

Palaeozoic Palaeobotany of Great Britain

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This volume represents the fruits of a 12-year review of Britain's Palaeozoic palaeobotany sites. It was done in collaboration with most of those palaeobotanists who have an interest in these sites, and who were consulted at both the site-selection and writing-up phases of the project. We recognize that without this collaboration, the project would be effectively meaningless, and we thank all those who have given their advice and suggestions. Certain people have provided particularly valuable input, however, and merit specific mention: Dr Dianne Edwards (University of Wales College of Cardiff) and Mr Peter Tarrant (Morville, Shropshire) for help on the Silurian and Devonian; Dr Albert Long (Berwick-on-Tweed), Dr Nick Rowe (Royal Holloway, University of London), the late Dr John Holmes (Université des Sciences et Techniques, Montpellier) and Mr Stan Wood (Edinburgh) for help on the Lower Carboniferous; Mr Cedric Shute (Natural History Museum, London) and Ms Gaynor Boon (Sheffield City Museum) for help on the Upper Carboniferous; and Professor Bob Wagner (Jardin Botanico de Córdoba) and Mr Tim Pettigrew (Tyne & Wear Museums Service) for help on the Permian. Most of the photographic illustrations were prepared by the photographic studios of the National Museum of Wales (Cardiff) and the Natural History Museum (London), to whom we are very grateful. Special thanks must go to Mr Cedric Shute of the Natural History Museum, for taking some of the photomicrographs. Line drawings for the volume were prepared by Ian Foulis Associates (Saltash).

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Access to the countryside

This volume is not intended for use as a field guide. The description or mention of any site should not be taken as an indication that access to a site is open or that a right of way exists. Most sites described are in private ownership, and their inclusion herein is solely for the purpose of justifying their conservation. Their description or appearance on a map in this work should in no way be construed as an invitation to visit. Prior consent for visits should always be obtained from the landowner and/or occupier.

Information on conservation matters, including site ownership, relating to Sites of Special Scientific Interest (SSSIs) or National Nature Reserves (NNRs) in particular counties or districts may be obtained from the relevant country conservation agency headquarters listed below:

English Nature,
Northminster House,
Peterborough PE1 1UA.

Scottish Natural Heritage,
12 Hope Terrace,
Edinburgh EH9 2AS.

Countryside Council for Wales,
Plas Penrhos,
Ffordd Penrhos,
Bangor,
Gwynedd LL57 2LQ.

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Preface

This volume summarizes the results of a survey of British Palaeozoic palaeobotany sites, undertaken between 1978 and 1990 as part of the Geological Conservation Review (GCR). The GCR was the first attempt to assess the scientific significance of all Britain's geological sites and has proved a landmark in the development of a coherent geological conservation strategy in this country. To ensure that the assessments were based on a firm logical and scientific foundation, the range of scientific interest was divided into ninety-seven discrete blocks, reflecting the natural divisions of stratigraphy, palaeogeography and geological process; Palaeozoic palaeobotany was one of these blocks.

The first stage in the survey was a review of the literature, to establish a comprehensive database of sites. From this, a provisional list of potentially significant sites was made and this was circulated to all relevant specialists in this country and abroad. At the same time, the sites were visited to assess their physical condition and whether the interest was still extant. In some cases, this excavation (so-called 'site-cleaning') was carried out to see if the interest of a site could be resurrected or enhanced. The comments made by the specialists and the field observations were then used to produce a second site list, which again was circulated for comment. This process of consultation continued until a consensus was reached among the specialists about which Palaeozoic sites were of sufficient palaeobotanical interest to justify conservation. The minimum criterion was that it was the best in Britain for yielding a particular assemblage of plant fossils. The resulting GCR sites were thus, at the very least, of national scientific importance, although many, such as Craig-y-Fro Quarry, Rhyndyffryn and the various Lower Carboniferous petrification sites, were also of international importance.

These GCR sites have been used as building-blocks for establishing a new set of Sites of Special Scientific Interest (SSSIs). If there was no other significant interest at or adjacent to the site, a proposal was made to establish it as an SSSI on the palaeobotanical interest alone. In many cases, however, a site showed other potentially significant features, or it adjoined another site of significance. In these cases, a composite proposed SSSI would be constructed from a set of GCR sites. Despite the heterogeneous nature of such sites, it is important to remember that the palaeobotanical interest is sufficient on its own to justify the conservation of the part of the site yielding the plant fossils. The SSSI proposals that have arisen out of this survey have been sent to the appropriate country conservation agencies (English Nature, Countryside Council for Wales, Scottish Natural Heritage), whose governing Councils are responsible for the final decision to notify them.

This volume is not intended to be a field guide to these sites, nor does it cover the practical problems of their future conservation. Its remit is to put on record the

Preface

scientific justification for conserving the sites, discussing the interest of the fossils found there, and placing them in a wider palaeobotanical context. Each site is dealt within a self-contained account, consisting of highlights (a précis of its special scientific interest), a general introduction (with a brief historical review of research carried out there), a brief statement as to the stratigraphical context, and a list of all reported plant macrofossil species (including a statement about preservation-types). A detailed interpretation of the significance of the site then follows. This interpretive section has unavoidably had to be couched in technical language, because the conservation value is mostly based on a specialist understanding of the fossils present. The account of each site ends, however, with a brief summary of the interest framed in less technical language, in order to help the non-specialist.

The inclusion of a site in this volume should not be taken as an indication of rights of access, nor should it be taken as an invitation to visit. The majority of the sites are in private ownership and prior permission to visit must always be obtained from the landowner and/or occupier. In many cases the sites are vulnerable to over-exploitation, and it is hoped that those that do visit them will treat them with the respect that should be given to any other part of our unique national heritage.

Finally, it must be emphasized that this volume does not provide a fixed list of the important Palaeozoic palaeobotany sites in Britain. Palaeobotany, like any other science, is an ever-developing pursuit with new discoveries being made continually. During the progress of this very survey, findings at three sites raised them from being of little apparent interest to being of national importance (Targrove Quarry, Kingswood End, Wadsley Fossil Forest). It is inevitable, therefore, that further sites worthy of conservation will be discovered in future years. There is also the problem of potential site loss, with at least one location having come under threat during the time of the survey (Nostell Priory Brickpit). This volume deals with our knowledge of the sites available at the time of the GCR survey (mainly during the 1980s) and must be seen in this context. Nevertheless, the account clearly demonstrates the value of British sites for Palaeozoic palaeobotany, and their important place in Britain's scientific and natural heritage.

Chapter 1

Introduction

Introduction

Palaeobotany is the study of the fragmentary fossilized remains of plants and, as such, can be undertaken for a variety of purposes. Plant fossils can be used for morphological studies and as evidence for whole-plant reconstructions, as well as providing the basis for evolutionary theory, palaeoecological reconstructions and interpretations, and biostratigraphy. This volume deals with the palaeobotany of the Palaeozoic Era, which represents the first 200 million years of land plant history. It was a time of major evolution and diversification of plants, both in a taxonomic and structural sense, as they adapted to terrestrial habitats. This, coupled with regional climatic and edaphic factors, led to geographical isolation of plant groups, regional floras and the complex ecological interrelationships that existed during the latter part of the Palaeozoic. A brief introduction to these points is necessary to appreciate the choice of sites listed in this volume and the species lists included in them. It will also be useful to explain briefly how plant fossils are formed, and how palaeobotanists study and name them. The reader in search of a more detailed understanding of plant fossils, explanations of the various systematic groups of plants and for interpretations of the fossil plants themselves may start by consulting one of the several available general texts on palaeobotany such as Taylor (1981), Thomas (1981a), Bassett and Edwards (1982), Stewart (1983), Meyen (1987), Thomas and Spicer (1987), Stewart and Rothwell (1992) and Taylor and Taylor (1992).

Palaeozoic vegetational history

The history of terrestrial vegetation can be divided into three broad phases, known as the Palaeophytic, Mesophytic and Cenophytic (Gothan and Weyland, 1954) and corresponding in time approximately to the Palaeozoic, Mesozoic and Cenozoic eras. The phases represent times of radiation of land vegetation, separated by major extinction events - the Permian-Triassic, and the K-T (Cretaceous-Tertiary) boundary events (Erwin, 1990; Halstead, 1990). These events had a major disruptive effect on vegetation, causing the extinction of many plant families (e.g. see Figure 7.1 for the Permian-Triassic event). However, the effective emptying of many habitats also had an accelerating effect on plant evolution, allowing the diversification of new groups that had previously found it difficult to compete with the

well-established communities of more primitive forms. For instance, the conifers and cycads first appeared in the Palaeozoic (Clement-Westerhof, 1988; Gao and Thomas, 1989), but it was not until the Mesozoic, when the well established pteridophyte-dominated forests had disappeared, that they underwent a major proliferation. The extinction events in the end proved to be a major driving-force in land plant evolution, by clearing the competitive 'log-jams' presented by the climax communities of the more primitive groups.

Being the first of these great phases in the evolutionary history of plants, the Palaeophytic is in many ways the most fundamental. It can be viewed from two perspectives - structural and taxonomic. Most of the major morphological and anatomical strategies that allowed plants to take advantage of the terrestrial habitats appeared at this time (Chaloner, 1970); only angiospermous flowers (probably) did not appear until the Mesozoic. The progressive appearance of these adaptations is summarized in Figure 1.1. They fall into three broad categories: reproduction-dispersal, architecture and water relations.

Reproduction and dispersal

Clearly, plants would only have been able to occupy terrestrial habitats when their propagules were able to reach and remain viable on land. The spores of most marine algae cannot survive out of water for any length of time. However, some freshwater green algae produce spores with a resistant wall, allowing them to disperse between isolated areas of freshwater, which would be a significant pre-adaptation to a more fully terrestrial life. This pre-adaptive hypothesis is supported by the fact that the earliest known resistant spores with a trilete mark are from the lower Silurian (upper Llandovery; Burgess, 1991), significantly pre-dating the other evidence for the existence of land plants.

In pteridophytic reproduction, an asexual sporophytic plant or generation produces spores which disperse and germinate to produce a gametophyte plant or generation. The gametophytes produce eggs and male gametes, which fuse to form a zygote, from which the next sporophyte generation grows. There is increasing evidence that some early land plants had sporophyte and gametophyte generations that looked essentially similar (Remy, 1991). However, this symmetry soon broke down and in vascular plants the sporophyte became much larger and the

		Ordovician (upper)		Silurian			Devonian			Carboniferous (lower)	
		Caradoc	Ashgill	Llandovery	Wenlock	Ludlow	Pridoli	Lower	Middle	Upper	Tournaisian
Reproduction	Resistant spores	—————									
	Ornamented spores	—————									
	Heterospory	—————									
	Radial seeds	—————									
	Platyspermic seeds	—————									
	Pre-pollen	—————									
	Seeds surrounded by cupule	—————									
	Seeds with micropyle	—————									
Vascular tissue	Simple vascular strand	—————									
	Exarch stele	—————									
	Stellate stele	—————									
	Endarch stele	—————									
	Polystele	—————									
	Secondary xylem	—————									
Epidermis	Cuticle	—————									
	Stomata	—————									
	Papillate cuticle	—————									
	Glandular trichomes	—————									
	Stomata with subsidiary cells	—————									
Leaves and enations	Spiny axis	—————									
	Non-vascularized microphylls	—————									
	Vascularized microphylls	-----									
	Forked microphylls	—————									
	Trifurcating lateral branches	—————									
	Wedge-shaped megaphylls	—————									
	Planated, frond-like leaves	—————									
	Leaf abscission	—————									
Leaves arranged in whorls	—————										
General habit	Slender dichotomous stems	—————									
	Encrusting, flat thalli	—————									
	Rooting structures	-----									
	Stems with lateral branches	—————									
	Tree-form (arborescence)	—————									

Figure 1.1 The progressive appearance of adaptations for life on land in plants.

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gametophyte an ephemeral, small object, known as a prothallus; in most pteridophytes, the 'plant that you see' is the sporophyte (the situation is reversed in mosses and liverworts). The problem with this reproductive strategy is that it restricts the plants (or at least the gametophyte generation) to damp conditions, as the motile male gametes have to swim to the egg. However, within this constraint the strategy has proved successful and still exists in a number of extant plant groups, most notably the ferns.

In the Devonian, a number of modifications to this basic pteridophytic reproductive strategy occurred. Instead of all gametophytes producing both eggs and male gametes, some plants produced separate male and female gametophytes, helping to reduce inbreeding. With only a few exceptions, the spores that produced the male and female gametophytes were produced in separate sporangia. Also, in many cases it proved advantageous for the gametophyte to be further reduced in size and retained within the spore wall, providing added protection to this vulnerable stage in the plant's life cycle. Thirdly, it became advantageous for the female spore and gametophyte to be larger than the male, as this allowed it to provide some food reserves to help in the early growth of the sporophyte; this asymmetry in spore size is known as heterospory.

Heterospory still occurs in a number of extant plant groups, such as the lycopsid *Selaginella* and the water-ferns *Marsilea* and *Pilularia*. However, it was in essence a transitory phase, eventually culminating in the situation where the female sporangium would contain just a single functional spore (megaspore); this is essentially what we now call the seed habit. There is, however, more to being a seed than just having a single megaspore, the most significant being that the spore (in a seed known as an embryo sac) is not released from the sporangium (or nucellus); rather, the whole structure is shed, usually after fertilization. This has obvious advantages, as the sexual phase of the reproductive cycle could take place in a more protected environment, on the parent plant. However, it also presents a problem, as a male gamete produced by a gametophyte on the ground is no longer able to find its own way to the egg. This was overcome by transporting the spore to the seed, either by wind or an animal vector. It was then 'captured' by a specialized structure in the apical part of the ovule (in primitive forms this was a lagenostome, in more advanced species a micropyle),

which provided a protected environment for the germination of the spore and the production of the gametes. Another feature of the early ovules and seeds was that they were enclosed by protective sheaves, an inner one known as an integument and sometimes an outer one known as a cupule.

The seed habit was one of the most significant developments for land vegetation, as it freed plants from needing wet conditions for their reproduction. It seems to have happened first in the Late Devonian and, although pteridophytic plants remained important for the rest of the Palaeozoic, seed plants (gymnosperms) soon came to dominate much of the Earth's vegetation, especially after the Permian-Triassic extinction event.

Plant architecture

When living in an aqueous environment, architecture is not a major problem for plants due to the support supplied by the water. On land, however, gravity causes clear problems. One solution, adopted by some early land plants, was to remain small, encrusting the land surface (e.g. *Parka*, *Nematoballus*). However, this is clearly restricting and any plant that could remain upright would have an adaptive advantage. Some plants seem to have done this by developing a zone of thickening, known as a sterome, around a terete stem; some mosses still use this strategy. More commonly, however, it was achieved by the development of a central strand of woody tissue (xylem) in the stem (it also functioned as a vascular structure - see below). The earliest example of a woody stele that we know of is from the Upper Silurian.

Various morphologies developed in the Devonian that helped maximize the strength of the xylem, while keeping its mass to a minimum. These included steles with a stellate cross-section (actinostele), and divided steles, consisting of several discrete strands (polystele). Nevertheless, there was a limit to the size of plant that could be supported by such structures. Some plant groups, most notably the lycopsids, overcame this by having additional support provided by other strengthened tissue in the stem, such as secondary cortex. This allowed the plants to grow to a considerable size (40 metres or more), and was a very efficient means of growth. However, the resulting trees were not particularly strong and would have been vulnerable to traumatic (e.g. storm) damage.

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Much stronger and, in the long run more successful, was the development of secondary wood, which first appears in the Middle Devonian.

Another restriction on size was the photosynthetic efficiency of the plant. If a plant consisted merely of terete axes, an increase in size would result in a reduction in the surface area to volume ratio. An early strategy to increase the surface area was the growth on the stem of emergences or spines, which had already appeared in the Silurian. These emergences progressively increased in size and became vascularized. These are what are called microphyllous leaves, such as seen today in clubmosses. However, there is a limit to the efficiency of this strategy, and an alternative approach appeared in the Middle Devonian – the megaphyllous leaf. The early phase in the evolution of megaphylls was where terete axes were clustered at the extremities of the plant, such as in the progymnosperm *Protopteridium*. In itself, this only marginally increased the available photosynthetic area, but improved when the axes formed into a flattened configuration, and then by filling the gaps with additional photosynthetic tissue (mesophyll).

Roots are another fundamental feature necessary for increasing plant size, both in providing anchorage, and as a means of obtaining water and nutrients. Unfortunately, roots are rarely preserved in the fossil record, and our understanding of the evolution of this organ is poor. Some of the Early Devonian land plants, such as *Rhynia*, had horizontal rhizome-like axes, from which slender rhizoids extended into the ground. By the Late Devonian, the progymnosperm *Archaeopteris* had roots very much like modern trees. How the latter developed is not known, but it was clearly a successful strategy.

Water relations

Plants living out of water are also faced with problems of water supply and control. The problem of supply was overcome by the most successful plants in tandem with that of mechanical support, discussed above. The stele consists, partially or exclusively, of xylem (tissue used mainly for the movement of water) and phloem (used for the movement of organic matter). Although tracheid-like tubes occurred in a number of algae that were becoming adapted to the land environment in the Silurian and Devonian (e.g. *Prototaxites*), and probably fulfilled a vascular function, only in the so-called vascular plants did this tissue form in

clusters, sufficient for it also to fulfil a mechanical function.

The problem of water loss was overcome by covering most of the exposed parts of the plant with a cutinized 'skin' known as a cuticle. Cuticles developed in most of the plants becoming adapted to the land in the Silurian and Devonian (e.g. *Nematoballus*, *Parka*). However, the vascular plants developed a strategy for controlling the passage of water between the plant and the atmosphere, which clearly gave them an adaptive advantage. This was achieved by having small pores in the cuticle. Most significantly, these pores (known as stomata) were surrounded by specialized cells called guard cells that could control the size of the pore.

Taxonomic radiation

The vascular plants were only one of a number of plant groups that were becoming adapted to terrestrial habitats in the Late Silurian and Early Devonian. However, the combination of resistant spores, a stele combining mechanical and vascular functions, and a cuticle with controllable stomata, clearly gave them an advantage over these other groups, and they rapidly came to dominate land vegetation.

The origin of the vascular plants is still not known for certain, although it is widely thought that the Chlorophycophyta ('green algae') may represent the ancestral stock. The Charales ('stoneworts'), in particular, have been advanced as possible ancestors. However, as their stratigraphical range only extends down to the Upper Silurian (Ishchenko, 1975), it is more likely that they share a common ancestor with the vascular plants, rather than being their ancestors.

Vascular plants first appeared in the Late Silurian (c. 420 Ma). The broad pattern of their subsequent evolution in the Palaeozoic is summarized in Figure 1.2. The earliest vascular plants form a plexus of phylogenetic lineages, that are difficult to place in a coherent taxonomic framework, but the scheme most widely used recognizes a series of classes, including the Rhyniopsida, Zosterophylloids, Trimerophytosida and Horneophytosida. These were all already present in the Early Devonian and presumably reflect the initial radiation of vascular plants into the previously empty terrestrial habitats.

These primitive classes had a relatively short life, all becoming extinct by the end of the

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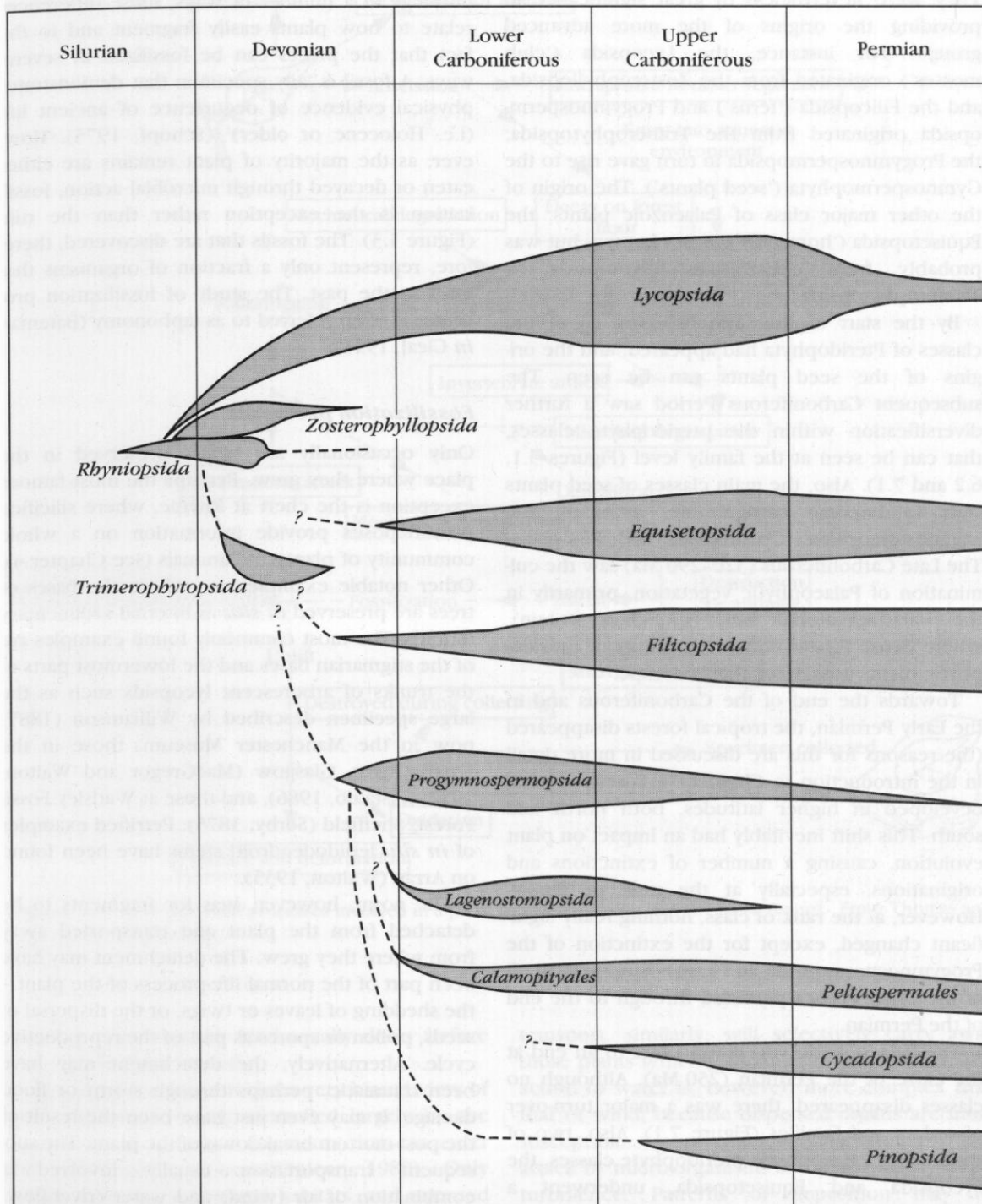


Figure 1.2 The ranges of the main plant classes through the Palaeozoic.

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Devonian (355 Ma). Although successful at times of relatively low competition, they proved unable to survive when more advanced forms appeared. They were nevertheless of great significance in providing the origins of the more advanced groups. For instance, the Lycopsidea ('club mosses') originated from the Zosterophylloids, and the Filicopsida ('ferns') and Progymnospermopsida originated from the Trimerophytoids; the Progymnospermopsida in turn gave rise to the Gymnospermophyta ('seed plants'). The origin of the other major class of Palaeozoic plants, the Equisetopsida ('horsetails'), is not known, but was probably from either the Rhyniopsida or Trimerophytoids.

By the start of the Carboniferous, all of the classes of Pteridophyta had appeared, and the origins of the seed plants can be seen. The subsequent Carboniferous Period saw a further diversification within the pteridophyte classes, that can be seen at the family level (Figures 5.1, 6.2 and 7.1). Also, the main classes of seed plants start to become recognizable, including the Lagenostomopsida, Cycadopsida and Pinopsida. The Late Carboniferous (320–290 Ma) saw the culmination of Palaeophytic vegetation, primarily in the palaeoequatorial belt (including Britain), where dense forests consisting mainly of pteridophytic plants dominated the landscape.

Towards the end of the Carboniferous and in the Early Permian, the tropical forests disappeared (the reasons for this are discussed in more detail in the introduction to Chapter 7). Forests instead developed in higher latitudes, both north and south. This shift inevitably had an impact on plant evolution, causing a number of extinctions and originations, especially at the rank of family. However, at the rank of class, nothing really significant changed, except for the extinction of the Progymnospermopsida and Lagenostomopsida; all of the other classes persisted through to the end of the Permian.

The Palaeophytic vegetation came to an end at the close of the Permian (250 Ma). Although no classes disappeared, there was a major turn-over of orders and families (Figure 7.1). Also, two of the leading Palaeophytic pteridophyte classes, the Lycopsidea and Equisetopsida, underwent a dramatic decline; they have managed to persist up to the present day, but only in very reduced numbers of species and genera.

Palaeobotanical problems

Palaeobotany differs from other branches of palaeontology in a number of ways; these differences relate to how plants easily fragment and to the fact that the pieces can be fossilized in several ways. A fossil is 'any specimen that demonstrates physical evidence of occurrence of ancient life (i.e. Holocene or older)' (Schopf, 1975). However, as the majority of plant remains are either eaten or decayed through microbial action, fossilization is the exception rather than the rule (Figure 1.3). The fossils that are discovered, therefore, represent only a fraction of organisms that lived in the past. The study of fossilization processes is often referred to as taphonomy (Bateman *in* Cleal, 1991).

Fossilization processes

Only occasionally are plants preserved in the place where they grew. Perhaps the most famous exception is the chert at Rhynie, where silicified peat deposits provide information on a whole community of plants and animals (see Chapter 4). Other notable examples are where the bases of trees are preserved *in situ* as internal sedimentary moulds. The most commonly found examples are of the stigmarian bases and the lowermost parts of the trunks of arborescent lycopsids such as the large specimen described by Williamson (1887) now in the Manchester Museum, those in the Fossil Grove, Glasgow (MacGregor and Walton, 1972; Gastaldo, 1986), and those at Wadsley Fossil Forest, Sheffield (Sorby, 1875). Petrified examples of *in situ* lepidodendroid stems have been found on Arran (Walton, 1935).

The norm, however, was for fragments to be detached from the plant and transported away from where they grew. The detachment may have been part of the normal life-process of the plant – the shedding of leaves or twigs, or the dispersal of seeds, pollen or spores as part of the reproductive cycle. Alternatively, the detachment may have been traumatic, perhaps through storm or flood damage. It may even just have been the result of the post-mortem breakdown of the plant. The subsequent transportation usually involved a combination of air (wind) and water (river-flow, current, tide) vectors, taking the fragment to its eventual site of burial in sediment. This site will normally have been subaqueous, usually in a lake or other form of non-marine standing-body of water, or occasionally in the sea; plant fragments

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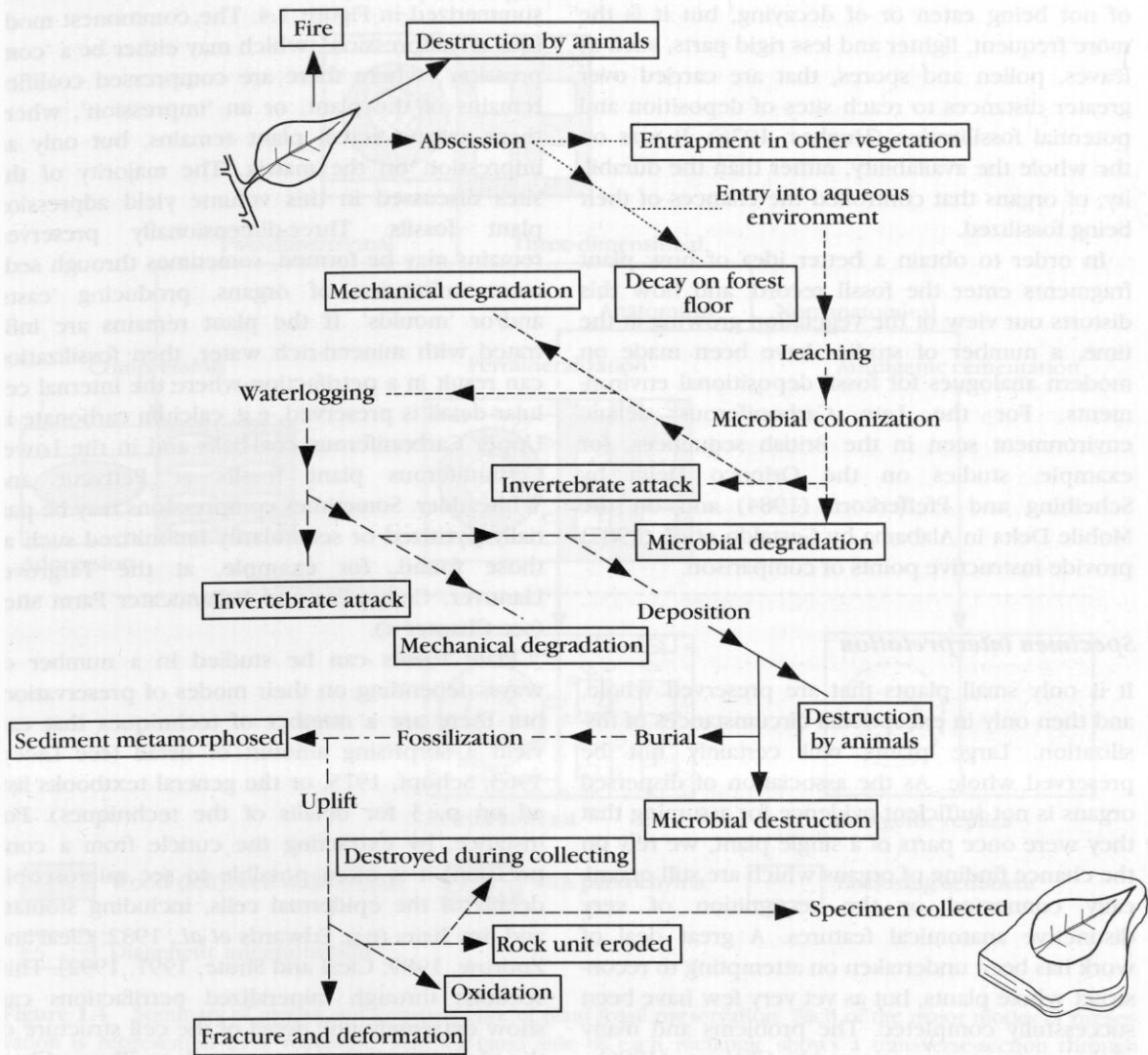


Figure 1.3 The potential processes involved in a plant fragment passing into the fossil record. From Thomas and Spicer (1987, figure 4.1).

coming to rest on dry land usually decay before they can become buried.

The fossil record provides a very biased view of past vegetation, being controlled largely by the availability of the plant fragments that can enter the fossilization process (Spicer, 1980). Only plants growing in lowland habitats, and exposed to winds or growing adjacent to flowing water, will normally be sampled. Wind will selectively carry fragments from the more exposed parts of the vegetation, so understorey plants will be under-represented in fossiliferous deposits. Water

transport, similarly, will selectively carry away those plants which grow near rivers or lakes. The action of water is, however, more complex than that of wind, because dispersed organs are more susceptible to mechanical fragmentation and attack by micro-organisms and re-sorting by water turbulence. Patterns of deposition may be extremely complex and only detectable by quantitative sampling and statistical analysis (Spicer and Hill, 1979).

Substantial selection and sorting of plant remains takes place during their transportation to

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places of active deposition. The more durable parts, such as wood, may stand the greater chance of not being eaten or of decaying, but it is the more frequent, lighter and less rigid parts, such as leaves, pollen and spores, that are carried over greater distances to reach sites of deposition and potential fossilization (Hughes, 1976). It was on the whole the availability, rather than the durability, of organs that controlled the chances of their being fossilized.

In order to obtain a better idea of how plant fragments enter the fossil record, and how this distorts our view of the vegetation growing at the time, a number of studies have been made on modern analogues for fossil depositional environments. For the Late Carboniferous deltaic environment seen in the British sequences, for example, studies on the Orinoco Delta by Scheihing and Pfefferkorn (1984) and on the Mobile Delta in Alabama by Gastaldo *et al.* (1987) provide instructive points of comparison.

Specimen interpretation

It is only small plants that are preserved whole, and then only in exceptional circumstances of fossilization. Large plants will certainly not be preserved whole. As the association of dispersed organs is not sufficient evidence for assuming that they were once parts of a single plant, we rely on the chance finding of organs which are still organically connected or the recognition of very distinctive anatomical features. A great deal of work has been undertaken on attempting to reconstruct whole plants, but as yet very few have been successfully completed. The problems and many of the successes are reviewed by Chaloner (1986).

Plant remains may be preserved in a number of ways, depending on the burial and the subsequent sedimentary and geological processes. Sometimes the remains are so durable that they survive virtually unchanged (cuticles, spore and pollen walls, charcoal). The majority are, however, altered in some way. Soluble compounds are quickly lost and microbial activity commences soon after death or abscission, so the degree of preservation depends to a large extent on the speed of fossilization. Many fossils contain organic residues that can be extracted and biochemically identified (Thomas, 1986). Some of these residues are very easily extractable. For example, lignin derivatives have been obtained from a wide range of sub-fossil woods and plant fossil compressions (Logan and Thomas, 1987).

The various modes of preservation in which Palaeozoic plant fossils are normally found are summarized in Figure 1.4. The commonest mode is as an 'adpression', which may either be a 'compression', where there are compressed coalified remains of the plant, or an 'impression', where there are no actual plant remains, but only an impression on the matrix. The majority of the sites discussed in this volume yield adpression plant fossils. Three-dimensionally preserved remains may be formed, sometimes through sediment infiltration of organs, producing 'casts' and/or 'moulds'. If the plant remains are infiltrated with mineral-rich water, then fossilization can result in a petrification where the internal cellular detail is preserved, e.g. calcium carbonate in Upper Carboniferous coal-balls and in the Lower Carboniferous plant fossils at Pettycur and Whiteadder. Sometimes compressions may be partially pyritized or secondarily limonitized such as those found, for example, at the Targrove, Llanover, Craig-y-Fro and Ballanucater Farm sites (see Chapter 4).

Plant fossils can be studied in a number of ways, depending on their modes of preservation, but there are a number of techniques that can yield a surprising amount of detail (see Lacey, 1963; Schopf, 1975, or the general textbooks listed on p. 3 for details of the techniques). For instance, by extracting the cuticle from a compression, it is often possible to see microscopic details of the epidermal cells, including stomata and tiny hairs (e.g. Edwards *et al.*, 1982; Cleal and Zodrow, 1989; Cleal and Shute, 1991, 1992). Thin sections through mineralized petrifications can show extremely fine detail of the cell structure of the plant fragment (e.g. the work on Rhynie Chert by Kidston and Lang, summarized in Chapter 4). It is only by careful and often painstakingly detailed studies that full interpretations of the fossilized plants are possible. By this means our knowledge of the once-living plants themselves and of the floral assemblages in which they grew has expanded rapidly in the last few decades.

Naming plant fossils

A consistent nomenclature is clearly vital for the interpretation and communication of information on plant fossils, especially when so much reliance and importance is placed on species lists; as indeed it is here in the site descriptions. However, the problem confronted in studying fossil plants is how to name and classify the very different plant

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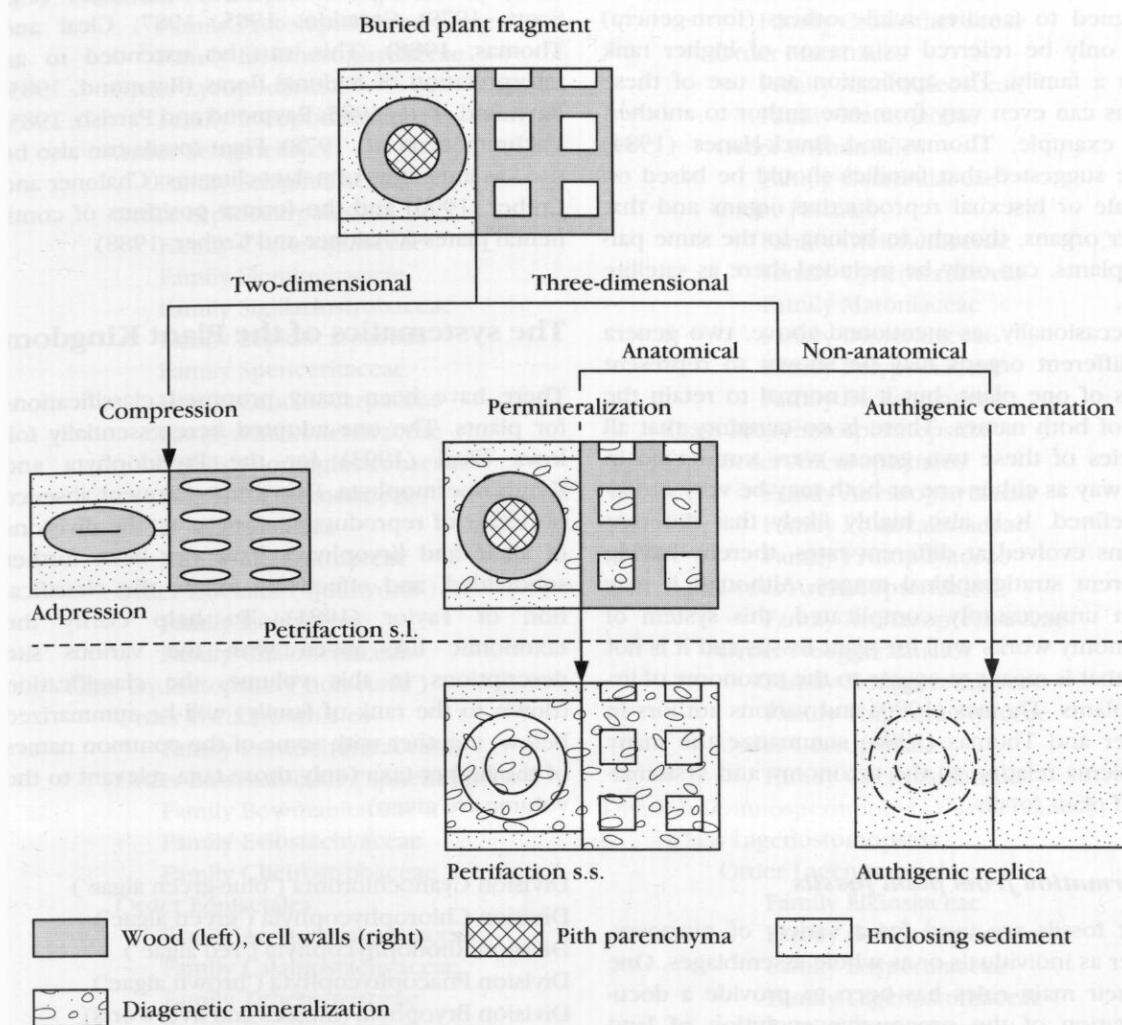


Figure 1.4 Summary of modes and nomenclature of plant fossil preservation. Each of the major modes of preservation is represented by a rectangle. The left-hand side of each rectangle shows a transverse-section through a hypothetical stem, and the right-hand side a close-up section showing cells. Based on Bateman *in* Cleal (1991, figure 2.2).

organs, or pieces of organs that were naturally shed, broken off, or traumatically detached from the parent plant prior to fossilization. To overcome this problem, palaeobotanists have developed a system of nomenclature for isolated organs, whereby different parts of plants are given different generic and specific names. Cleal (1986b) and Thomas (1990) have given general discussions on this, and Collinson (1986) has reviewed the problems relating to the use of modern generic names for plant fossils. The taxonomy of plant fossils, therefore, differs from that of living plants in many respects and has its own

'rules' (Greuter *et al.*, 1988). Species lists must, therefore, be treated with caution when they are being used for an estimate of species diversity or a comparison of assemblages. The number of genera or species of fossils will not necessarily equate to the number of different plant species that gave rise to the remains making up the assemblage and certainly does not equate to the number of different plant species that grew in the original vegetation.

Much debate has centred on the concept of the genus as applied to the isolated fossil organs of plants and to their inclusion in any taxonomic

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hierarchy. Some genera based on organs may be assigned to families, while others (form-genera) can only be referred to a taxon of higher rank than a family. The application and use of these terms can even vary from one author to another. For example, Thomas and Brack-Hanes (1984) have suggested that families should be based on female or bisexual reproductive organs and that other organs, thought to belong to the same parent plants, can only be included there as satellite taxa.

Occasionally, as mentioned above, two genera of different organs may be shown to represent parts of one plant, but it is normal to retain the use of both names. There is no certainty that all species of these two genera were connected in this way as either one or both may be very broadly defined. It is also highly likely that different organs evolved at different rates, thereby having different stratigraphical ranges. Although it may seem unnecessarily complicated, this system of taxonomy works well for plant fossils and it is not one that is meant to equate to the taxonomy of living plants. Thomas (1990) and various authors in Spicer and Thomas (1986) summarize the many problems relating to the taxonomy and systematics of plant fossils.

Information from plant fossils

Plant fossils are used for a variety of purposes, either as individuals or as whole assemblages. One of their main roles has been to provide a documentation of the progressive evolution of land vegetation. This has been particularly important during the early phases of this process, in the Silurian and Devonian (see Chapters 3 and 4). Its value diminishes for later parts of this history; as plants made greater inroads into the hinterland, far away from areas of sediment deposition, the proportion of the total land vegetation that could find its way into the fossil record became less and less. Nevertheless, it is the only direct means that we have of looking at this evolutionary history and, provided its message is interpreted in the appropriate geological context, it can provide a means of testing indirect phylogenetic models, developed using methods such as cladistic and DNA analyses.

Plant fossils can also be used to interpret the living communities from which they were derived i.e. palaeoenvironmental analyses. Here the interrelationships between the fossil assemblages and the lithology of the sediments may provide

evidence of different living assemblages (e.g. Scott, 1979; Gastaldo, 1985, 1987; Cleal and Thomas, 1988). This can be extended to an interpretation of regional floras (Raymond, 1985; Raymond *et al.*, 1985; Raymond and Parrish, 1985; Vakhrameev *et al.*, 1978). Plant fossils can also be used as indicators of palaeoclimates (Chaloner and Creber, 1990) and the former positions of continental plates (Chaloner and Creber, 1988)

The systematics of the Plant Kingdom

There have been many proposed classifications for plants. The one adopted here essentially follows Cleal (1993) for the Pteridophyta and Gymnospermophyta. Due to the frequent absence of details of reproductive structures, the divisions of algae and bryophytes have not been further subdivided, and effectively follow the classification of Taylor (1981). To help clarify the taxonomic lists given with the various site descriptions in this volume, the classification (down to the rank of family) will be summarized below, together with some of the common names of the higher taxa (only those taxa relevant to the volume are given).

- Division Cyanochloronta ('blue-green algae')
- Division Chlorophycophyta ('green algae')
- Division Rhodophycophyta ('red algae')
- Division Phaeophycophyta ('brown algae')
- Division Bryophyta (mosses and liverworts)
- Division Pteridophyta
 - Class Rhyniopsida
 - 'rhyniophytoid fossils'
 - Order Rhyniales
 - Family Rhyniaceae
 - Class Zosterophylloidsida
 - Order Zosterophyllales
 - Family Zosterophyllaceae
 - Class Horneophytoidsida
 - Order Horneophytales
 - Family Horneophytaceae
 - Class Trimerophytoidsida
 - Order Trimerophytales
 - Family Trimerophytaceae
 - Class uncertain
 - Order Barinophytales
 - Family Barinophytaceae
 - Class Lycopsida ('club-mosses')
 - Order Drepanophycales
 - Family Drepanophytaceae

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- Order Protolpidodendrales
 - Family Protolpidodendraceae
 - Family Eleutherophyllaceae
- Order Lycopodiales
 - Family Lycopodiaceae
- Order Selaginellales
 - Family Selaginellaceae
- Order Lepidocarpaceae
 - Family Cyclostigmaceae
 - Family Flemingitaceae
 - Family Sigillariostrobaceae
 - Family Lepidocarpaceae
 - Family Spenceritaceae
 - Family Caudatocarpaceae
 - Family Pinakodendraceae
 - Family Sporangiostrubaceae
 - Family Pleuromeiaceae
- Order Miadesmiales
 - Family Miadesmiaceae
- Order Isoetales ('quillworts')
 - Family Isoetaceae
 - Family Chaloneriaceae
- Class Equisetopsida ('horsetails')
 - Order Pseudoborniales
 - Family Pseudoborniaceae
 - Order Bowmaniales ('sphenophylls')
 - Family Bowmaniaceae
 - Family Eviostachyaceae
 - Family Cheirostrobaceae
 - Order Equisetales
 - Family Archaeocalamitaceae
 - Family Calamostachyaceae
 - Family Tchernoviaceae
 - Family Gondwanostachyaceae
 - Family Equisetaceae
 - Family Echinostachyaceae
- Class Filicopsida ('ferns')
 - Order Cladoxylales
 - Family Cladoxylaceae
 - Order Ibykales
 - Family Ibykaceae
 - Order Coenopteridales
 - Family Rhacophytaceae
 - Family Zygotpteridaceae
 - Family Stauropteridaceae
 - Family Corynepteridaceae
 - Family Biscalitheaceae
 - Order Botryopteridales
 - Family Psalixochlaenaceae
 - Family Tedeleaceae
 - Family Botryopteridaceae
 - Family Sermeyaceae
 - Order Urnatopteridales
 - Family Urnatopteridaceae
- Order Crossothecales
 - Family Crossothecaceae
- Order Marattiales
 - Family Asterothecaceae
 - Family Marattiaceae
- Order Osmundales
 - Family Osmundaceae
- Order Filicales
 - Family Gleicheniaceae
 - Family Cynepteridaceae
 - Family Matoniaceae
 - Family Dipteridaceae
 - Family Polypodiaceae
 - Family Dicksoniaceae
- Class Progymnospermopsida
 - Order Aneurophytales
 - Family Aneurophytaceae
 - Family Protokalonaceae
 - Family Protopityaceae
 - Order Archaeopteridales
 - Family Archaeopteridaceae
 - Order Noeggerathiales
 - Family Noeggerathiaceae
 - Family Tingiostachyaceae
 - Order Cecropsidales
 - Family Cecropsidaceae
- Division Gymnospermophyta ('seed plants')
 - Class Lagenostomopsida
 - Order Lagenostomales
 - Family Elkinsiaceae
 - Family Genomospermaceae
 - Family Eospermaceae
 - Family Lagenostomaceae
 - Family Physostomaceae
 - Unnamed Class
 - Order Calamopityales
 - Family Calamopityaceae
 - Order Callistophytals
 - Family Callistophytaceae
 - Order Peltaspermales
 - Family Peltaspermaaceae
 - Family Cardiollepidaceae
 - Family Umkomasiaceae
 - Order Leptostrobales
 - Family Leptostrobaceae
 - Order Arberiales ('glossopterids')
 - Family Arberiaceae
 - Family Caytoniaceae
 - Order Gigantonomiales ('gigantopterids')
 - Family Emplectopteridaceae
 - Class Cycadopsida
 - Order Trigonocarpaceae ('medullosans')
 - Family Trigonocarpaceae
 - Family Potonieaceae

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- Order Cycadales ('cycads')
 - Family Cycadaceae
- Class Pinopsida
 - Order Cordaitanthales ('cordaites')
 - Family Cordaitanthaceae
 - Family Rufforiaceae
 - Family Vojnovskyaceae
 - Order Dicranophyllales
 - Family Dicranophyllaceae
 - Family Trichopityaceae
 - Order Pinales ('conifers')
 - Family Emporiaceae
 - Family Utrechtiaceae
 - Family Majonicaceae
 - Family Ullmanniaceae
 - Family Voltziaceae

The choice of GCR sites

The British Isles has an outstanding number of sites that yield Upper Palaeozoic plant fossils, especially from the Upper Silurian, Lower Devonian, and Carboniferous. Many of these, such as the Rhynie Chert locality, are of national and international importance and have been known to the scientific community for a great many years. If palaeobotany is to survive as a viable research subject in Britain then these important sites must be conserved and maintained for further studies to be possible. A full rationale for conserving sites of palaeobotanical importance, the methods for selecting them and the problems in managing them have been discussed in detail by Cleal (1988).

Based on the presence of certain broad guidelines, only those sites which could be regarded as nationally or internationally significant have been chosen for inclusion in this volume. They include the following:

1. Sites yielding a unique assembly of species which have contributed significantly to our understanding of plant fossils (e.g. Perton Lane, Whiteadder).
2. Sites where species are exceptionally well-preserved, showing structural features not seen elsewhere (e.g. Pettycur).
3. The best available sites in Britain for showing the major plant fossil assemblages (e.g. Teilia Quarry).

The sites selected have been chosen to include an adequate cover of the range of Britain's plant fossil assemblages. The list is the result of selection from the vast number of sites known at present but, of course, the collection of new and exciting

species at existing sites, the reinterpretation of existing specimens, or the discovery of new sites may bring about its modification in the future.

The survey resulted in the selection of 42 sites, as summarized in Table 1.1. The distribution of the sites in Britain is shown in Figure 1.5, using the site codes given in Table 1.1.

Table 1.1 The Palaeozoic palaeobotany GCR sites

Geological System	Site Name	Site Code
Permian	Kimberley Railway Cutting	P3
	Middridge Quarry	P2
	Stairhill	P1
U. Carboniferous	Jockie's Syke	U6
	Llanbradach Quarry	U5
	Nostell Priory Brickpit	U4
	Cattybrook Claypit	U3
	Wadsley Fossil Forest	U2
	Nant Llech	U1
	L. Carboniferous	Victoria Park
Glencartholm		L15
Wardie Shore		L14
Teilia Quarry		L13
Moel Hirradug		L12
Puddlebrook Quarry		L11
Glenarbuck		L10
Loch Humphrey Burn		L9
Laggan		L8
Kingswood		L7
Pettycur		L6
Kingwater		L5
Weak Law		L4
Oxroad Bay		L3
Whiteadder		L2
Lennel Braes	L1	
Devonian	Plaistow Quarry	D10
	Sloagar	D9
	Bay of Skail	D8
	Rhynie	D7
	Auchensail Quarry	D6
	Ballanucater Farm	D5
	Craig-y-Fro Quarry	D4
	Llanover Quarry	D3
	Turin Hill	D2
	Targrove Quarry	D1
Silurian	Freshwater East	S7
	Perton Lane	S6
	Capel Horeb Quarry	S5
	Cwm Craig Ddu Quarry	S4
	Rockhall Quarry	S3
	Llangammarch Wells Quarry	S2
	Pen-y-Glog Quarry	S1

Introduction

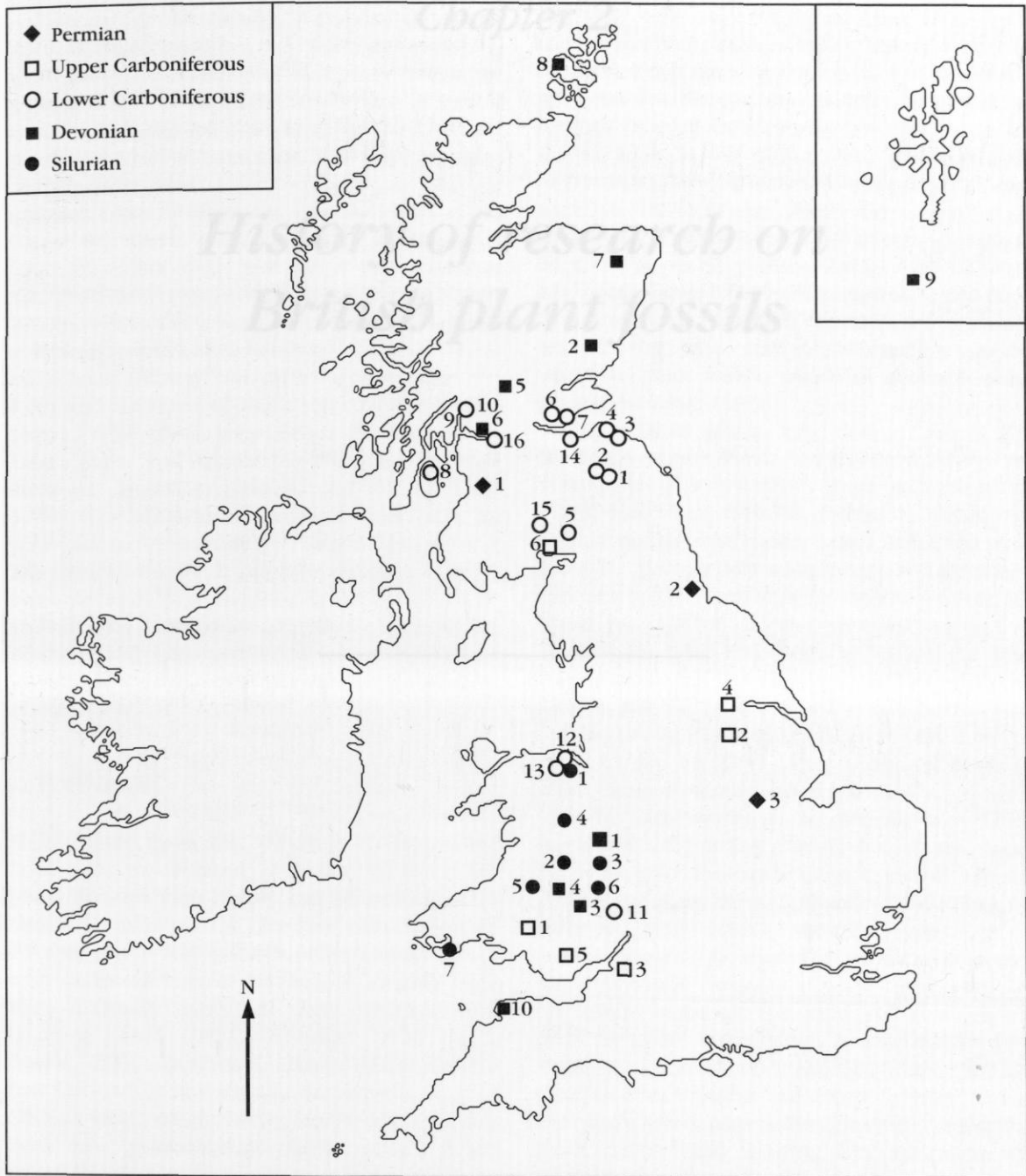


Figure 1.5 The distribution of the GCR Palaeozoic palaeobotany sites in Britain. See Table 1.1 for site names.

Chapter 2

History of research on British plant fossils

SILURIAN

British sites, particularly in Wales and the Welsh Borders, have played a key role in developing ideas about the evolution of land plants during the Silurian (440–410 Ma). This may be due, at least in part, to it being the type area for much of the Silurian and having been subject to more intensive investigation than other outcrops of this age (Bassett, 1984; Holland and Bassett, 1989). It has meant that there is a long history of records of plant fragments from these strata, dating back to the mid-nineteenth century (e.g. Phillips, 1848; Brodie, 1869, 1871; see Lang, 1937 for a more complete account of the early records). However, no serious attempt was made to investigate the form and structure of these difficult fossils until Lang's (1937) classic monograph. For many years, Lang's paper was regarded as the definitive statement on Silurian vegetation, and not until the 1970s was any attempt made to re-evaluate his observations, principally by Dianne Edwards (e.g. Edwards, 1979a, 1982; Edwards and Davies, 1976; Edwards and Rogerson, 1979; Edwards *et al.*, 1979, 1986; Fanning *et al.*, 1988, 1990, 1991). Edwards and her co-workers are continuing to investigate the fossil evidence for Silurian terrestrial vegetation.

DEVONIAN

Plant fossils from the Devonian (410–355 Ma) have been investigated in Britain for over 150 years, but this long history can be broken down into three main phases. The first effectively started with the work of Hugh Miller (Rosie, 1981), who collected from a number of Scottish localities. Although there had been earlier records (Fleming, 1811, 1831; Williams, 1838; De la Beche, 1839; Murchison, 1839), Miller was the first to describe and discuss such fossils in detail (Miller, 1841, 1849, 1855, 1857). His contributions to palaeobotany have been largely overshadowed by his work on vertebrate palaeozoology. However, he was probably the first palaeontologist in the world to treat Devonian plant fossils seriously, and he laid the foundations for the studies of later nineteenth century workers (e.g. Dawson, 1888).

Considering the poor preservation of most Devonian plant fossils, it is not surprising that many of the nineteenth century palaeobotanists had difficulty interpreting them. For a time, it

became widely believed that the 'fossil plants of the Devonian rocks in Europe resemble generically, with very few exceptions, those of the coal-measures' (Lyell, 1865, p. 542). The discovery of 'conifer' wood (now known in fact to be from a progymnosperm) in the Middle Devonian of Scotland tended to reinforce this misconception (Miller, 1841; M'Nab, 1871). Some geologists such as Dawson (1859, 1870, 1871) argued that at least some of the Devonian fossils represented truly simple and primitive plants, but others just regarded them as poorly preserved fragments of more advanced plants. Despite this confusion, the nineteenth and early twentieth centuries saw a gradual accumulation of a pool of information on the Devonian plant fossils, which is admirably summarized by Arber (1921).

The second phase of research on British Devonian plant fossils commenced with the description of the Rhynie Chert assemblage by Kidston and Lang (1917b, 1920a, b, 1921a, b). This was the first unequivocal evidence that Devonian plants really were simple and primitive, and provided a significant impetus to the further investigation of the less well-preserved adpression assemblages from elsewhere. In Britain, the field was dominated at this time by Lang. Following the work at Rhynie, he continued to collaborate with Kidston on the Scottish assemblages (Kidston and Lang, 1923a, b, 1924). After Kidston's death in 1924, Lang continued to work on the Scottish sites, but later moved on to material from Wales and the Welsh Borders. During this second phase, Devonian palaeobotany became an established discipline and many of our presently held views on early land plant evolution were developed.

From about 1945, there was a lull in the investigation of British Devonian plant fossils. During the mid-1960s, however, the third and most recent phase in their investigation began, mainly as a result of the work of Dianne Edwards. She has instigated new work on many of the classic Devonian plant adpression localities, collecting fresh material and applying new and improved techniques to its study. She has also searched out new localities, such as Auchensail Quarry (see also Edwards and Richardson, 1974; Edwards and Rose, 1984; Edwards *et al.*, 1986). This has all provided significant new information on the morphological variation and anatomy of many of these plants. Recent attempts at biostratigraphical (Banks, 1980), palaeoecological (Edwards, 1980b) and palaeogeographical analyses (Raymond *et al.*, 1985; Edwards, 1990) have leaned heavily on this

new data. There has also been significant recent progress on the Rhynie fossils, mainly through the work of Lyon (1957, 1962, 1964), Bhutta (1972, 1973a, b), El-Saadawy and Lacey (1979a, b), Remy (1978, 1980a, b, 1991), Remy and Remy (1980a, b), Remy *et al.* (1980b), D.S. Edwards (1980, 1986), Edwards and Lyon (1983), Lyon and Edwards (1991) and Remy and Hass (1991a, b). This was mainly as a result of using new techniques, particularly serial sectioning using acetate peels, which allowed far more refined reconstructions of the plants to be achieved.

Despite the recent resurgence of interest, there are many aspects of British Devonian palaeobotany that remain neglected. For instance, other than papers by Chaloner (1972), Edwards (1976) and Allen and Marshall (1986), there has been no recent work on the Middle Devonian plant fossils from northern Scotland. This is despite there being numerous sites available for further collecting. The British Upper Devonian assemblages have been even more neglected, the only recent references to them being by Long (1973) and Fairon-Demaret and Scheckler (1987). There is evidently considerable potential for further work in this country.

LOWER CARBONIFEROUS

Plant adpressions were reported from the Lower Carboniferous (355–320 Ma) of Britain in the early to mid-nineteenth century, in particular from the Burdiehouse Limestone near Edinburgh (e.g. Lindley and Hutton, 1831–1837; Miller, 1857). However, intensive work on fossils from these strata did not start until the late nineteenth century, principally by Kidston (Edwards, 1984). Kidston's immense contribution to the subject culminated in his classic monographs published between 1923 and 1925, which remain the definitive publications on the Lower Carboniferous adpression palaeobotany of Britain (those parts of this monograph not published before his death were subsequently updated and published by Crookall, 1955–1975). Probably the most significant aspect of Kidston's work, other than the fact that he placed on record so many fossils of this age, was his analysis of the frond architecture of the early pteridosperms and his consequent refinement of their classification.

The next major phase of work on the British fossils of this age was by Walton (1926, 1931, 1941), Benson (1904, 1933, 1935a, b) and later Lacey

(1962). They mainly concentrated on sites in Wales and south-west England, although Walton also reported on adpressions from the Clyde Plateau Volcanic Formation near Glasgow (Walton *et al.*, 1938). Walton's work was particularly important for helping establish reconstructions of the plants, especially for determining the connection between foliage and fructifications. Lacey's work is also of considerable significance, if only because it is one of the few attempts to prepare cuticles from plant fossils of this age.

Most recently, the only significant contribution to British Lower Carboniferous adpression palaeobotany has been Rowe's (1988a, b, c) work on material from the Drybrook Sandstone in the Forest of Dean. Although previously studied by Lele and Walton (1962b), Rowe has applied new techniques to provide a fresh insight into the fossils.

The first records of British Lower Carboniferous petrifications were in the early nineteenth century, by Witham (1831, 1833), who described material from a number of sites in the Cementstone Group of southern Scotland. Witham's work is mainly significant in having developed the method of thin sectioning rocks, which was not only important for the future development of palaeobotany, but was perhaps more significant for petrology and mineralogy. The first major advance in this field for palaeobotany, however, was the discovery in the 1870s of the petrifications from the Pettycur Limestone. The work of Williamson and Scott at this site established it as of international significance (Williamson, 1872, 1873, 1874a, b, 1877, 1880, 1883, 1895; Williamson and Scott, 1894, 1895; Scott, 1897, 1901); until the discoveries 40 years later at Rhynie (see Chapter 4), it provided some of the oldest evidence of cell structure in plants and was central to ideas about early plant evolution.

Various other petrification sites were discovered in Scotland during the late nineteenth and early twentieth centuries, but these were mainly found by chance. The first concerted effort to search for new sites was by Gordon (1935a, b, 1938, 1941), who discovered petrifications at various localities in the volcanogenic deposits exposed along the south-east coast of Scotland. Gordon described a variety of new taxa from both these new and some of the old localities, his work on the ferns being particularly important. Other major contributions to Lower Carboniferous petrification palaeobotany during the mid-twentieth century were by Calder (1934, 1935, 1938), Walton (1935,

1949a, b, c, 1957, 1969), Beck (1958), Chaphekar (1963) and Chaphekar and Alvin (1972).

In more recent years, by far the most important work on Lower Carboniferous petrifications has been by Long (1959-1987) on the Cementstone Group sites. By utilizing the peel method, Long has revolutionized our view of the Early Carboniferous plants, particularly of the seed plants. His views on the evolution of these plants have not always met with universal acceptance, but the quality of his observations and the degree to which other palaeobotanists have had to use them in developing their ideas concerning seed plant evolution, in particular, are indisputable.

Another approach to the study of the British Lower Carboniferous petrification sites has been by Scott, who has integrated the analysis of species distribution and sedimentology to develop ideas about the plant ecology of the time (Scott *et al.*, 1984, 1985, 1986; Scott and Rex, 1987; Rex and Scott, 1987). Scott's work has produced particularly interesting results from exposures of the volcanogenic strata in southern Scotland, such as the Pettycur Limestone and the Oxroad Bay tuffs. He has also instigated the collection of additional new material from many of these sites, which have been worked on mainly by other palaeobotanists (Rothwell and Wight, 1989; Galtier and Scott, 1986a, b; Meyer-Berthaud, 1986; Meyer-Berthaud and Galtier, 1986a, b; Bateman, 1988; Bateman and Rothwell, 1990). The review paper by Scott *et al.* (1984) provides one of the best sources of information on the distribution of Lower Carboniferous petrifications in Britain.

UPPER CARBONIFEROUS

Upper Carboniferous (320-290 Ma) plant fossils have been known from Britain since at least the seventeenth century, the first published account usually being credited to Lhuys (1699). A number of subsequent publications by British naturalists during the eighteenth and early nineteenth centuries, described Upper Carboniferous plant fossils, the most widely quoted being Artis (1825) and Lindley and Hutton (1831-1837) (for a fuller account of early British work on these fossils, see Kidston, 1923a and Andrews, 1980). Unlike continental Europe, however, Britain failed to produce any significant contributors to the subject until the mid-nineteenth century. The first major British palaeobotanist to deal with the adpression plant

fossils was Kidston, whose impressive list of publications started in the 1880s (Crookall, 1938; Edwards, 1984) and culminated in his classic 1923-1925 monographs. During the first half of the twentieth century, notable contributions were also made by Arber (1904b, 1912, 1914, 1916).

Most of this work was of a floristic nature, documenting assemblages and species distributions; Kidston's work on fern fructifications and pteridosperm frond architectures being the most significant exceptions. More botanically orientated, morphological/anatomical study was instead concentrated on the Langsettian coal-balls from Yorkshire and Lancashire. Petrified plant fossils were first noted in coal-balls in the 1850s by Binney, but their true significance was established first by Williamson in a series of papers starting in the 1860s, and later by Scott. The results of this main phase of British coal-ball work is admirably summarized by Scott (1920-1923).

After this 'golden period' of British Upper Carboniferous palaeobotany, ending in the mid-1920s, interest in the subject suffered a decline. Crookall attempted to continue Kidston's work on the adpressions, although this amounted mainly to further documenting the distribution of species in Britain. His main achievement was the 1955-1975 monographs, which described those plant groups not covered in the Kidston volumes. However, they were published some time after Crookall's main phase of work, in the 1930s, and despite some attempts to update them, they have a rather archaic feel. It is also worth mentioning here the work of Dix (1933, 1934, 1935) on the biostratigraphy and Davies (1929) on the palaeoecology of the Upper Carboniferous plant fossils, although in both cases their publications are weakened by a failure to document fully the taxa they were recording.

The most significant recent contributions to Upper Carboniferous palaeobotany in Britain have been on the lycopsids, by Chaloner (much of whose work is summarized by Chaloner *in* Boureau *et al.*, 1967), Thomas (1967a, b, 1970, 1977, 1978a, b, 1981b) and Boulter (1968). There has also been some recent interest in the ferns and pteridosperms (Thomas and Crampton, 1971; Cleal and Laveine, 1988; Shute and Cleal, 1989; Cleal and Shute, 1991, 1992). Finally, there has also been interest in the use of plant fossils for Late Carboniferous palaeoecology (e.g. Scott, 1977, 1978, 1979) and biostratigraphy (Wagner and Spinner, 1972; Cleal, 1978, 1984b, 1986c, 1987b; Cleal and Thomas, 1988).

History of research on British plant fossils

Coal-ball work also underwent somewhat of a decline after the 1930s. Contributions were made by Holden and Long (reviewed briefly by Andrews, 1980). The most significant work has, however, been that of Holmes on some of the herbaceous ferns found in the coal-balls (reviewed by Holmes, 1989).

PERMIAN

Most work on the Permian (290–250 Ma) palaeobotany of Britain has been on the Marl Slate and

its equivalents. The best historical account of studies on these fossils is by Stoneley (1958), who notes records dating back to the mid-nineteenth century (Sedgwick, 1829; Lindley and Hutton, 1937; King, 1850; Kirkby, 1862, 1864, 1867). Stoneley provides the only attempt at a monographic analysis of these fossils, although a useful review is also provided by Schweitzer (1986). Individual taxa have also been dealt with by Townrow (1960) and Poort and Kerp (1990).