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 been 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. 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 Any part of the plant capable of growing into a new organism, such as a spore, seed, or cutting plants could not start to live there. 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

		Ordovician (upper)		Silurian				Devonian			Carboniferous (lower)	
		Caradoc	Ashgill	Llandovery	Wenlock	Ludlow	Pridolí	Lower	Middle	Upper	Tournaisian	Viséan
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.

looked essentially similar (Remy, 1991). However, this symmetry soon broke down and in vascular plants the sporophyte became much larger and the 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 occurred to this basic pteridophytic reproductive strategy. 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. Other features 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*, *Nematothallus*). 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, this 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. 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 conifers. 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 as they are found in most arborescent plants.

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. *Nematothallus*, *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, Zosterophyllopsida, Trimerophy-

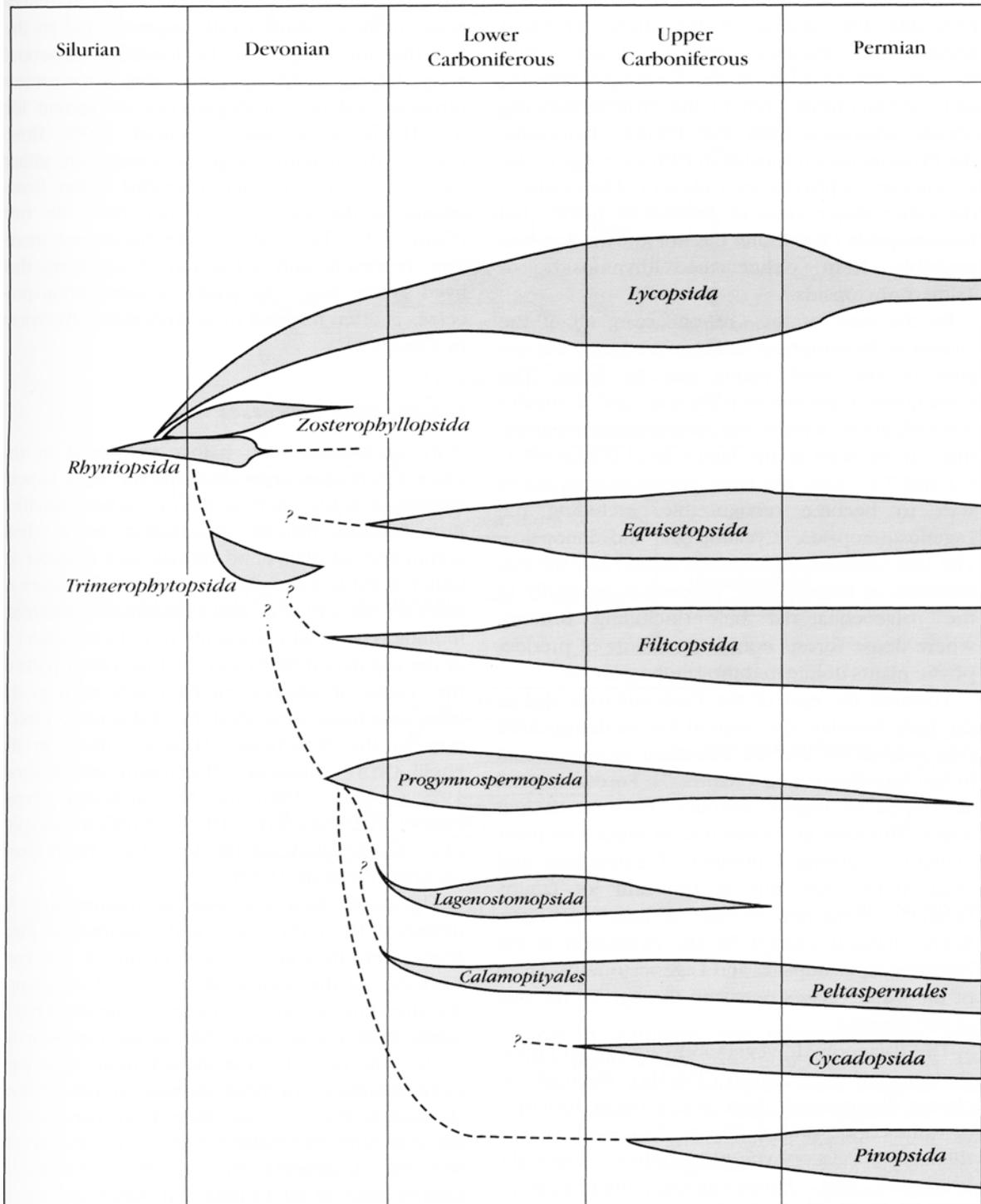**Figure 1.2** The ranges of the main plant classes through the Palaeozoic.

topsida and Horneophytopsida. 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 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 Lycopsida ('club mosses') originated from the Zosterophyllopsida, and the Filicopsida ('ferns') and Progymnospermopsida originated from the Trimerophytopsida; 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 Trimerophytopsida.

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. 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. 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. Also, two of the leading Palaeophytic pteridophyte classes, the Lycopsida 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. 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 it 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
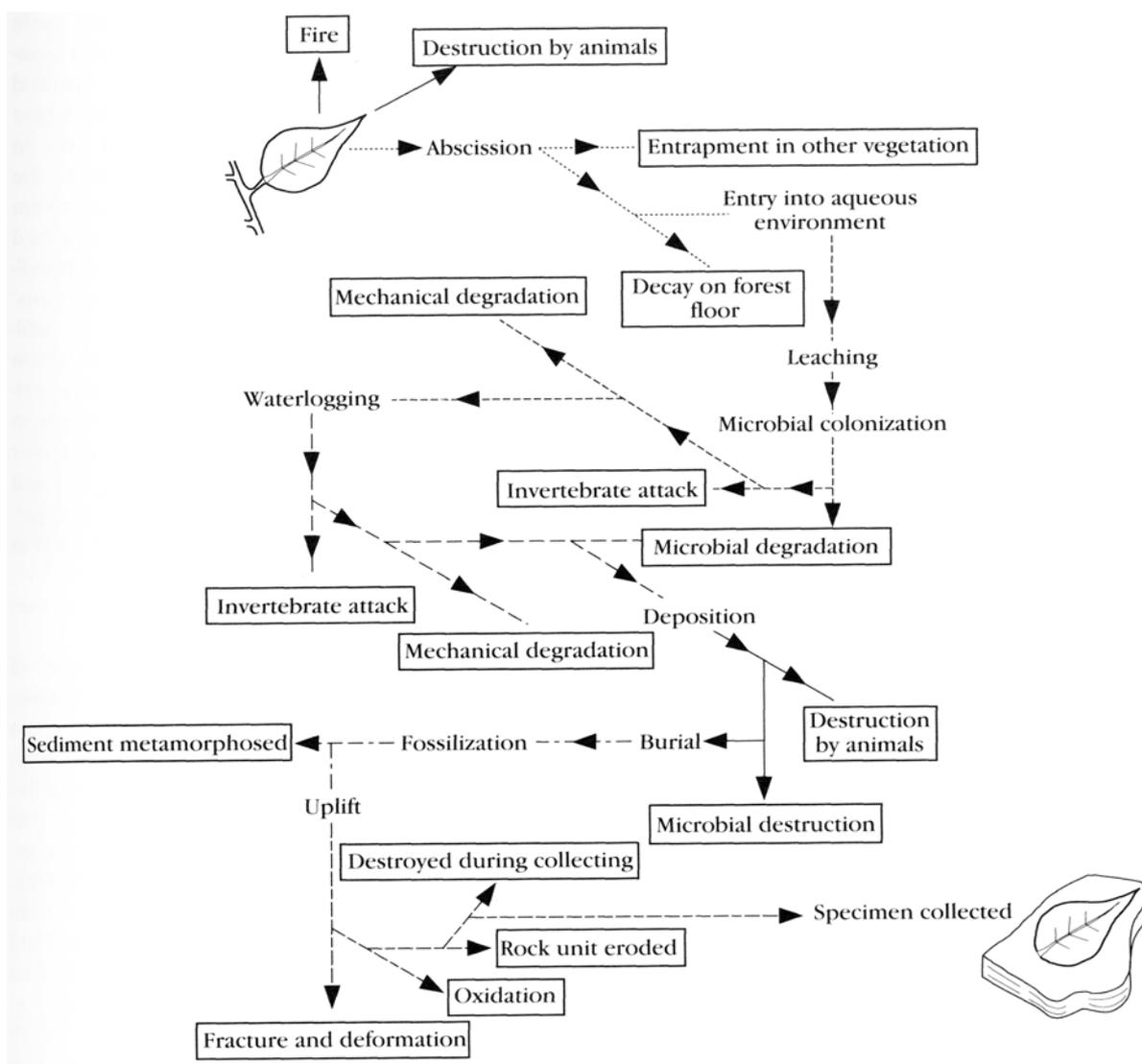
Figure 1.3 The potential processes involved in a plant fragment passing into the fossil record.. From Thomas and Spicer (1987, fig. 4.1).

the fragment to its eventual site of burial in sediment. This site will normally have been sub-aqueous, usually in a lake or other form of non-marine standing-body of water, or occasionally in the sea; plant fragments 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 the fossiliferous deposit. 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 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 is 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 petrifaction 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.

Plant fossils can be studied in a number of ways, depending on their modes of preservation, but there are a number of techniques than can yield a surprising amount of detail (see Lacey, 1963; Schopf, 1975, or the general textbooks listed above 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 petrifactions 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.

Buried plant fragment

Two-dimensional   Three-dimensional

Anatomical   Non-anatomical

Compression   Permineralization   Authigenic cementation

Adpression

Petrifaction s.l.

Petrifaction s.s.   Authigenic replica

Wood (left), cell walls (right)   Pith parenchyma   Enclosing sediment
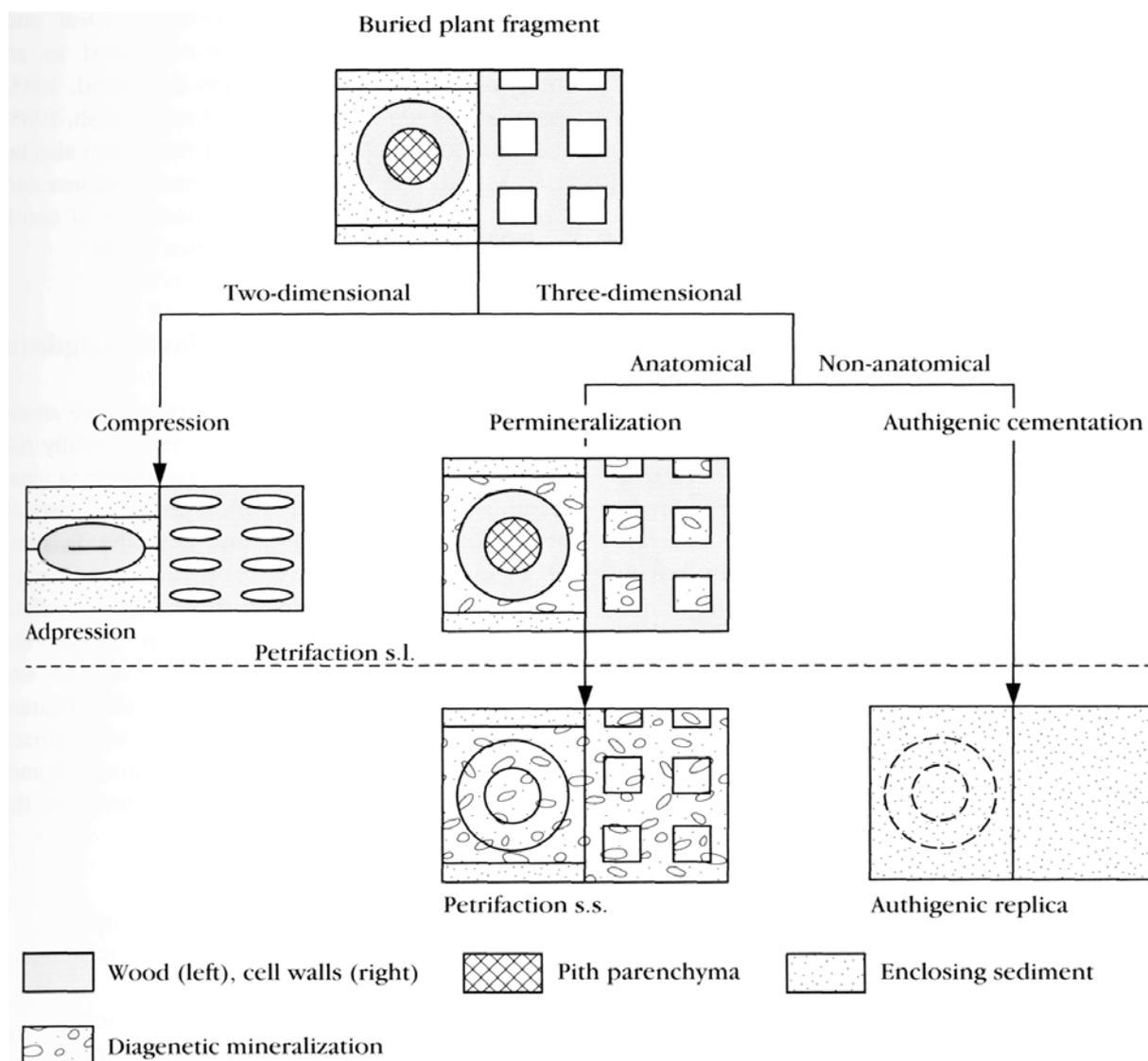
Diagenetic mineralization

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, fig. 2.2).

However, the problem confronted in studying fossil plants is how to name and classify the very different plant 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 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. 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 Zosterophyllopsida
      Order Zosterophyllales
        Family Zosterophyllaceae
    Class Horneophytopsida
      Order Horneophytales
        Family Horneophytaceae
    Class Trimerophytopsida
      Order Trimerophytales
        Family Trimerophytaceae
    Class uncertain
      Order Barinophytales
        Family Barinophytaceae

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Class Lycopsida ('club-mosses')
  Order Drepanophycales
    Family Drepanophycaceae
  Order Protolepidodendrales
    Family Protolepidodendraceae
    Family Eleutherophyllaceae
  Order Lycopodiales
    Family Lycopodiaceae
  Order Selaginellales
    Family Selaginellaceae
  Order Lepidocarpales
    Family Cyclostigmaceae
    Family Flemingitaceae
    Family Sigillariostrobaceae
    Family Lepidocarpaceae
    Family Spenceritaceae
    Family Caudatocarpaceae
    Family Pinakodendraceae
    Family Sporangiostrobaceae
    Family Pleuromeiaceae
  Order Miadesmiales
    Family Miadesmiaceae
  Order Isoetales ('quillworts')
  Family Isoetaceae
  Family Chaloneriaceae
Class Equisetopsida ('horsetails')
  Order Pseudoborniales
    Family Pseudoborniaceae
  Order Bowmanitales ('sphenophylls')
    Family Bowmanitaceae
    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 Zygopteridaceae
    Family Stauropteridaceae
    Family Corynepteridaceae
    Family Biscalithecaceae
  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 Callistophytales
      Family Callistophytaceae
    Order Peltaspermales
      Family Peltaspermaceae
      Family Cardiolepidaceae
      Family Umkomasiaceae
    Order Leptostrobales
      Family Leptostrobaceae
    Order Arberiales ('glossopterids')
      Family Arberiaceae
      Family Caytoniaceae
    Order Gigantonomiales ('gigantopterids')
      Family Emplectopteridaceae
  Class Cycadopsida

Order Trigonocarpales ('medullosans')
   Family Trigonocarpaceae
   Family Potonieaceae
Order Cycadales ('cycads')
   Family Cycadaceae
Class Pinopsida
   Order Cordaitanthales ('cordaites')
      Family Cordaitanthaceae
      Family Rufloriaceae
      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	L16
	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 Skaill	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
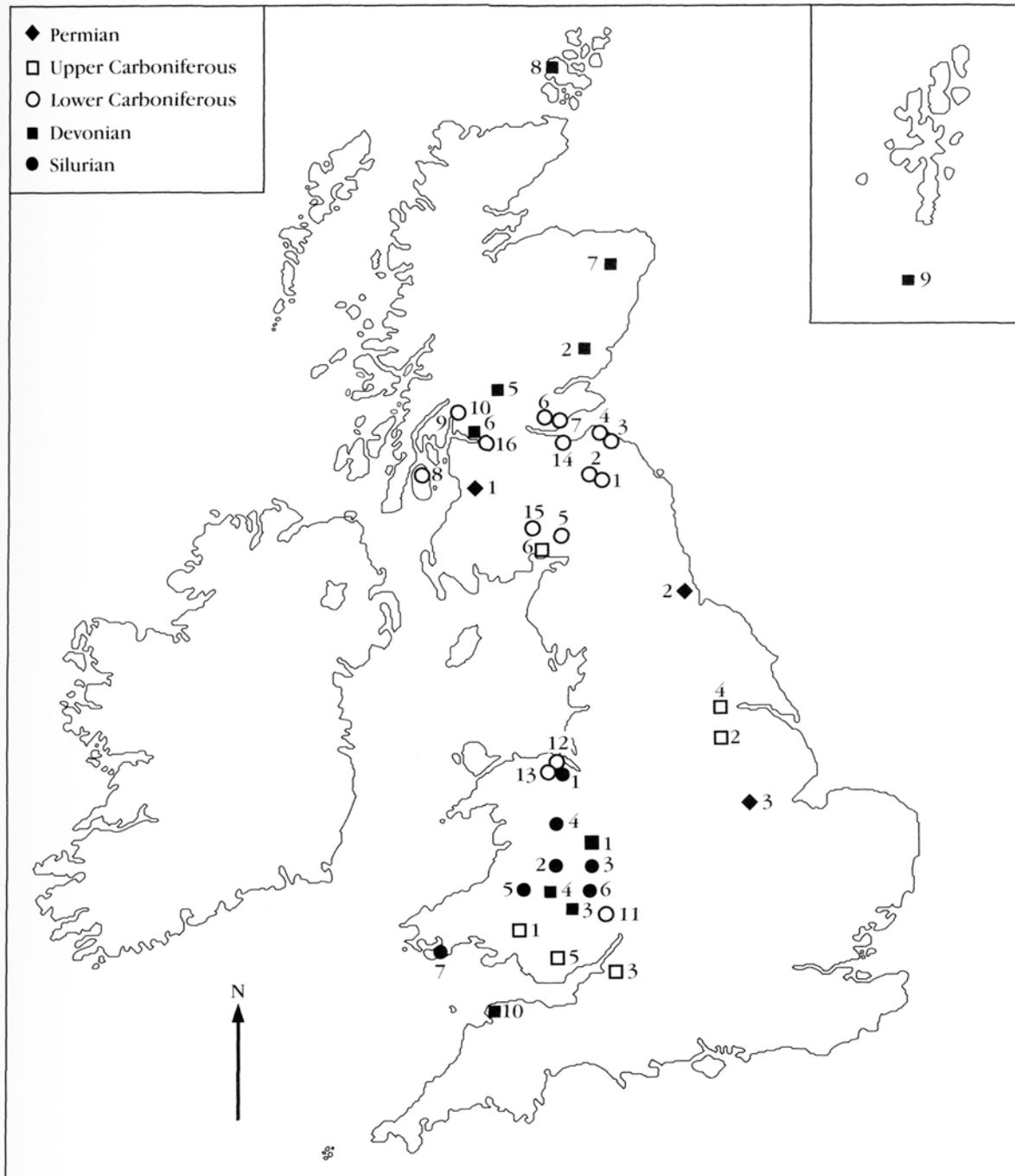
Figure 1.5 The distribution of the GCR Palaeozoic palaeobotany sites in Britain. See Table 1.1 for site names.