

Introduction

The popular image of a ‘typical’ fossil is often the remains of an animal – a seashell or a dinosaur bone. Animals, especially invertebrates, do indeed tend to be more commonly found as fossils, but plants can be fossilised given the right conditions. Plants probably first appeared on land more than 450 million years ago, during the Ordovician Period, and since that time their remains have found their way into muds, silts and sands, to be preserved as fossils (Fig. 1.1 shows the standard stratigraphical names for the time intervals referred to in this book). These plant fossils give us our only direct view of the vegetation of the past and from this we can infer the history of the evolution of plants and floras.

What is a plant?

This may seem obvious but, when you examine the problem in detail, it is not. Early naturalists divided living organisms into two kingdoms, animals and plants. Animals were thought of as mobile organisms whose nutrition was based on the consumption of other organisms, whereas plants were static, green organisms whose food was generated by internal processes (mainly photosynthesis). Although this was satisfactory for classifying most of the organisms that we meet on a day-to-day basis, it soon became evident that the distinction was not clear-cut. Fungi were the most obvious discrepancy because their nutrition is based on a saprophytic existence – the decomposition of plant and animal residues. Fungi were therefore eventually assigned to their

own kingdom. As biologists looked more closely at the microscopic world, the position became even more complex.

Many authors today do not regard plants as a systematically coherent group of organisms. The organisms that most of us would refer to as land plants are instead sometimes referred to as embryophytes, which are formally defined as those organisms that have alternating sexual (gametophyte) and asexual (sporophyte) generations, and where the gametophyte produces an embryo (alternating generations, Fig. 4.2). Some simple algal organisms have alternating sexual and asexual generations, but they do not produce embryos. Animals produce embryos but of a fundamentally different type, consisting of a hollow ball of cells that is usually detached from the tissue of the mother; the embryophyte embryo, in contrast, is a solid structure that remains embedded in the maternal tissue.

Whilst accepting this formal definition of embryophytes, for convenience we will continue through the rest of this book to refer to them as plants. In this context, plants consist of charophytes, bryophytes and vascular plants (also known as tracheophytes), together with some primitive non-vascular plants found mainly in Early Palaeozoic floras. Bryophytes, which today include mosses, hornworts and liverworts, are perfectly adapted to life on land but have never developed into large organisms, as have the vascular plants. Vascular plants include most land vegetation such as ferns, sphenophytes (‘horse-tails’), lycophytes (‘club mosses’), gymnosperms and angiosperms. Their main defining feature is a

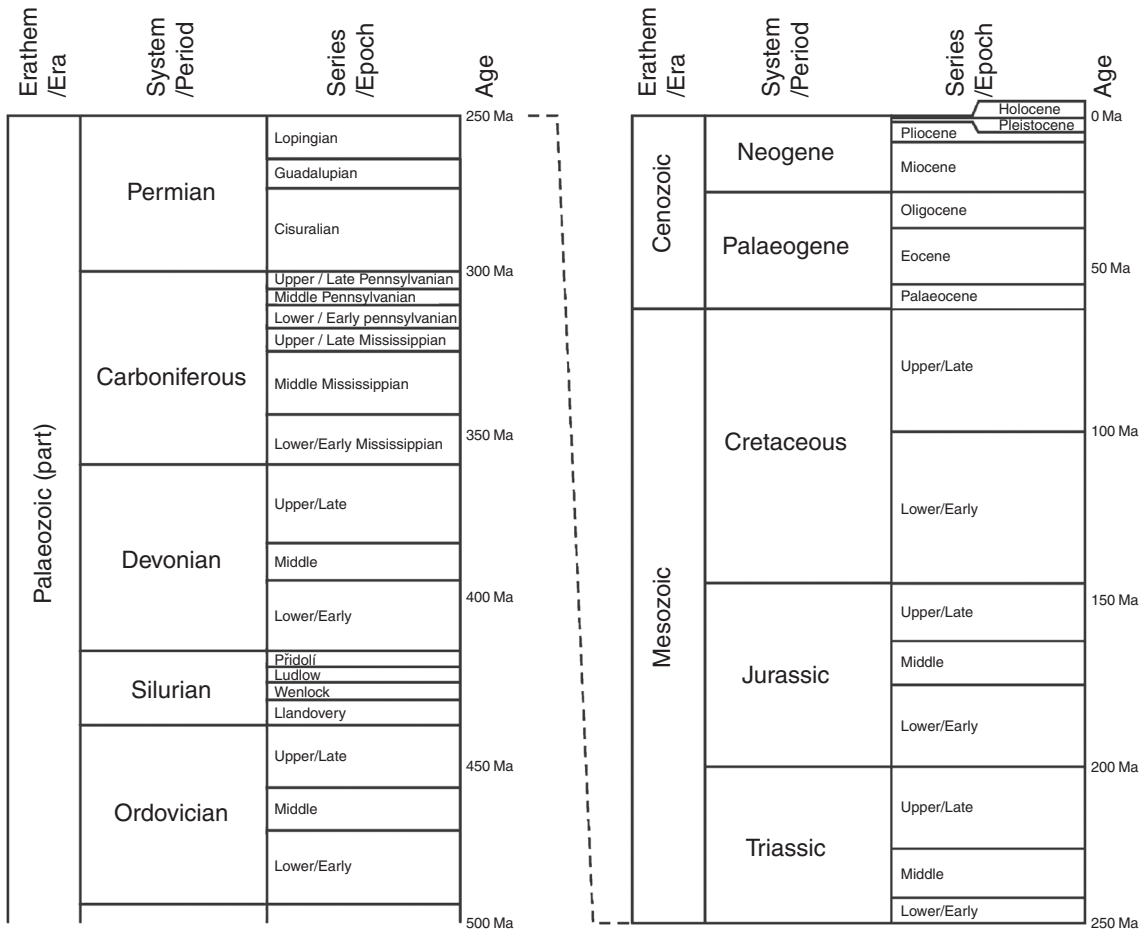


Fig. 1.1 Subdivisions of the global geological record, based on the 'International Stratigraphic' Chart published by the International Commission on Stratigraphy. The lowest Palaeozoic subdivision (the Cambrian System/Period) is not shown. The approximate dates given at the right of the two columns, based mainly on radiometric dating, are given in millions of years (denoted as Ma).

stem with vascular tissue, which assists in supporting the plant and in the transport of nutrients and water around its body; most vascular plants also have a dominant sporophyte phase (although some primitive vascular plants appear to have had sporophytes and gametophytes of similar size, see Chapter 4).

How do plant fragments get into the fossil record?

Very occasionally, whole plants became entrapped in sediment and preserved where they were growing; such fossils are referred to as autochthonous

or T⁰ assemblages (examples are shown in Figs. 1.2 and 5.20). More usually, we find fragments (leaves, seed, branches, etc.) that have been detached from the plant. The process of fragmentation may be part of the natural strategy of the plant, such as the deciduous shedding of leaves in many angiosperm trees. More often, however, it was the result of traumatic external influences, such as storm damage.

The detached fragment may have fallen to the ground near where the parent plant was growing, in which case the fossil is described as hypautochthonous. Such situations tend to be rare because the ground surrounding a growing plant tends to be exposed and the tissue of the



Fig. 1.2 a. *Calamites* stem preserved *in situ* in a Middle Pennsylvanian fluvio-lacustrine sequence at Brymbo Quarry, near Wrexham, Wales. b. *In situ* silicified coniferous trees near Agua del Zorro, Mendoza Province, Argentina. The trees were discovered by Charles Darwin in 1835, while on his travels around the world aboard the *Beagle* and are described in two of his publications (Darwin, 1839, 1844). This Triassic site, now known as 'Darwin's Fossil Forest', is protected by Provincial and National laws. Photos by B. A. Thomas (a) and M. A. Urreta (b).

detached plant fragment will normally decay rapidly. Preservation is more likely when the plant remains are transported away from the place of growth usually by air (wind) or water (rivers), to where they can be rapidly covered by sediment, such as in a lake or river delta – these form allochthonous fossils.

Because of the effects of this fragmentation and transportation, most plant fossil assemblages normally represent a mixture of plant fragments from different habitats rather than a single natural assemblage of plants. Reconstructions of original vegetation can only be directly achieved with autochthonous or hypautochthonous assemblages, such as 'fossil forests' of tree stumps where the landscape has been subjected to a sudden catastrophic inundation by sediment. Most peat deposits are hypautochthonous and so, if their component plant remains can be identified such as in coal balls (discussed later in this chapter, and in Chapter 2), they can also often give a reasonably accurate picture of what the local vegetation looked like. The study of spores and pollen (paleontology) in peat can be similarly useful here, provided the plants that produced the different types of pollen and spores are known – an assumption that is reasonable in Cenozoic and most Mesozoic floras, but can be problematic in Palaeozoic floras that include extinct and sometimes poorly understood plant groups.

A consequence of the fossilisation process is that most plant fossils are only fragments of the original plant. Even some of the larger organs,

such as fronds of ferns or Palaeozoic gymnosperms, may have been fragmented. Reconstructions of plants depend on piecing together the chance finds of attached organs, such as a leaf and a seed, a leaf and a stem, and a stem and a cone. Mostly, we know nothing of the seeds that were borne by the plant that produced a particular leaf, let alone the appearance of the whole plant. This has consequences for naming plant fossils, which we will deal with in Chapter 3.

Types of plant fossil

When the plant fragment becomes trapped within the sediment, it undergoes various changes, which can affect what sort of detail is retained. Palaeobotanists have developed a range of terms to describe the different modes of preservation (Fig. 1.3).

Most plant fossils represent fragments of plant that have become trapped in sediment where anaerobic conditions prevent microbial breakdown of their tissues. They are then flattened by the weight of the overlying sediment, although retain their overall shape. Such fossils are known as adpressions (Fig. 1.4a). The plant tissue itself is converted to a thin layer composed mainly of carbon and is called a phytolite. If the phytolite is still preserved, the fossil is known as a compression, but if the layer is lost either through geological changes (e.g. additional compression and/or heat) or weathering after the

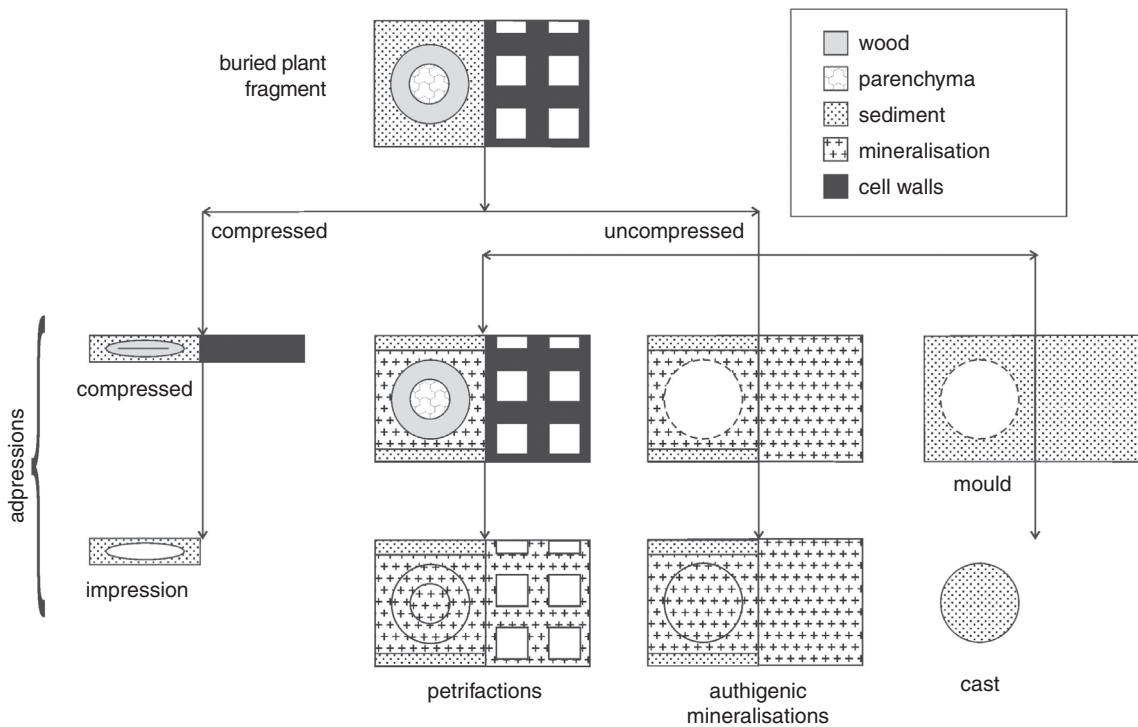


Fig. 1.3 A hypothetical stem fossil consisting of a woody cylinder with an internal core of soft cellular tissue (parenchyma) preserved in different ways. Each mode of preservation is represented by a rectangle, the left-hand side of which represents the stem in transverse section in the sediment, showing the distortion in shape that it has undergone during fossilisation. The right-hand side of the rectangle is a schematic representation of cells in close-up to show the level of anatomical detail that is preserved.

fossil has become exposed, it is known as an impression. In many cases, a particular assemblage may include both fossils that retain the phytolite (i.e. compressions) and others where it is lost (i.e. impressions). For instance, when a specimen is broken open, one half will often carry the phytolite, while the other half (the counterpart) will just show an impression of the plant fragment. Where the matrix is soft,

the phytolite can often become detached from the rock, leaving parts of the specimen as a compression and other parts as an impression. In such cases, the general term adpression is used.

This process of compression destroys most evidence of cellular-structure. The only notable exception is the cuticle (the outer 'skin' of the plant, Fig. 1.5), which sometimes survives because of its make-up of relatively non-biodegradable aliphatic

Fig. 1.4 Different types of preservation in plant fossils. a. Adpression. Scale bar = 10 mm. This specimen of *Paripteris gigantea* (Sternberg) Gothan has some pinnules with the carbonised plant tissue still intact (i.e. compressions), whilst others have lost the tissue (i.e. impressions). Specimen from the Faisceau de Meunière (Middle Pennsylvanian Series) in the Dechy Mine, Douai, northern France (Laboratory for Palaeobotany, University of Lille, France, Specimen 947). Photo by J.-P. Laveine. b. Silicified cast of fossil wood. Scale bar = 20 mm. Its woody texture, including some knots, is clearly visible but without evidence of the structure of the wood, it can be difficult to be sure of the type of tree that it originated from. Specimen from Lower Cretaceous strata near Sevenoaks, Kent, England (NMW Specimen 50.140 G.1). Photo by NMW Photography Department. c. Authigenic mineralisation in a siderite nodule of a *Lepidostrobus cone*, from an unknown locality, probably of Middle Pennsylvanian age. Scale bar = 30 mm (NMW Specimen 58.464.G440). Photo by C.J. Cleal. d. Transverse section through a petrified stem of a small Mississippian lycophyte *Oxroadia gracilis* Alvin showing detailed cell anatomy of the stele and cortex. Scale bar = 0.1 mm (Bateman Collection, Specimen OBD (2.15)038bT/2). Photo by R. Bateman.

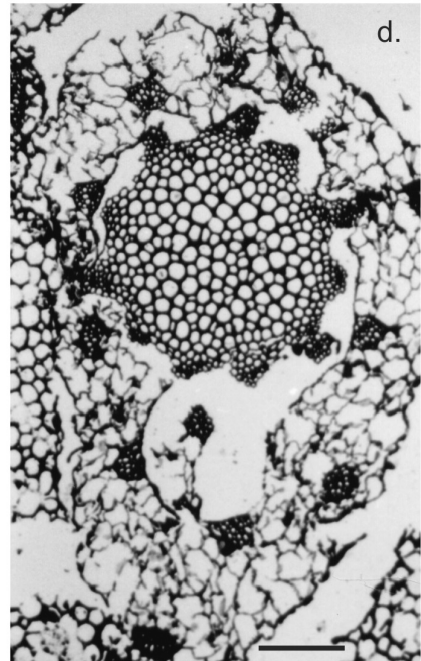
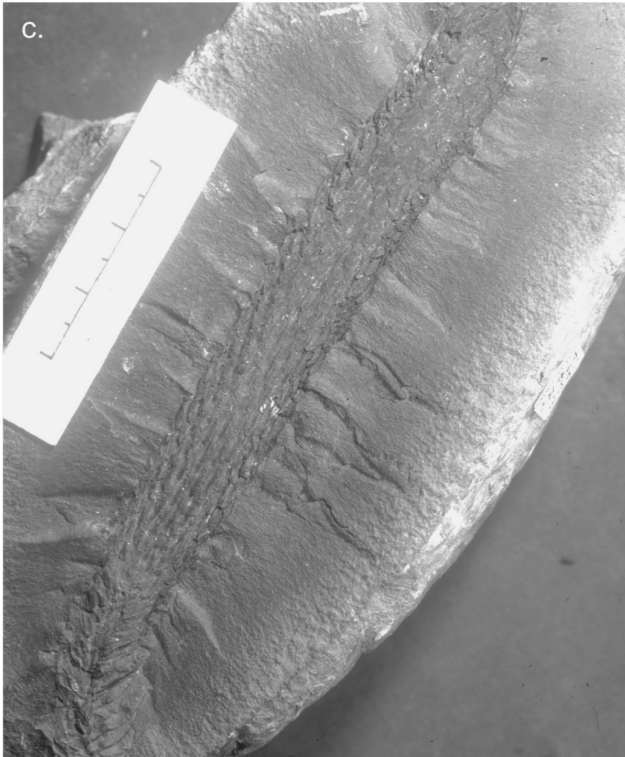
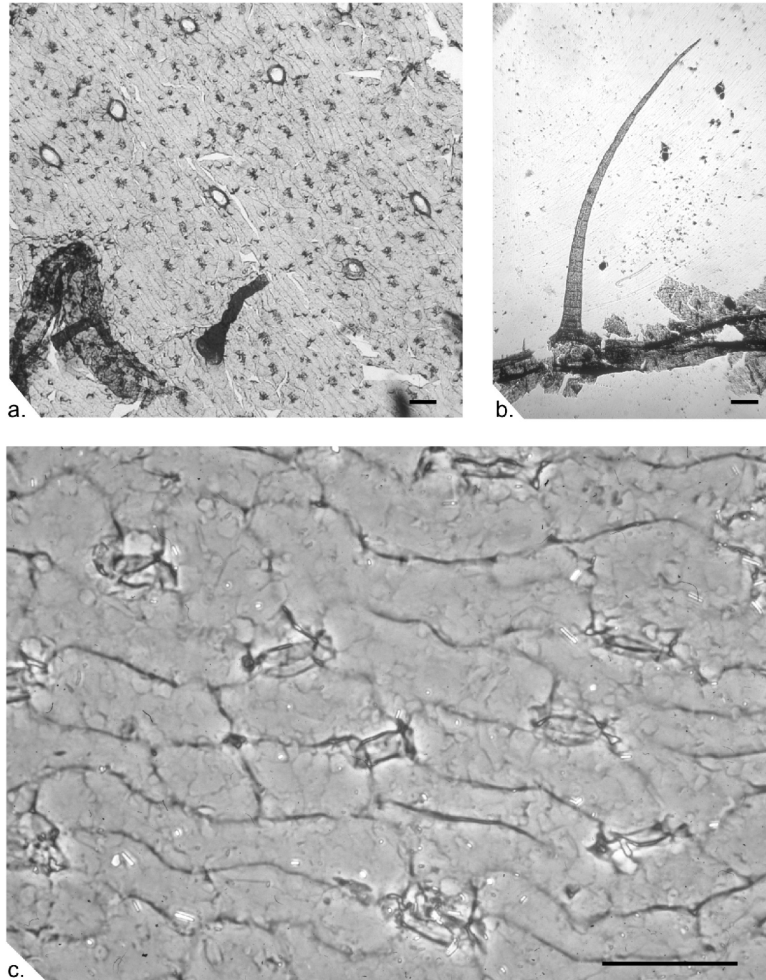


Fig. 1.5 Examples of cuticles prepared from Carboniferous pteridosperm fronds. a. Lower cuticle from *Neuropteris flexuosa* Sternberg frond, stained with safranin, showing hair bases, an attached hair and stomata. Scale bar = 200 μm . Lloyd Cove Seam (Middle Pennsylvanian Series), Brogan's Pit, near Pt Aconi, Cape Breton, Canada (E. L. Zodrow Collection, Specimen 981 GF-353). b. Unstained epidermal hair from rachis of *Odontopteris barroisii* Bertrand. Scale bar = 50 μm . Heiligenwald Formation (Middle Pennsylvanian Series), St Barbara Colliery, Saarland Coalfield, Germany (Saarbrücken Mining School Collections, Specimen C/4054). c. Lower (abaxial) cuticle from frond of *Neuropteris ovata* Hoffmann showing stomata. Scale bar = 50 μm . Photographed using phase contrast. Kallenberg Seam, Luisenthal Formation (Middle Pennsylvanian Series), Itzenplitz Colliery, Saarland Coalfield, Germany (Saarbrücken Mining School Collections, Specimen C/3638). Photos by C. J. Cleal.



polymers. Where the fossil has been subjected to too much heat and/or compression even the cuticle will be destroyed. The cuticle itself does not consist of cells, but often bears the impression of the outer layer of cells of the plant (the epidermis) that it covered. The epidermis includes many structures that are important for understanding the systematic position and ecology of the plants (e.g. epidermal hairs and the stomata or 'breathing pores'), and so the study of cuticles has become an important facet of palaeobotany.

Under certain circumstances the plant fragment may be preserved with little or no compression having taken place. One way this can happen is if the sediment around the plant fragment hardens quickly before significant compression

has occurred. The plant tissue itself will subsequently rot away or become reduced to just the carbon residue of the tissue, but there will still be the cavity remaining within the rock that will represent the original shape of the plant fragment. Fossils such as this, known as moulds, are most typically formed around robust parts of plants such as wood and seeds. In some cases, the cavity is subsequently filled up with fine sediment or mineral growth, resulting in a cast of the plant fragment (Fig. 1.4b).

Another type of cast occurs where stems have a central core that is either hollow or made of soft, easily decayed cellular tissue. Sediment may fill the central cavity before the rest of the tissue has decayed producing a sediment-cast of the internal

cavity, normally referred to as a pith-cast. Sphenophytes and cordaites are particularly prone to this mode of preservation. Sometimes stems are infilled when the remains of the plants are still in the position of growth, which can give an idea of the original density of the vegetation. Other stems may have been transported away by water and these generally collapse a little before becoming infilled with sediments (see Chapters 6 and 8).

Moulds and casts tend not to preserve fine details of the plant fragments, but there can be exceptions. If the chemistry is right, a piece of plant falling into water and sediment can act as a nucleus for mineral precipitation, and a nodule can form around it; siderite (iron carbonate) is the most common mineral to form such nodules. If this mineralisation happens quickly, the resulting nodule can form a mould around the plant fragment, preserving fine detail, even sometimes including cellular detail of the epidermis and some sub-epidermal layers. Such fossils are known as authigenic mineralisations (Fig. 1.4c). One of the most notable fossil floras preserved in this way is the Pennsylvanian-age Mazon Creek flora of Illinois, USA, which has been the subject of a number of important studies, the most recent being by Wittry (2006).

An analogous mode of preservation is where a plant fragment or small animal is trapped in the resin produced by various types of tree. After the volatile oils have evaporated the resin hardens and is known as amber. Only quite small plant fragments are normally preserved in amber, but extremely fine preservation occurs as they are entrapped very quickly; such fossils have proved particularly useful for the study of fossil flowers (Fig. 10.17a).

The best-preserved plant fossils are where little compression occurred and even the cellular detail of the tissue is preserved; these are known as petrifications (Fig. 1.4d). They form when fluids containing minerals (e.g. calcite or silica) in solution have percolated through the body of the plant before significant decay has occurred. The cells themselves become impregnated by the mineral, which crystallises to preserve their form. The cell wall is sometimes retained as a thin layer of coal around the mineral replacement of the cell contents (cell lumen) or is itself replaced by mineral. Either way, the detailed anatomy of the plant

fragment is revealed when a section is cut through the fossil. Examples of petrifications occur throughout the fossil record of plants. Notable examples include the Early Devonian Rhynie Chert flora from Scotland that has provided critical evidence for understanding the early evolution of land plants (discussed in Chapter 4); the Carboniferous and Permian coal ball floras from the USA, Europe and China that have allowed us to gain a better understanding of the very earliest tropical rainforests; and the Jurassic Rajmahal Hills flora of India, that has clarified many aspects of Mesozoic plants.

Petrifications only occur under unusual conditions, such as in habitats associated with volcanic activity or where the plant fragments have been soaked in sea water. They are therefore much rarer than adpressions and casts, and tend to represent vegetation growing in extreme habitats. Consequently, if we only looked at petrifications, we would get a very biased understanding of past vegetation. Where they do occur, however, petrifications provide critical anatomical evidence that illuminates parts of the evolutionary history of plants and thus complements the more complete adpression record.

Fire might seem an unlikely way of preserving plant fossils and normally of course it will completely incinerate plant tissue. Under certain conditions in natural wildfires, however, temperatures are so high that the plant tissue is quickly charred leaving a charcoal-like substance called fusain. Wood is the most commonly found plant remains preserved as fusain and this will often reveal fine detail of the cell structure. However, sometimes quite delicate plant structures have also been found preserved as fusain, most notably early flowers of Mesozoic age. Although very fragmentary and delicate, by suitable preparation such fossils can reveal fine details of the flowers (e.g. Fig. 10.8) – a great deal of our understanding of the early evolution of flowers has been obtained from such fossils.

Where are plant fossils found?

Plant remains can be found fossilised in most types of sedimentary rock, especially those made up of fine sediment, in a range of different localities (Fig. 1.6). However, the most abundant and



Fig. 1.6 Plant fossil sites. a. Coastal exposure at Cayton Bay, Yorkshire, England. Collecting at this classic Middle Jurassic plant bed in 1970 (left to right: J. Watson, K. Sporne, M. Boulter and M. Mortimer). b. Exposure at Edrom on the banks of the Whiteadder River, Berwickshire, Scotland. This site has yielded a diverse assemblage of Mississippian plant petrifications, especially of early seed-plants. c. The field at Rhynie in Scotland, that has yielded the classic Early Devonian macroflora discussed in Chapter 4. There are normally no exposures of this plant bed, but there have been occasional excavations to collect further material (e.g. Fig. 2.11). d. Road cutting near Beckley, West Virginia, USA. Bill Gillespie (centre) and Mitch Blake collecting from the Early Pennsylvanian Pocahontas No. 2 Coal. e. Disused clay pit at Czerwionka-Leszczyn, Upper Silesia, Poland, where Middle Pennsylvanian plants can be found. f. Spoil tip from abandoned underground coal mine. Middle Pennsylvanian flora from near Radstock, England, being collected by Deborah Spillards and Chris Cleal. Photos by B. A. Thomas (a, f) and C. J. Cleal (b–e).



Fig. 1.7 Middle Pennsylvanian sequence at Point Aconi, Cape Breton, Canada. This shows a coal seam (the Point Aconi Seam), underlain by a seat earth (fossil soil), and overlain by mudstones that were deposited when water and sediment flooded the area and destroyed the peat-forming vegetation. Photo by B. A. Thomas.

best preserved tend to occur in rocks that were deposited in non-marine environments. Rocks formed from sediment deposited in river deltas provide some of the best opportunities to find plant fossils, especially the muds and silts deposited in lakes within the deltas. If the water table remains generally high in the delta sediment, plant fragments will be much slower to decay and thus stand a greater chance of being preserved within the sediment. If both sedimentation rates and decomposition of the plant litter are slow, peat can accumulate and over geological time this can result in coal (Fig. 1.7). If sedimentation rates are more rapid, the plant fragments will be buried in sands or mud, and when these

deposits are turned into solid rock the plant remains are preserved, usually as adpressions or casts, as described above. Both rapid and slow sedimentation rates can occur in repeated sedimentary successions, such as the cyclothems that result from a rhythmic raising and lowering of sea-levels during glacial-interglacial cycles. A number of times in the fossil record such sedimentary changes have resulted in the formation of seams of coal separated by sandstones and mudstones containing plant fossils. The prime examples of this type of sequence can be found in the Pennsylvanian coal-bearing sequences ('Coal Measures') of Europe and eastern North America.

Although the coal/peat consists almost exclusively of plant remains, it is usually very difficult to study them because they are all crushed together in a confused mass, so one can rarely discern the shape of any of the pieces of plant that make up a lump of coal. It is possible to macerate coal using strongly oxidising acids so that some of the plant material can be extracted, but the remains are usually so broken up that they are difficult to study. Pollen, spores and cuticles are the most common types of fossils studied in this way. The only circumstances where anatomical details of the component plant remains of coal can be studied are when the seam has been impregnated with mineral matter, petrifying some of the plant tissues. Such mineralisation is not widespread but where it does occur it can produce extremely fine preservation of the plant tissue. The best known examples of such preservation are the Pennsylvanian-age coal balls of Europe and North America (examples of such coal ball petrifications are shown in Figs. 5.11, 7.6c, 8.11e).

If the water table is lower, plant decay is much quicker and peat tends not to build up. Low water table conditions can often be recognised by the oxidisation of the sediment, often resulting in red-coloured rocks (red beds). Plant fragments may still be preserved in the sediment in such situations, but on the whole they are less common than when the water table has been higher. If they are found in such red-beds, the carbon phytolite is usually lost and the fossil is preserved as an impression.

Volcanic landscapes tend to be very unstable and their sedimentary deposits are often subject to considerable reworking. On the face of it, this would seem to be an unlikely setting in which to find plant fossils. However, the ground waters in such environments are often mineral-rich and so can petrify plant fragments. An example of this is the Rhynie Chert deposit, formed when an Early Devonian peat accumulation was inundated by mineral-rich waters, preserving in exquisite detail the internal anatomy of some of the very early land plants (see Chapter 4).

Lagoonal and coastal deposits may contain fragments of plants that had drifted from the coastal vegetation. An example here is the Jurassic Stonesfield 'Slate' flora of Oxfordshire, where plant fossils including conifer and fern fragments are found with the remains of marine animals such as bivalves. Another is the Sheppey flora from Kent, which has Tertiary plant remains associated with sharks' teeth, crabs and other animal remains. The diversity and preservation of other drifted floras is sometimes much poorer although coastal and lagoonal deposits may preserve remains of vegetation that is different from that found in deltaic deposits of the same age. For instance, the Stonesfield flora is quite different from that found in the deltaic deposits in Yorkshire, despite being of similar Middle Jurassic age.

Bias in the fossil record

Although fossils are the only direct record that we have of organisms that lived in the past, they provide a very incomplete picture. This problem has been known about since the nineteenth century and Charles Darwin discussed it extensively in his book *On the Origin of Species*. The fossil record provides a particularly incomplete picture of past vegetation, especially of plants growing in drier or upland habitats. It is probably at its best when plants were first starting to migrate onto land, in Silurian and Early Devonian times, as the wet habitats being colonised were well suited for fossilisation. As soon as plants adapted to drier habitats, bias in the record becomes significant and only those plants that continued to occupy wetter

habitats, such as riverbanks and deltas, and lake shores, are well represented as fossils. Since many of the main evolutionary developments in plants have been adaptations to life in drier regimes (especially reproductive adaptations such as seeds and flowers, see Chapters 8–10), there is a very real problem in using the fossil record directly to develop models that explain the evolutionary history of plants.

There are two main types of evidence that suggest the fossil record is incomplete. Firstly, sedimentary rocks sometimes yield tiny fragments of plants that have travelled a much greater distance than the larger specimens that make up the vast bulk of the plant fossil record, and probably represent the vegetation growing in more elevated and thus drier habitats. Fusained plant fragments produced by wildfires, for instance, can travel great distances along rivers and can often preserve surprisingly fine morphological details including some internal anatomy. Spores and pollen grains can also travel vast distances and give us information about the plants growing in drier habitats away from the sedimentary basins. The problem here, however, is that we do not know which groups of plants produced some of the spores and pollen grains. Nevertheless, from both of these sources of information we are fairly certain that in late Carboniferous times there were forests in upland areas with various seed-plants, including conifers and cycads, long before those plants are represented in the main fossil record.

There are also indirect means of judging the incompleteness of the plant fossil record. One example is known as 'the molecular clock'. By determining the rate at which genes randomly mutate, it is possible to use the number of genetic differences between two organisms to estimate how long ago they shared a common ancestor. Such evidence suggests that the flowering plants diverged from the other seed-bearing plants as long ago as Triassic times, if not earlier. However, this is in marked contrast to the evidence of the fossil record, in which the oldest unequivocal occurrence of flowering plants is in rocks of Early Cretaceous age. So, either the molecular clock has been 'running fast', or there were flowering plants growing in upland areas for millions of

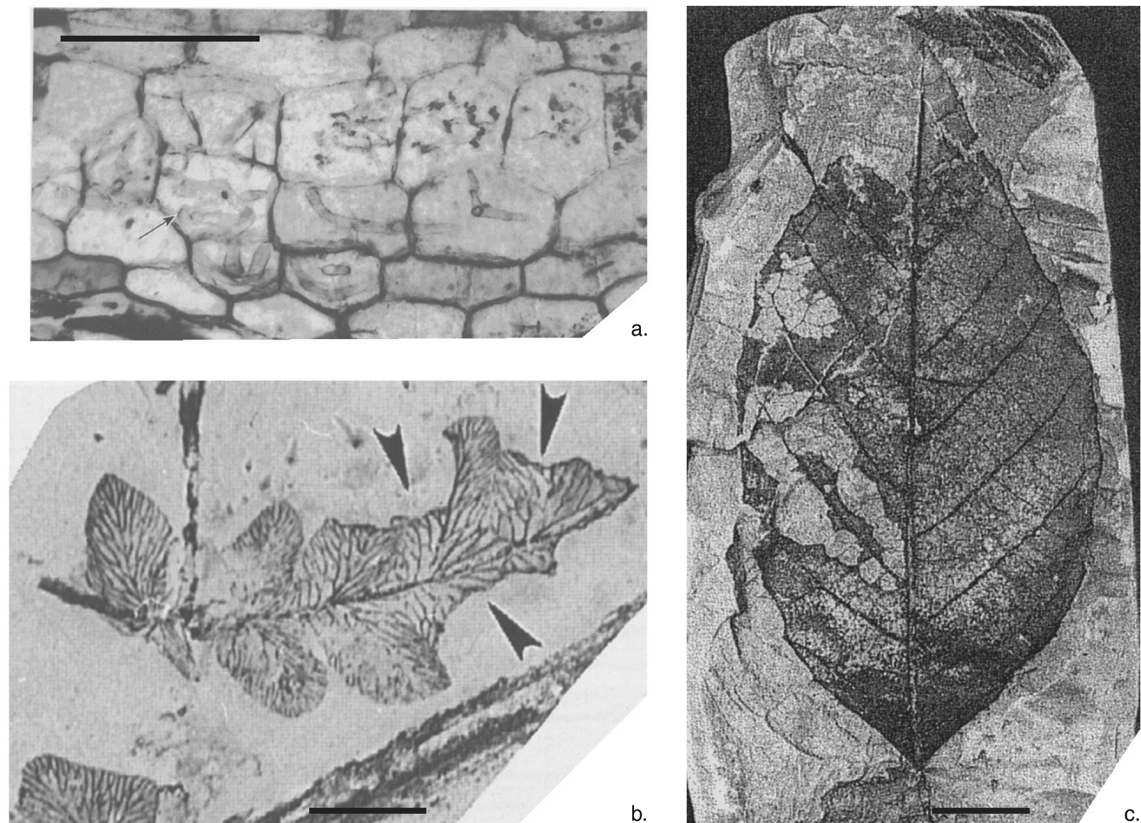


Fig. 1.8 Fungi and insect damage. a. Section of a root of the taxodiaceous conifer *Metasequoia milleri* (Middle Eocene, British Columbia, Canada) showing coiled hyphae and arbuscules of mycorrhizal fungi in the inner cortex. Scale bar = 100 μ m. Photo by R. A. Stockey. b. Feeding traces on the filiclean fern *Cynepteris lasiphora*, Triassic System, south-eastern USA. Scale bar = 5 mm. Photo by S. R. Ash. c. Leaf mines in an angiosperm leaf from the Branksome Sand Formation, Bournemouth, England. Leaf mines are linear tunnels or blotch-like excavations caused by specialised larvae eating the mesophyll (photosynthetic cells) and/or the epidermal cells. The cuticle is left intact. Scale bar = 10 mm. Photo reproduced with permission from Lang *et al.* (1995).

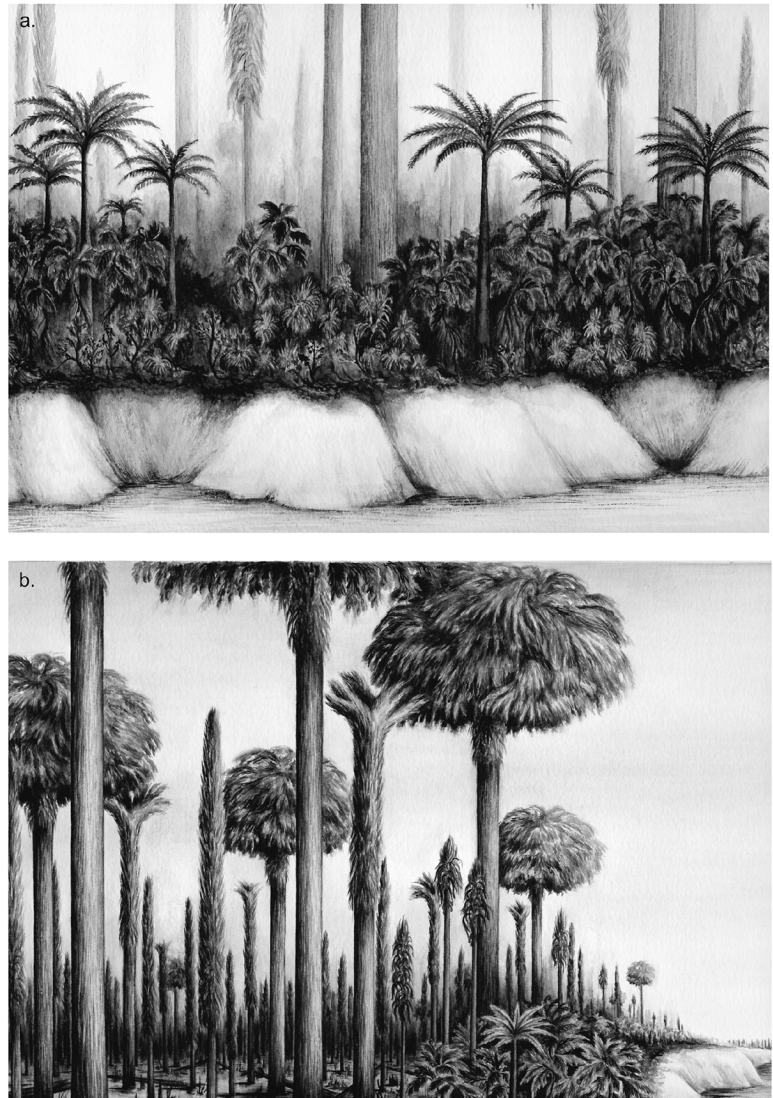
years before they appeared in the lowland habitats that are sampled by the fossil record.

Even when trying to interpret the vegetation that gave rise to a particular fossil assemblage, bias in its composition becomes a real issue. The plants will have been subjected to varying degrees of damage due to fungal or animal attack (Fig. 1.8) that may affect different groups of plants in different ways. Delicate plants such as mosses and liverworts are for this reason rarely represented in the fossil record, and consequently our understanding of the evolutionary history of these groups is much poorer than that of more robust plants such as ferns.

Most assemblages are allochthonous, often derived from two or more original habitats, and

these may not be representative of the overall vegetation of the area. For instance, in the Pennsylvanian Coal Measures of Europe and North America, most fossils are found in the mudstones and siltstones, and represent a mixture of the vegetation that grew along the banks of these palaeotropical rivers. However, the vast bulk of the forests consisted of giant lycophytes ('club mosses') growing in the swamp areas behind the raised levees and these found their way into the sediment nowhere near as often as the riparian plants. Only by studying the hypautochthonous peat (now converted into coal) have we been able to get a more representative picture of what the Coal Forests as a whole looked like (Fig. 1.9).

Fig. 1.9 Reconstructions of the Pennsylvanian palaeotropical Coal Forests. a. Diverse vegetation growing on the river bank, from where the bulk of the plant fragments found preserved as adpressions were derived. b. A more representative view of the Coal Forests, showing that most of the vegetation consists of arborescent lycophytes, and the riverbank vegetation is only a minor component. Drawings by A. Townsend. *For the colour version of part b., please refer to the plate section.*



Autochthonous and hypautochthonous assemblages may sometimes give a more representative picture of the vegetation that grew in an area, although even here bias exists. For instance, where an area of forest has been killed by being inundated by flood water and sediment leaving the stumps of the larger trees in place (resulting in what we call a fossil forest) the understory and climbing plants are usually washed away.

Most plant fossil assemblages should not, therefore, be confused with a vegetation assemblage (flora) as a modern-day botanist would see it. To

express this difference between a plant fossil assemblage and a living flora, palaeobotanists have coined various terms over the years, none of which has received universal acceptance. In this book we use the term macroflora for an assemblage of plant macrofossils (i.e. fossils that can be seen with the naked eye, in contrast to microfossils that have to be examined under the microscope) found in a particular locality and in a particular stratigraphical unit. Similarly, an assemblage of pollen and spores extracted from a particular stratigraphical unit at a particular unit is described as a palynoflora.

Why do we study plant fossils?

There is evidence that man had come into contact with the fossilised remains of plants even in pre-historic times; for example, a piece of fossilised wood was found in a Scottish neolithic hearth, which had presumably been placed there by an unsuspecting prehistoric cook! The serious study of plant fossils, however, started in the eighteenth century, and developed as a major discipline in the nineteenth century (for a more detailed discussion of this subject, see Chapter 2).

The fossil record, even though incomplete and biased, is the only direct means of finding out what plants grew in the past. Most other sources are based around extrapolations into the past from present-day data, which require many assumptions in the analysis. With the fossil record, we can see the actual remains of extinct plants that lived in the past and, even with its limitations, it still has much to tell us of the evolutionary history of plants.

There is other information that the record can provide. Biogeographical studies can help in palaeogeographical reconstructions. The apparent anomalies in the distribution of Palaeozoic plant fossils relative to the distribution of the continents today was one of the arguments used by Alfred Wegener in developing his continental drift model in the 1920s. Wegener's hypothesis formed the basis for the plate tectonics model now used to explain many large-scale processes in earth sciences. This topic will be dealt with in more detail in Chapter 11.

Changes in the distribution of floras through time can also be an extremely valuable proxy for past climate change, as can changes in leaf shape (leaf physiognomy), especially among the angiosperms. Variations in stomatal density have been used to estimate both long- and short-term fluctuations in atmospheric CO₂. Even the presence of charcoalfied plant fossils is now thought to provide an important constraint on estimates of atmospheric O₂; there cannot have been wild-fire (which is thought to generate most charcoal) if atmospheric O₂ was below a certain level.

Plant fossils can be used to estimate the relative ages of the rocks in which they are found by

comparing the patterns of appearances and disappearances through the stratigraphical successions – a science known as biostratigraphy. Animal fossils such as ammonites and corals are generally used for such work in marine strata. Animal groups have also been used in non-marine deposits (good examples are the non-marine bivalves in the Pennsylvanian successions of western Europe). Generally, however, plant fossils are of more use in non-marine rocks, especially those of the Late Palaeozoic age, where there seems to have been a very rapid turnover of species. The distribution of plant and spore fossils in non-marine and near-shore marine deposits has been particularly important in helping to correlate the two environments.

There can also be a simple economic imperative to study plant fossils. Their biostratigraphical value has proved useful in exploration for natural resources such as oil. Plant remains are also the basis of one of the world's most important energy resources – coal. Most coals are the remains of peat generated in swamps and forests, and maximising their exploitation can depend on understanding how that peat was formed. This in turn depends on understanding the vegetational dynamics of the original forests, which can only be determined by the study of the plant fossils.

Plant fossils are, therefore, an important tool for the botanist trying to understand the evolution of plant-life, the geologist wanting a means of correlating strata and establishing past continental positions, the climatologist who wants to know about past climates and atmospheres and the mining engineer who needs help in the exploitation of coal reserves. One reason for the continuing fascination of the subject is that it relates directly to so many different fields.

Recommended reading

Banks (1964), Cleal (1991), Delevoryas (1966), DiMichele & Falcon-Lang (2011), Doyle *et al.* (2001), Gordon (1935), Jones & Rowe (1999), Meyen (1987), Rex (1983), Rex & Chaloner (1983), Schopf (1975), Stace (1989), Stearn (1992), Stewart & Rothwell (1993), Taylor & Taylor (1993), Thomas & Spicer (1987), Walton (1936).