evidence of animals, such as a trackway of dinosaur footprints, an ancient worm burrow, or a string of faecal pellets (excrement). Rarely, some trace fossils indicate movements of plants.

004118.p0007 The study of fossils is palaeontology (US, paleontology), and it is carried out by palaeontologists. Specialist subdivisions of palaeontology include palaeobiology (the study of how ancient plants and animals lived and evolved), palaeoecology (the study of ancient plants and animals in their environments), palaeopathology (the study of ancient diseases from their indications in fossils), palaeobiogeography (the study of the distributions of ancient organisms), ichnology (the study of trace fossils), palaeobotany (the study of ancient plants), palynology (the study of ancient pollen and spores) and micropalaeontology (the study of ancient microscopic organisms, mainly plankton in seas and lakes). Related disciplines include stratigraphy (dating of rocks and division of geological time), palaeoclimatology (the study of ancient climates), systematics (the study of the relationships and evolution of groups) and macroevolution (the study of large-scale patterns of evolution). **See also**: Geological time: dating techniques; Geological time: principles; Microevolution and macroevolution: introduction; Palaeoenvironments

004118.s0003 Modes of Preservation – Normal and Exceptional

004118.p0008 When a plant or an animal dies, it is must likely that it will not end up as a fossil. If it is fossilized, all that is normally preserved are the hard parts – bones, shells, wood and the like. In rare cases, soft parts may be preserved, and these exceptional cases of preservation are crucially important in reconstructing the life of the past. Understanding the balance between normal, incomplete, preservation and exceptional preservation allows palaeontologists to reconstruct a full picture of the life of the past.

004118.s0004 Hard parts and soft parts

004118.p0009 Fossils are typically the hard parts – shells, bones, woody tissues – of previously existing plants and animals. In many cases, these skeletons, materials used in supporting the bodies of the animals and plants when they were alive, are all that is preserved. Skeletons may nonetheless give useful information about the appearance of many extinct animals since they can show the overall body outline and may hint at the location of muscles, and woody tissues of plants may allow whole tree trunks and leaf venation to be preserved in some detail. The fossil record is biased in favour of organisms that have hard parts. Soft-bodied organisms may represent up to 60% of the individuals in a marine setting, and these would all be lost under normal conditions of fossilization.

There is a variety of hard materials in plants and animals 004118.p0010
that contribute to their preservation (**Table 1**). These include inorganic mineralized materials, such as forms of calcium carbonate, silica, phosphates and iron oxides. Calcium carbonate ($CaCO_3$) makes up the shells of foraminifera, some sponges, corals, bryozoans, brachiopods, molluscs, many arthropods and echinoderms. Silica (SiO_2) forms the skeletons of radiolarians and most sponges, while phosphate, usually in the form of apatite ($CaPO_4$), is typical of vertebrate bone, conodonts and certain brachiopods and worms. There are also organic hard tissues, such as lignin, cellulose, sporopollenin and others in plants and chitin, collagen and keratin in animals, which may exist in isolation or in association with mineralized tissues.

Exceptional preservation 004118.s0005

There are many famous examples of exceptional preser- 004118.p0011
vation, such as the mammoths from Siberia preserved with their flesh intact and, supposedly, still edible after 15 000 years. Older cases include the Late Jurassic Solnhofen beds of southern Germany which have yielded specimens of *Archaeopteryx*, the first bird, with feathers preserved, and the Cambrian Burgess Shale of Canada, 500 million years old, with its weird arthropods and worm-like creatures. Such fossil-bearing formations, termed Lagerstätten, have produced hundreds of remarkable fossil specimens, and in some cases soft parts are preserved. In the most spectacular cases, such as the Mid-Cretaceous Santana Formation of Brazil, soft tissues such as muscle, and even the gills of fishes, which are composed of labile forms of organic carbon, may be preserved. And the famous Eocene deposits at Messel, near Darmstadt, Germany, yield fossils showing original colour patterns as well as blood cells. Usually, the rather more decay-resistant soft tissues, such as chitin and cellulose, are fossilized. **See also**: Mesozoic birds; Messel; Solnhofen.

Plant and animal tissues decay in a sequence that de- 004118.p0012
pends on their volatile content, and the process of decay can only be halted by mineralization (**Figure 1**). In the process of fossilization, then, it is possible to think of a race between rates of decay and rates of pre-burial mineralization: the point of intersection of those rates determines the quality of preservation of any particular fossil.

Early mineralization of soft tissues may be achieved in 004118.p0013
pyrite, phosphate or carbonate, depending on three factors: (1) rate of burial, (2) organic content and (3) salinity (**Figure 2a**). Early diagenetic pyritization (**Figure 2b**) of soft parts is favoured by rapid burial, a low organic content, and the presence of sulfates in the sediment. Early diagenetic phosphatization (**Figure 2c**) requires a low rate of burial and a high organic content. Soft-part preservation in carbonates (**Figure 2d**) is favoured by rapid burial in organic-rich sediments; at low salinity levels, siderite is deposited, and at high salinity levels, carbonate is laid down

in the form of calcite. In rare cases, decay and mineralization do not occur, when the organism is instantly encased and preserved in a medium such as amber (**Figure 2e**) or asphalt.

004118.p0014 Mineralization of soft tissues occurs in three ways. Rarely, soft tissues may be replaced in detail, or replicated, by phosphates. Permineralization occurs very early, probably within hours of death, and may preserve highly labile structures such as muscle fibres (**Figure 2b**), as well as more refractory tissues such as cellulose and chitin. The commonest mode of mineralization of soft tissues is by the formation of mineral coats of phosphate, carbonate or pyrite, often by the action of bacteria. The mineral coat preserves an exact replica of the soft tissues which decay away completely. The third mode of soft tissue mineralization is the formation of tissue casts during early stages of sediment compaction. Examples of tissue casts include siliceous and calcareous nodules which preserve the form of the organism and prevent it from being flattened or dissolved.

004118.p0015 The mode of accumulation of fossils also determines the nature of fossil Lagerstätten. Fossil assemblages may be produced by concentration, the gathering of remains by normal processes of sedimentary transport and sorting to form fossil-packed horizons, or by conservation, the fossilization of plant and animal remains in ways that avoid scavenging, decay and diagenetic destruction. Exceptionally preserved fossil assemblages are produced mainly by processes of conservation. Certain sedimentary regimes, in the sea or in lakes, are stagnant, where sediments are usually anoxic, and are devoid of animals that might scavenge carcasses. In other situations, termed obrution deposits, sedimentation rates are so rapid that carcasses are buried virtually instantly, and this may occur in rapidly migrating river channels or at delta fronts and other situations where turbidites are deposited. Some unusual conditions of instant preservation are termed conservation traps. These include amber, fossilized resin that oozes through tree bark, and may trap insects and tar pits and peat beds, where plants and animals sink in and their carcasses may be preserved nearly completely.

004118.s0006 Taphonomy

004118.p0016 Critical to an understanding of fossils is the study of taphonomy, the processes that go on between the death of an organism, and its discovery as a fossil. Any fossil that is found in the rocks has passed through a sequence of stages: (1) decay of the soft tissues of the plant or animal; (2) transport and breakage of hard tissues; and (3) burial and modification of the hard tissues.

Decay 004118.s0007

Decay processes typically operate from the moment of death until either the organism disappears completely, or until it is mineralized, although mineralization does not always stop decay. If mineralization occurs early, then a great deal of both the hard and soft parts may be preserved in detail, and the specimens are identified as exceptionally preserved (see above). If mineralization occurs late, as is usually the case, decay processes will have removed or replaced all soft tissues and may also affect many of the hard tissues. 004118.p0017

Decay processes exist because dead organisms are valuable sources of food for other organisms. When large animals feed on dead plant or animal tissues, the process is termed scavenging, and when microbes, such as fungi or bacteria, transform tissues of the dead organism, the process is termed decay. Well-known examples of scavengers are hyenas and vultures, both of which strip the flesh from large animal carcasses. After these large scavengers have had their fill, smaller animals, such as meat-eating beetles, may continue the process of defleshing. In many cases, all flesh is removed in a day or so. Decay is dependent on three factors. 004118.p0018

The first factor controlling decay is the supply of oxygen. In aerobic (oxygen-rich) situations, microbes break down the organic carbon of a dead animal or plant by converting carbon and oxygen into carbon dioxide and water. Microbial decay can also take place in anaerobic conditions, i.e., in the absence of oxygen, and in these cases nitrate, manganese dioxide, iron oxide, or sulfate ions are necessary to allow the decay to occur. 004118.p0019

The second set of factors controlling decay, temperature and pH, may be most important. High temperatures promote rapid decay. Decay proceeds at normal high rates when the pH is neutral, as is the case in most sediments, since this creates ideal conditions for microbial respiration. Decay is slowed down by conditions of unusual pH, such as those found in peat swamps, which are acidic. Fossils preserved in peat or lignite (brown coal) become tanned, like leather, and many of the soft tissues are preserved. Examples are the famous 'bog bodies' of northern Europe, in which skin and internal organs are preserved, and silicified fossils in the lignite of the Geiseltal deposit in Germany (Eocene), which show muscle fibres and skin. **See also**: Soils and decomposition. 004118.p0020

Decay depends, thirdly, on the nature of the organic carbon, which varies from highly labile to highly decay-resistant. Most soft parts of animals are made from volatiles, forms of carbon that have molecular structures that break down readily. Other organic carbons, termed refractories, are much less liable to break down, and these include many plant tissues, such as cellulose. 004118.p0021

The normal end result of scavenging and decay processes is a plant or animal carcass stripped of all soft parts. In rare 004118.p0022 cases, some of the soft tissues may survive, and these are examples of exceptional preservation (see above).

004118.s0008 ## Breakage and transport

004118.p0023 The hard parts left after scavenging and decay have taken their toll may simply be buried without further modification, or they may be broken and transported. There are several processes of breakage, some physical (disarticulation, fragmentation and abrasion) and some chemical (bioerosion, corrosion and dissolution).

004118.p0024 Skeletons that are made from several parts may become disarticulated, separated into their component parts. For example, the multi-element skeletons of vertebrates may be broken up by scavengers and by wave and current activity on the sea bed (**Figure 3a**). Disarticulation happens only after the scavenging or decay of connective tissues that hold the skeleton together. This may occur within a few hours in the case of crinoids, where the ligaments holding the separate ossicles together decay rapidly. In trilobites and vertebrates, normal aerobic or anaerobic bacterial decay may take weeks or months to remove all connective tissues.

004118.p0025 Skeletons may also become fragmented, i.e., individual shells, bones or pieces of woody tissue break up into smaller pieces (**Figure 3b**), usually along lines of weakness. Fragmentation may be caused by predators and scavengers such as hyenas, which break bones, or crabs, which use their claws to snip their way into shelled prey. Much fragmentation is caused by physical processes associated with transport: bones and shells may bang into each other and into rocks as they are transported by water or wind. Wave action may cause such extensive fragmentation that everything is reduced to a fine sand.

004118.p0026 Shells, bones and wood may be abraded by physical grinding and polishing against each other and against other sedimentary grains. Abrasion removes surface details, and the fragments become rounded (**Figure 3c**). The degree of abrasion is related to the density of the specimen (in general, dense elements survive physical abrasion better than porous ones), the energy of currents and grain size of surrounding sedimentary particles (large grains abrade skeletal elements more rapidly than small grains), and the length of exposure to the processes of abrasion.

004118.p0027 Under certain circumstances, shells, bones and wood may undergo bioerosion, the removal of skeletal materials by boring organisms such as sponges, algae and bivalves (**Figure 3d**). Minute boring sponges and algae operate even while their hosts are alive, creating networks of fine borings by chemical dissolution of the calcareous shell material. This process continues after death, and some fossil shells are riddled with borings which may remove more than half of the mineral material of any single specimen. Other boring organisms eat their way into logs, and heavily modify the internal structure.

Before and after burial, skeletal materials are commonly corroded and dissolved by chemical action (**Figure 3e**). The minerals within many skeletons are chemically unstable, and they break down after death while the specimen lies on the sediment surface, and also for some time after burial. Carbonates are liable to corrosion and dissolution by weakly acidic waters. The most stable skeletal minerals are silica and phosphate. 004118.p0028

Burial and modification 004118.s0009

Animal and plant remains are typically buried after a great deal of scavenging, decay, breakage and transport. Sediment is washed or blown over the remains, and the specimen becomes more and more deeply buried. During and after burial, the specimen may undergo physical and chemical change. 004118.p0029

The commonest physical change is flattening by the weight of sediment deposited above the buried specimen, and it may occur soon after burial. The flattening forces flatten the specimen in the plane of sedimentary bedding. The nature of flattening depends on the strength of the specimen: the first parts to collapse are those with the thinnest skeleton and largest cavity inside. Greater forces are required to compress more rigid parts of skeletons. Ammonites, for example, have a wide body chamber cavity which would fill up with sand or water after the soft body is decayed. This part collapses first (**Figure 3f**) and, because the shell is hard, it fractures. The other chambers are smaller, fully enclosed, and hence mechanically stronger: they collapse later. Plant fossils such as logs are usually roughly circular in cross-section, and they flatten to a more ovoid cross-section after burial. The woody tissues are flexible and they generally do not fracture, but simply distort. 004118.p0030

Physical effects such as flattening, and chemical effects that occur after burial, are termed diagenesis. In sedimentological terms, diagenesis may occur very soon after burial (e.g. flattening and some chemical changes) or long after, often thousands or millions of years later, as a result of the passage of chemicals in solution through rock containing fossils. Fossils may also be deformed by metamorphic processes, often millions of years after burial and diagenetic alteration. 004118.p0031

The calcium carbonate in shells occurs in four forms: aragonite, calcite (in two varieties – high magnesium (Mg) calcite, and low Mg calcite), and combinations of aragonite plus calcite. The commonest diagenetic process is the conversion of aragonite into calcite. After burial, pore fluids within the sediment may be undersaturated in $CaCO_3$, and the aragonite dissolves completely, leaving a void representing the original shell shape. Later, pore fluids which are supersaturated in $CaCO_3$ allow calcite to crystallize within the void, thus producing a perfect replica of the original shell. This process of replacement of aragonite by calcite occurs commonly, and may be detected by the change of 004118.p0032 the crystalline structure of the shell (**Figure 3g**). The regular layers of aragonite needles have given way to large irregular calcite crystals (sparry calcite) or tiny irregular calcite crystals (micrite).

004118.p0033 A common diagenetic phenomenon is the formation of carbonate concretions, bodies that form within sediment and concentrate $CaCO_3$ (calcite) or $FeCO_3$ (siderite). Carbonate concretions generally form early during the burial process, and this is demonstrated by the fact that enclosed fossils are uncrushed, having been protected from compaction by the formation of the concretion. Carbonate concretions form typically in black shales, sediments deposited in the sea in anaerobic conditions. Black shales contain abundant organic carbon, and when this is buried, bacterial processes of anaerobic decay begin. These decay processes reduce oxides in the sediment, and produce bicarbonate ions which may combine with any calcium or iron ions to generate carbonate and siderite concentrations. Such concentrations may grow rapidly to form concretions around the source of calcium and iron ions, usually the remains of an organism.

004118.p0034 Another early diagenetic mineral which occurs in anaerobic marine sediments is pyrite (FeS_2). It is also produced as a byproduct of anaerobic processes of microbial reduction within shallow buried sediments. Pyrite may replace soft tissues such as muscle in cases of rapid burial, and replaces hard tissues under appropriate chemical conditions. Wood, for example, may be pyritized, and dissolved aragonite or calcite shells may be entirely replaced by pyrite. In both cases, the original skeletal structures are lost.

004118.p0035 Phosphate is a primary constituent of vertebrate bone and other skeletal elements. In some cases, masses of organic phosphates are modified by microbial decay, which releases phosphate ions into the sediment. These may combine with calcium ions to form apatite, which can entirely replace dissolved calcareous shells. In other cases, the microbial processes enable soft tissues, and entirely soft-bodied organisms, to be replaced by phosphate. Coprolites, fossil dung, may also be phosphatized. In these cases, apatite has been liberated from the organisms themselves, and from surrounding concentrations of organic matter, and the replacement destroys most, or all, of the original skeletal structures. **See also**: Fossils and fossilization.

004118.s0010 Completeness

004118.p0036 Is the fossil record good enough to record the past history of life, or is it so hopelessly incomplete that it gives only rare glimpses of what was going on? Both viewpoints are current, and there are strong arguments on both sides. The question cannot be answered directly, although new quantitative techniques are inching towards an answer. **See also**: Fossil record: quality

A proponent of the viewpoint that the fossil record is good might use a number of arguments. He would note that our view of the fossil record has not changed much in the past hundred years. By 1900, all the main fossil groups had been found, and their order in the rocks had been established. The oldest fossil bird, *Archaeopteryx*, was found in 1860, and it is still the oldest fossil bird, despite some counterclaims. By 1900, the oldest fossil fishes were known from the Silurian period, some 430 million years ago. Since then, isolated remains of some what older, Ordovician, fishes have been found, some 460 million years old. The story is similar for other groups: in many places older representatives have been found, or an unusual new group is named, but the broad pattern is unchanged. The argument then is that, despite huge efforts by collectors and palaeontologists, not much has changed. Therefore, we are aware of all that we need to know of those groups of organisms, which are potentially fossilizable. 004118.p0037

The opposite view, often advanced by nonpalaeontologists, is that fossils are incomplete in two ways: 004118.p0038

1 Most plants and animals that ever lived are not preserved as fossils.
2 Those fossils that are preserved are mostly incomplete, being indications merely of the hard parts.

Linked to these observations is the fact that some habitats, such as shallow carbonate seas, are much better represented in the fossil record than others, such as many terrestrial settings. In addition, many processes, such as erosion, subduction of whole masses of the Earth's crust during continental drift, metamorphism (heating and folding of rocks), have a more and more serious effect on ever-older rocks. These two observations indicate processes that can exert systematic biases against both terrestrial and ancient organisms. **See also**: Palaeoenvironments 004118.p0039

The double incompleteness, of specimens and of anatomy, could be fatal, if one is required to have full representation of every individual organism. Fortunately, it is enough to have one dinosaur out of a hundred million to know time and place and anatomy. Similarly, surprisingly many terrestrial fossils are known (think of the hundreds of dinosaur and land mammal skeletons in museums around the world), and fossil Lagerstätten, such as the Cambrian Burgess Shale, dramatically fill many of the gaps in older parts of the fossil record. 004118.p0040

These observations on completeness are not overwhelming and convincing, since they are merely qualitative. Quantitative assessments, based on comparisons of evolutionary trees and the rock record, are beginning to resolve the question, and to give information on relative completeness of the fossil record of different groups and different time slices. The general result of the quantitative studies is that the fossil record gives an accurate picture of 004118.p0041 the past history of life, and that different palaeoenvironments are more comparable than might be expected. **See also**: History of palaeontology; Tiering on land – trees and forests (late Palaeozoic); Tiering in the sea – reefs and burrows (late Palaeozoic)

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Glossary

Body fossil#A fossil that preserves part, or all, of the body of an ancient animal or plant.

Diagenesis#The physical and chemical modifications that occur in rocks, and fossils, after burial.

Extinction#The disappearance of a species, or other larger group of plants or animals.

Lagerstätte (pl. Lagerstätten)#A fossil deposit of exceptional preservation (this is a specialized use of a German word that originally referred to a rich mineral deposit).

Palaeontology (US, paleontology)#The study of ancient life.

Permineralization#The conversion of soft or hard tissues of an organism to mineral.

Sedimentary rock#A rock, such as sandstone or limestone, that was once a sediment such as sand or mud, and which has not been subsequently modified substantially after burial.

Skeleton#The supporting hard tissues in an organism, either internal or external.

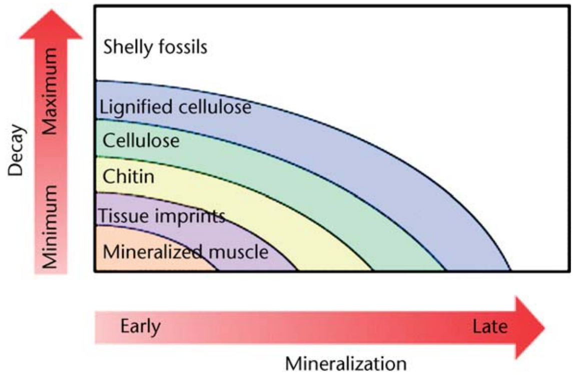
Taphonomy#The study of the processes that occur between death and burial of an organism, and its inclusion in sedimentary rock.

Trace fossil#Evidence of activity of an ancient animal or plant, such as a burrow, track or faecal pellet.

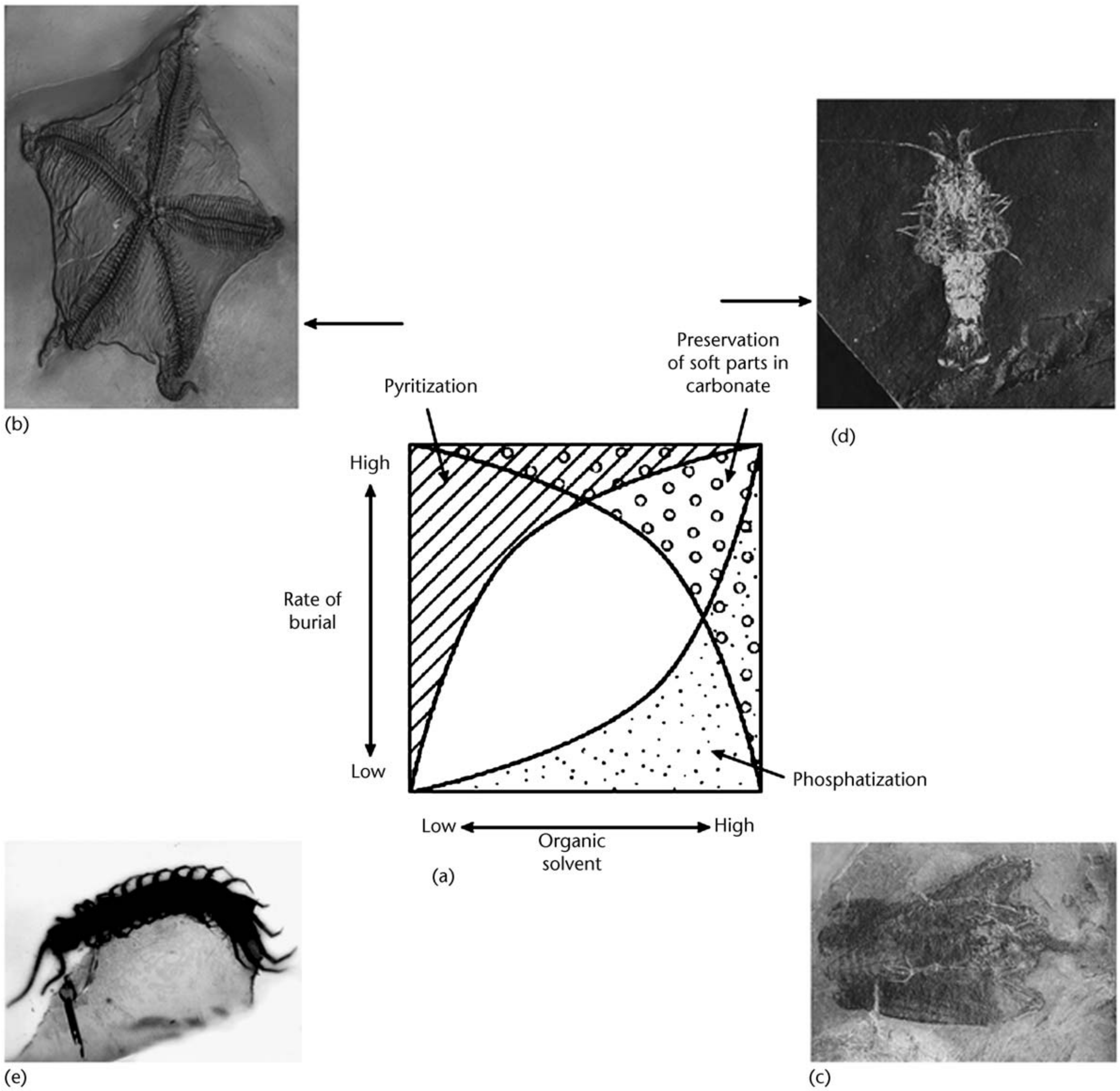
Turbidite#Sequence of sandstones and mudstones deposited by a gravity flow process underwater, usually in the deep sea.

Table 1 Mineralized materials in protists, plants and animals. The commonest occurrences are indicated with XX, and lesser occurrences with X

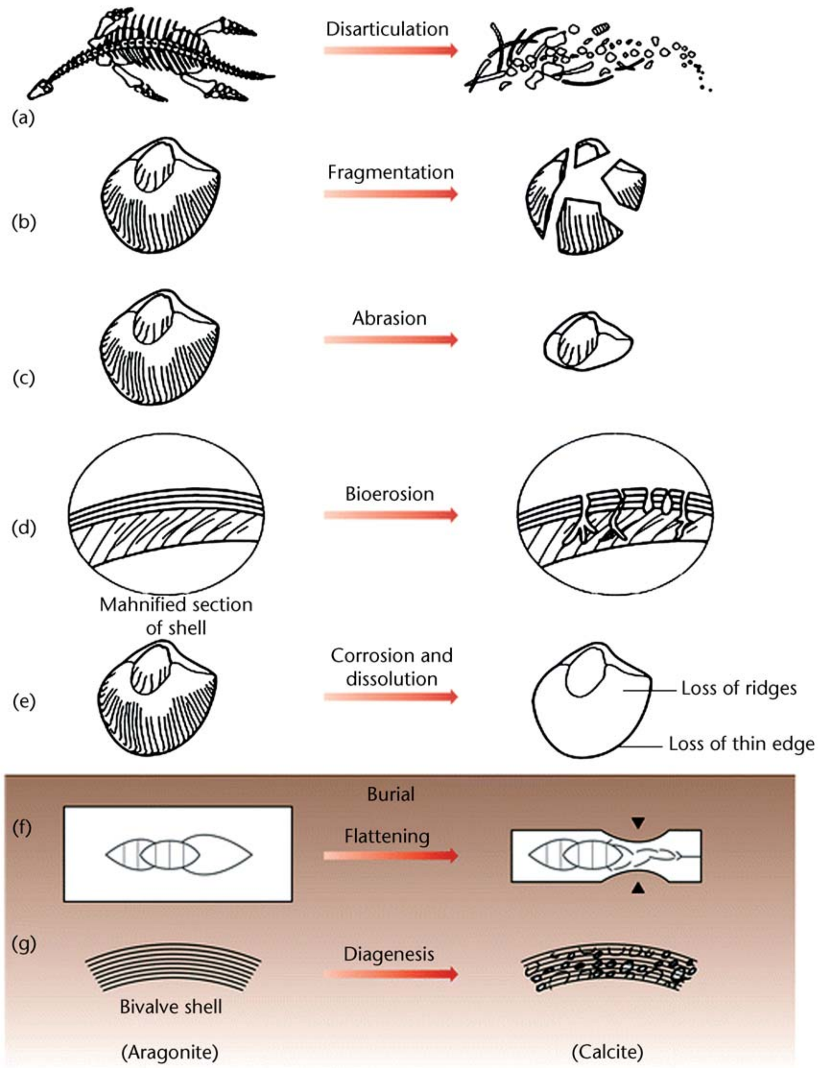
	Inorganic					Organic			
	Carbonates								
	Aragonite	Calcite	Phosphates	Silica	Iron oxides	Chitin	Cellulose	Collagen	Keratin
Prokaryotes	XX	X	X		X		X		
Algae	XX	XX		X		X	XX		
Higher plants		X		X	X		XX		
Protozoa		XX		XX	XX	X	X		
Fungi		X	X		X	XX	XX		
Porifera	X	XX		XX	X			XX	
Cnidaria	XX	XX				X		X	
Bryozoa	XX	XX	X			XX		X	
Brachiopoda		XX	XX			XX		X	
Mollusca	XX	X	X	X	X	X		X	
Annelida	XX	XX	XX		X	X		XX	
Arthropoda		XX	XX	X	X	XX		X	
Echinodermata		XX	X	X				XX	
Chpodata		X	XX		X		X	XX	XX



004118.f0001 **Figure 1** The relative rates of decay (vertical axis) and mineralization (horizontal axis) determine the kinds of tissues that may be preserved. At minimum decay rate and with very early mineralization, highly labile muscle tissues may be preserved. When decay has gone to a maximum, and when mineralization occurs late, all that is left are the nonorganic tissues such as shells.



004118.f0002 **Figure 2** The conditions for exceptional preservation. (a) Rate of burial and organic content are key controls on the nature of mineralization of organic matter in fossils. Pyritization (high rate of burial; low organic content) may preserve entirely soft-bodied worms, as in an example of the starfish *Loriolaster* (b) from the Early Devonian Hunsrückschiefer of Germany. Phosphatization (low rate of burial; high organic content) may preserve feathers as in (c), an unidentified bird from the Eocene of Germany. Soft parts may be preserved in carbonate (high rate of burial; high organic content), such as the limbs and antennae of a shrimp (d), from the Carboniferous of Scotland. If decay never starts, small animals may be preserved organically and without loss of material, as in a centipede in amber from the Early Tertiary of the Baltic region (e).



004118.f0003 **Figure 3** Processes of breakage and diagenesis of fossils. Dead organisms may be disarticulated (a) or fragmented (b) by scavenging or transport, abraded (c) by physical movement, bioeroded (d) by borers, or corroded and dissolved (e) by solutions in the sediment. After burial, specimens may be flattened (f) by the weight of sediment above, or various forms of chemical diagenesis, such as the replacement of aragonite by calcite (g) may take place.