

# *Mesozoic and Tertiary Palaeobotany of Great Britain*

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# *Access to the countryside*

## *JNCC policy statement*

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. 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 not 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:

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

English Nature,  
Northminster House,  
Peterborough PE1 1UA.

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



# *Conserving our fossil heritage*

## *– JNCC policy statement*

Fossils are a key part of our natural heritage and form a major scientific, educational and cultural resource. They are fundamental to understanding the evolution of life and the character of ancient environments. Fossils also provide a basis for comparing the ages of rocks the world over.

The discovery, collection and study of the fossilized remains of ancient life can be enjoyable and stimulating activities that give people a fascinating insight into the geological and biological history of the Earth. However, the available fossil resource is finite. It is only through maintaining a prudent approach to the management of important fossil sites that future generations will be able to experience, study and enjoy this resource.

### **RESPONSIBLE FOSSIL COLLECTING**

In most circumstances, responsible fossil collecting is not harmful to the conservation of fossil sites. It can actually benefit our understanding of geology. This is particularly true where the fossils are relatively common or the sites in which they are found are subject to high levels of natural or artificial degradation, such as coastal cliffs that are being eroded or quarries that are being actively worked. In such situations collecting fossil specimens that might otherwise be destroyed can be beneficial to science, provided that they are properly documented and made available for study. Responsible fossil collecting can therefore be a valuable activity in the sustainable management and safeguard of our fossil heritage.

### **IRRESPONSIBLE FOSSIL COLLECTING**

Irresponsible collecting provides no scientific or educational gain and is therefore an unacceptable activity resulting in irreparable damage to our fossil heritage. It will pose a clear threat where fossils are rare or the fossil source is limited in extent, for example in a cave or a river channel deposit. Collecting without proper recording and curation, inexperienced collecting, over-collecting and inappropriate use of power tools and heavy machinery are likely to reduce or even destroy the scientific value of such sites. Unless the activity is undertaken in an appropriate manner, the statutory nature conservation agencies, the Countryside Council for Wales, English Nature, Environment and Heritage Service and Scottish Natural Heritage, will oppose fossil collecting on the small number of Sites of Special Scientific Interest / Areas of Special Scientific Interest where this activity would



## *Fossil collecting code of good practice*

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cause significant damage to the features of special interest.

### **CODE OF GOOD PRACTICE**

Adopting a responsible approach to collecting is essential for conserving our fossil heritage. The basic principles set out below should be followed by all those intending to collect fossils.

**Access and ownership** – permission to enter private land and collect fossils must always be gained and local bylaws should be obeyed. A clear agreement should be made over the future ownership of any fossils collected.

**Collecting** – in general, collect only a few representative specimens and obtain these from fallen or loose material. Detailed scientific study will require collection of fossils *in situ*.

**Site management** – avoid disturbance to wildlife. Many invertebrates and lower plants live on or under loose rocks that should be replaced in their original positions whenever possible. Do not leave the site in an untidy or dangerous condition for those who follow.

**Recording and curation** – always record precisely the locality at which fossils are found and, if collected *in situ*, record relevant details of the position of the rock layer from where the fossil was collected. Ensure that these records can be directly related to the relevant specimens. Where necessary, seek specialist advice on specimen identification and care. Fossils of prime scientific importance should be placed in a suitable repository, normally a museum with adequate curatorial and storage facilities.

### **ACHIEVING POSITIVE MANAGEMENT**

In order to achieve the successful management of the fossil heritage of the United Kingdom, the statutory nature conservation agencies will:

- Promote the responsible approach outlined in the *Code of Good Practice*, above.
- Encourage the placement of scientifically important fossils into a suitable repository (such as a museum) in order to ensure their proper curation, long-term security and accessibility.
- Recognize the contribution that responsible fossil collectors can make to geological and palaeontological study.
- Encourage collaboration within the geological community to ensure that maximum educational and scientific gain is made from our fossil resource.
- Support and encourage initiatives that increase awareness and understanding of the value of our fossil resource and the need to conserve it.
- Increase awareness and understanding of the differing management needs of fossil sites. In particular, encourage landowners and occupiers to become advocates for conservation of the fossil resource.
- Review the need for export and import controls on the international trade in fossil specimens.



1997



# Preface

There is such a diversity of rocks, minerals, fossils and landforms packed into the piece of the Earth's crust we call 'Britain' that it is difficult not to be impressed by the long, complex history of geological change to which they are testimony. But if we are to improve our understanding of the nature of the geological forces that have shaped our islands, further unravel their history in 'deep time' and learn more of the history of life on Earth, we must ensure that the most scientifically important of Britain's geological localities are conserved for future generations to study, research and enjoy. Moreover, as an educational field resource and as training grounds for new generations of geologists on which to hone their skills, it is essential that such sites continue to remain available for study. The first step in achieving this goal is to identify the key sites. This is the aim of the Geological Conservation Review.

The GCR, launched in 1977, is a world-first in the systematic selection and documentation of a country's best Earth science sites. No other country has attempted such a comprehensive and systematic review of its Earth science sites on anything near the same scale. After over two decades of site evaluation and documentation, we now have an inventory of over 3000 GCR sites, selected for 100 categories covering the entire range of the geological and geomorphological features of Britain.

This volume, detailing the Mesozoic and Tertiary Palaeobotany GCR sites, is the 22nd to be published in the intended 42 volume GCR series. Not only does it contain the descriptions of key localities that will be conserved for their contribution to our understanding of the palaeontology and palaeobiology of plants, but also provides an excellent summary of the floral realms in Britain and the considerable research that has been undertaken on it. The book will be invaluable as an essential reference book to those engaged in the study of these rocks and will provide a stimulus for further investigation. It will also be helpful to teachers and lecturers and for those people who, in one way or another, have a vested interest in the GCR sites: owners, occupiers, planners, those concerned with the practicalities of site conservation and indeed the local people for whom such sites are an environmental asset. The conservation value of the sites is mostly based on a specialist understanding of the stratigraphical, palaeontological and sedimentological features present and is therefore, of a technical nature. The account of each site ends, however, with a brief summary of the geological interest, framed in less technical language, in order to help the non-specialist. The first chapter of

## Preface

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the volume, used in conjunction with the glossary, is also aimed at a less specialist audience. This volume is not intended to be a field guide to the sites, nor does it cover the practical problems of their ongoing conservation. Its remit is to put on record the scientific justification for conserving the sites.

This volume deals with the state of knowledge of the sites available at the time of writing, in 1998–2000, and must be seen in this context. Palaeontology, like any other science, is an ever-developing pursuit with new discoveries being made, and existing models are subject to continual testing and modification as new data come to light. Increased or hitherto unrecognized significance may be seen in new sites. Indeed, during the progress of writing this book, new sites have been proposed for the Palaeobotany GCR lists, and it is possible that further sites worthy of conservation will be identified in future years. Nevertheless, there is still much more to learn and the sites described in this volume are as important today as they have ever been in increasing our knowledge and understanding of the palaeobotany of Britain. This account clearly demonstrates the value of these sites for research, and their important place in Britain's scientific and natural heritage. This, after all, is the *raison d'être* of the GCR Series of publications.

N.V. Ellis

GCR Publications Manager

December 2000



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## *Chapter 1*

# *Introduction to the Mesozoic and Tertiary palaeobotany of Great Britain*

*C.J. Cleal and B.A. Thomas*

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## OVERVIEW

In a previous volume of the Geological Conservation Review Series (Cleal and Thomas, 1995), we dealt with the best British sites that demonstrate the palaeobotany of the Palaeozoic Era, c. 543–c. 251 million years (Ma) ago – for a discussion of this age range see GCR volumes by Rushton *et al.*, 1999 and Smith, 1995 and references therein. In the present volume, we deal with most of the rest of the history of land vegetation in Britain, covering almost 250 million years of Earth history from the start of the Mesozoic Era (c. 251 Ma) to the end of the Tertiary sub-Era (i.e. to the end of the Neogene Period (1.8 Ma) – for discussion of the end point of the Neogene Period see Daley and Balson, 1999, pp. 237–9). Quaternary sites in Britain with important features of palaeobotanical interest are described in the regional Quaternary volumes of the GCR Series (see, for example, Campbell and Bowen, 1989; Gordon and Sutherland, 1993; Bridgland, 1994; Campbell *et al.*, 1998; Huddart and Glasser, in press).

## INTRODUCTION

Following the catastrophic collapse of land vegetation shown in the record of fossil plants across the Permian–Triassic boundary (c. 251 Ma), a new type of land vegetation developed that included many groups of ferns and gymnosperms (e.g. cycads and conifers) that still have representatives alive today. The oldest unequivocal evidence of angiosperms (flowering plants) in Britain is from early Tertiary rocks, but elsewhere in the world the oldest fossil examples are from the Upper Jurassic or Lower Cretaceous series (e.g. Sun *et al.*, 1998). By the end of the Tertiary sub-Era, British vegetation was essentially of a modern aspect, dominated by angiosperms and, to a lesser extent, conifers.

In order to provide a context for the choice of GCR sites described in this volume, we will first discuss some of the general palaeobotanical background. A brief explanation is given of how plant fossils are formed, and how palaeobotanists study and name them. More exhaustive accounts of the various systematic groups of plants, and how to interpret plant fossils, can be found in Thomas (1981), Meyen (1987), Thomas and Spicer (1987), Stewart and Rothwell (1993), Taylor and Taylor (1992), and Cleal and Thomas (1999).

## MESOZOIC–TERTIARY VEGETATIONAL HISTORY

The start of the Mesozoic Era is marked by a dramatic change to life on Earth, with some 96% of the known species of animal and plant becoming extinct (Erwin, 1993). Among the gymnosperms, for instance, there are 19 families described from the Permian System, but only three of these range through into the Triassic System. However, the cause of this biological catastrophe remains something of a mystery. There is no obvious evidence of an asteroid impact, such as found at the Cretaceous–Tertiary boundary. It is more likely that there was a very marked climate change and possible drop in atmospheric oxygen levels. One postulated cause for this is large-scale volcanicity in Siberia and southern China. Alternatively, changing circulation patterns may have caused stagnant, deep oceanic waters to rise to near the surface (known as the 'big belch'), introducing carbon dioxide and hydrogen sulphide into the atmosphere. Whatever its cause, it was the most dramatic of all mass extinctions for land vegetation and marks the change from the primitive Palaeozoic floras to floras of a recognizably modern aspect that start in the following Triassic Period.

In contrast, the better-known Cretaceous–Tertiary ('K/T') event had relatively little impact on land vegetation. The K/T event was probably the result of asteroid impact and/or intense volcanicity, which must obviously have had some short-term effect on plant life, owing to increased darkness and lower temperatures. However, it did not significantly affect the plant propagules (spores and seeds), which were able to germinate when more favourable conditions returned. An examination of the plant fossil record reveals that very few families became extinct at this event. Of those that did disappear (e.g. the bennettites – Krassilov, 1978), most were suffering a marked decline during the Cretaceous Period, probably as a result of competition from the angiosperms.

The palaeobotanical history of Mesozoic to Tertiary times is thus a relatively uninterrupted progression from the devastated early Triassic vegetation to the modern, angiosperm-dominated vegetation of late Tertiary times. As discussed below, most post-Permian plant groups can in fact be directly traced to Palaeozoic ancestors and there were few major evolutionary develop-



ments at this time. The only notable exception is the rise of the angiosperms during the Mesozoic Era.

### Lycophytes and sphenophytes

The lycophytes and sphenophytes were major groups during the Palaeozoic Era and in the tropics included large, tree-sized plants. However, these arborescent forms underwent a significant decline with the contraction of the tropical swamp forests (coal forests) towards the end of the Palaeozoic Era and they became extinct at the end of the Permian Period.

During the Triassic Period, one group of lycophytes, *Pleuromeia*, developed to a height of up to 2 m. Otherwise, however, Mesozoic lycophytes appear to have been small, herbaceous plants very similar to the living clubmosses such as *Selaginella* and *Lycopodium* (Skog and Hill, 1992).

The sphenophytes (known informally as 'horsetails') also never really developed as arborescent forms after the Palaeozoic Era. Most post-Palaeozoic forms in fact resemble strongly the living horsetails and are normally placed in the same genus (*Equisetum*) or in a fossil genus (*Equisetites*) for material that is morphologically indistinguishable from the living genus. Although never achieving great species diversity, the sphenophytes have remained a remarkably successful and persistent group that today still occurs in most parts of the world.

### Ferns

Ferns were a major component of Late Palaeozoic vegetation, but underwent a dramatic decline at the end of the Permian Period. Only three families persisted into the Mesozoic Era – the Osmundaceae, Marattiaceae and Gleicheniaceae – and these have survived to the present day, albeit with a relatively restricted distribution. In the early part of the Mesozoic Era, a number of other still-surviving families appeared, including the Matoniaceae, Dipteridaceae, Schizaeaceae, Cyathaceae and Dicksoniaceae. These flourished during the Jurassic and Cretaceous periods but then declined markedly in Tertiary times, partly in response to competition from more modern ferns sometimes known as the 'Polypodiaceae', and partly in response to the increasing number of herbaceous angiosperms. The origins of the

Polypodiaceae are not clear but they first appear unequivocally in the Tertiary fossil record (Collinson, 1986a). Today, the Polypodiaceae have spread around the world, into all but the most inhospitable environments, and their diversification and proliferation is in many ways analogous to that of the angiosperms.

Although most Mesozoic groups of ferns have survived to the present day, albeit with restricted diversity, there is one notable exception. The Tempskyaceae was an unusual group of tree ferns that flourished in late Mesozoic times, but became extinct towards the end of the Cretaceous Period. Some members of the group grew up to 6 m tall but did not have a true trunk. Rather, there was a false trunk consisting of intertwined stems and roots. Modern tree ferns have large fronds that form an apical crown to the plant. However, *Tempskya* had what were probably small fronds that were spread over the upper part of the trunk. We know nothing of the reproductive biology of these plants and so their affinities are unknown.

Water ferns (Marsiliales, Salviniaceae) first appear in the fossil record in late Mesozoic times. Although very small plants, they had a high potential to become fossilized, because they lived in water and we have consequently a good record of the group for the Tertiary sub-Era.

More comprehensive reviews of post-Palaeozoic ferns can be found in Tidwell and Ash (1994) and Collinson (1996a) (see also Chapter 3 of the present volume).

### Gymnosperms

The Mesozoic Era was a time of maximum diversity and abundance for those groups of gymnosperms with large, usually dissected leaves, and their foliar remains dominate many floras of this age. However, they underwent a rapid decline during the later part of the Mesozoic Era as the angiosperms came to dominance, and today there are only two groups remaining, the Cycadales and Gnetales.

The cycads and bennettites are often regarded as typifying Mesozoic vegetation. Their foliage looks superficially similar, although there are important anatomical differences that can be recognized if cuticles are preserved. More importantly, they had fundamentally different reproductive structures and it is now clear they were only very distantly related. Other major



groups of large-leafed gymnosperms that are typical of the Mesozoic Era, and which occur at GCR sites described in this volume, are the Leptostrobales (alternatively known as the Czekanowskiales) and Caytoniaceae. However, all of these groups except the cycads became extinct by the end of the Mesozoic Era. Further details of these plants can be found in the introduction to Chapter 3.

The conifers have in contrast remained important elements of the land vegetation through to the present day, although competition with angiosperms has tended to push them more to higher latitude floras. Conifers had started to become abundant during the Permian Period but, like the ferns, underwent a dramatic decline at the Permian–Triassic boundary. Following this decline, however, many new conifer families rapidly appeared, including most of those that are still with us today (Miller, 1988). The only modern family that was relatively late to appear was the Cupressaceae, whose oldest known examples are early Tertiary in age.

There are a number of other now extinct families of conifer that have been recognized in the Mesozoic Era. Most are only known from a few fragmentary remains of cone showing distinctive structures. However, one family is better known and was clearly a major component of Late Triassic to Early Cretaceous vegetation, the Cheirolepidiaceae (Watson, 1988). These trees seem to have favoured flat coastal fringes throughout much of the world, except for the northern high latitudes. They declined rapidly in the Late Cretaceous, possibly because rising sea levels drowned their favoured habitats around the coasts, and they became extinct by the end of the Cretaceous Period.

Another typically Mesozoic group of gymnosperms is the ginkgos. Leaves, many of which look remarkably like those of the one still-living species *Ginkgo biloba* L. (the maidenhair tree), are found in Mesozoic rocks throughout much of the world. It was clearly a dominant plant of the time but, like some of the other gymnosperms, seems to have suffered from competition with the angiosperms in the later part of the Mesozoic Era. By modern times, they had almost become extinct and seem to have survived mainly because Chinese and Japanese monks regarded the maidenhair tree as sacred and planted them in their temple gardens. Today, the maidenhair tree is making somewhat

of a comeback as it is proving very adaptable to gardens and parks, and has been widely planted in Europe, North America and the Far East. Further details of the living maidenhair tree and its fossil ancestors can be found in Hori *et al.* (1997).

### Angiosperms

Flowering plants now constitute the dominant plant group, with at least 240 000 extant species. They live in a greater range of environments, show a greater range of growth habits and morphological variation, and are represented by more families, genera and species than any other group of living vascular plants. They are the basic diet of most herbivorous animals, and humans rely on them for agriculture, horticulture, wood and many pharmaceutical products.

The definition of what makes a flowering plant might seem easy, but it is not. Many do not have the showy flowers normally associated with angiosperms, the most obvious examples being grass. In fact, no single character can be used to define the angiosperms, but the following features, when taken together, are usually regarded as evidence of angiosperm affinity (Friis *et al.*, 1987, pp. 1–6).

1. Pollen with clear apertures combined with a tectate columellate wall organization.
2. Leaves with a reticulate venation, with an ordered pattern of vein hierarchy (stronger to weaker veins) often with ultimate free-ending veinlets.
3. Wood with vessels (in rare cases of doubt detailed anatomical study is usually conclusive).
4. Flowers with closed carpels and receptive stigmas.
5. Fruits as products of closed carpels with receptive stigmas.
6. Seeds contained within fruits, or being bitegmic (resulting from two protective layers around the embryo sac), or as possessing endosperm (unique to angiosperms as a product of double fertilization).

The higher dicotyledonous flowering plants (known as the 'Eudicot' clade) are easily recognized, especially by their pollen having three or more apertures. However, basal angiosperms



can be harder to recognize. For instance, vessels occur in some ferns and the gymnosperms *Gnetum*, *Ephedra* and *Welwitschia*, but are absent from the angiosperms *Tetracentron* (Hamamelideae) and some of the Winteraceae (Magnoliales). Some ferns (e.g. *Hausmania*) and gymnosperms (e.g. *Sagenopteris*, *Gnetum*) have laminated leaves with reticulate venation (although not with the hierarchical pattern seen in angiosperms), while many angiosperms have other types of venation. Some angiosperms have non-ectate pollen, while some conifers, notably the Cheirolepidiaceae, are known to have ectate pollen (although not the apertures seen in angiosperm pollen). Nevertheless, even with these exceptions, the six characters provide at least a general guide to the angiospermous affinities of plant fossils.

The origin of angiosperms remains a hotly debated issue. The oldest macrofossils that have reasonable angiosperm credentials are from the very Late Jurassic or Early Cretaceous rocks of China (Sun *et al.*, 1998), although there are also some possible earlier remains such as the leaf from the Middle Jurassic strata of Stonesfield (see Chapter 3). However, it has been argued that the group started earlier in the Mesozoic Era or possibly even in Late Palaeozoic times (e.g. Anderson and Anderson, 1997). In this scenario, the absence of angiosperm remains from the fossil record in these earlier strata is a result of their early evolution in 'upland' habitats, which are less likely to be preserved in the fossil record. Whatever the explanation, angiosperms do not become important components of the fossil record until Late Cretaceous times. Because the Late Cretaceous strata in Britain are exclusively marine (deposits of this age being formally referred to as 'the Chalk' owing to the fact that such strata in western Europe are dominantly composed of this marine rock type), the earliest good evidence of angiosperms in this country is not until the early part of the Tertiary sub-Era, when they dominate the plant macrofossil assemblages (see Chapter 7). For further discussions on the evolutionary history of angiosperms, see Beck (1976), Friis *et al.* (1987), Hughes (1994), Crane *et al.* (1995) and Taylor and Hickey (1996).

### PALAEOBOTANICAL PROBLEMS

Palaeobotany suffers somewhat different problems from other branches of palaeontology

owing to the ease with which plants fragment after death and the different ways the fragments can become fossilized (Figure 1.1). The study of the fossilization processes is often referred to as 'taphonomy' (Bateman, 1991).

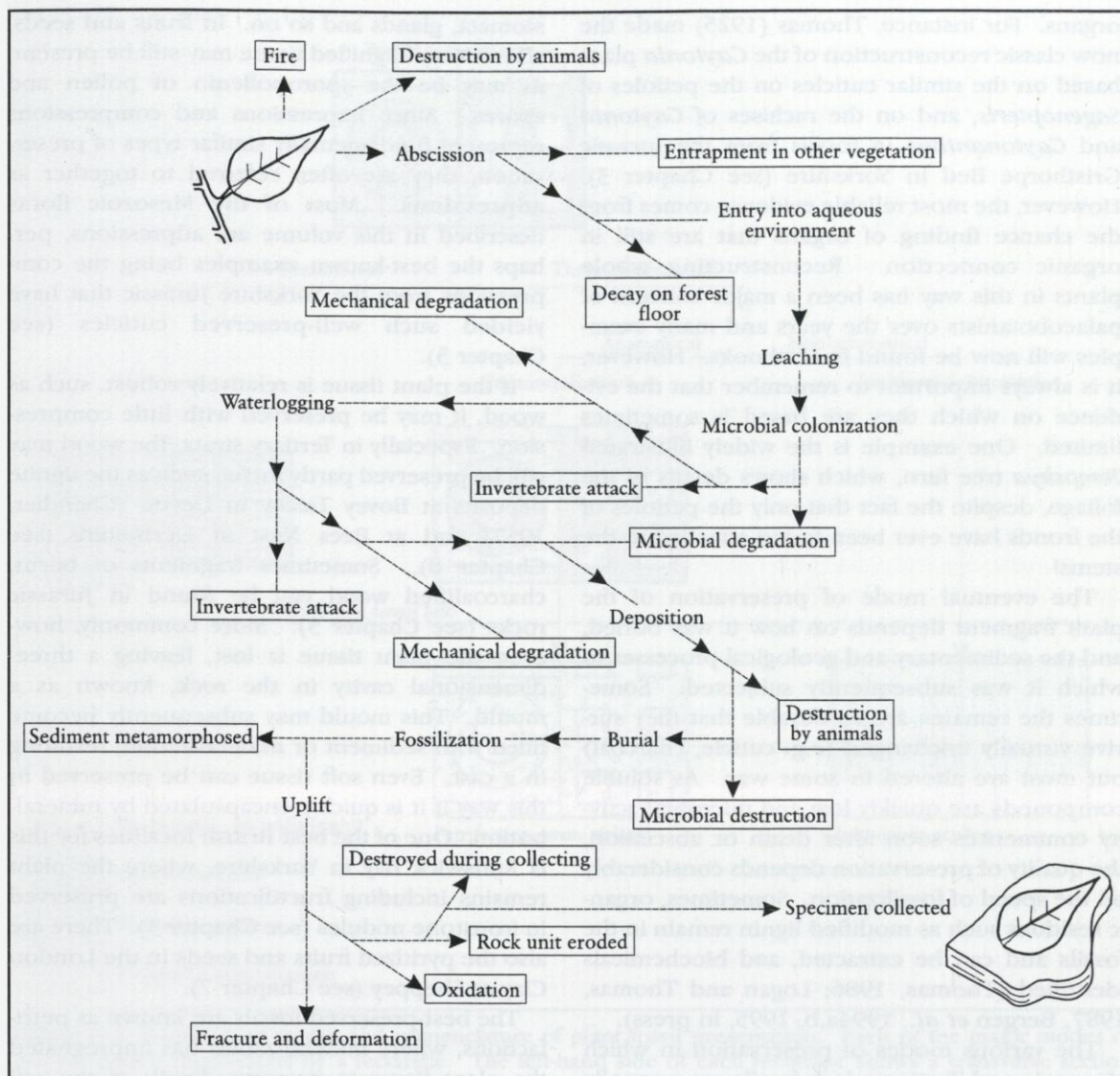
### Plant taphonomy

Plants are rarely preserved where they grew. There can be exceptions, such as the fossil conifer forests at Kingbarrow on the Isle of Portland. However, most plant fossils represent fragments that have become 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, such as the shedding of leaves or twigs, or the dispersal of seeds, pollen or spores as part of the reproductive cycle (Thomas and Cleal, 1999). Alternatively, the detachment may have been traumatic, perhaps through storm damage or flood damage. Whatever the means of detachment, however, the fragment will usually then be transported by a combination of air (wind) and water (river-flow, current, tide) to its eventual resting place in sediment or will form peat. This place of burial will normally be subaqueous, such as a lake or other non-marine standing body of water, or occasionally under 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 fossilized. 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 that 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, separation through having different buoyancies, 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 (e.g. Spicer and Hill, 1979).

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





**Figure 1.1** The potential process involved in a plant fragment passing into the fossil record. (After Thomas and Spicer, 1987, fig. 4.1.)

to places of active deposition. Although the more durable parts (e.g. wood) stand a greater chance of not being eaten or of decaying, it is the lighter and less rigid parts (e.g. leaves, fruits, seeds) that are most commonly found as identifiable fossils (Hughes, 1994). This is partly because the plants produce such parts more abundantly. It is a combination of availability, and the durability, of plant parts that controlled the chances of their being fossilized.

## Specimen preservation

Only small plants are preserved whole and then

only in exceptional circumstances; large plants are never preserved whole. Most extinct plants must therefore be reconstructed from direct or indirect evidence in the fossil record (Chaloner, 1986). Experience has shown that the association of dispersed organs is not, on its own, proof that they were once parts of a single plant. Continual association with the exclusion of other species of the same genera can be a strong pointer, especially if the association is confirmed to be real by mathematical analysis (e.g. Spicer and Hill, 1979). However, this still needs to be backed-up by the presence of distinctive anatomical or morphological characters on different



organs. For instance, Thomas (1925) made the now classic reconstruction of the *Caytonia* plant based on the similar cuticles on the petioles of *Sagenopteris*, and on the rachises of *Caytonia* and *Caytonanthus* in fossils from the Jurassic Gristhorpe Bed in Yorkshire (see Chapter 3). However, the most reliable evidence comes from the chance finding of organs that are still in organic connection. Reconstructing whole plants in this way has been a major concern of palaeobotanists over the years and many examples will now be found in textbooks. However, it is always important to remember that the evidence on which they are based is sometimes limited. One example is the widely illustrated *Tempskya* tree fern, which shows details of the foliage, despite the fact that only the petioles of the fronds have ever been found attached to the stems!

The eventual mode of preservation of the plant fragment depends on how it was buried, and the sedimentary and geological processes to which it was subsequently subjected. Sometimes the remains are so durable that they survive virtually unchanged (e.g. cuticle, charcoal) but most are altered in some way. As soluble compounds are quickly lost and microbial activity commences soon after death or abscission, the quality of preservation depends considerably on the speed of fossilization. Sometimes, organic residues such as modified lignin remain in the fossils and can be extracted, and biochemicals identified (Thomas, 1986; Logan and Thomas, 1987; Bergen *et al.*, 1994a,b, 1995, in press).

The various modes of preservation in which Mesozoic and Tertiary plant fossils are normally found are summarized in Figure 1.2. The most common are adpressions, where the plant fragment has been subjected to vertical pressure from overlying sediment. If the plant tissue has been lost and all that is left is the impression of the plant in the rock matrix, the fossil is known as an **impression**. However, if the compressed plant tissue is still remaining in the form of a thin, coalified layer (known as a phytolite) the fossil is known as a **compression** (the counterpart of a compression after the rock has been split is usually an impression). Compressions have the advantage that, provided there has not been significant thermal or chemical alteration, some original plant material may be preserved. In leaves, the cuticles can be separated from the fossil and may show considerable detail of the epidermal structure of the plant including hairs,

stomata, glands and so on. In fruits and seeds, scleratic and lignified tissue may still be present, as may be the sporopollenin of pollen and spores. Since impressions and compressions represent fundamentally similar types of preservation, they are often referred to together as **adpressions**. Most of the Mesozoic floras described in this volume are adpressions, perhaps the best-known examples being the compressions from the Yorkshire Jurassic that have yielded such well-preserved cuticles (see Chapter 3).

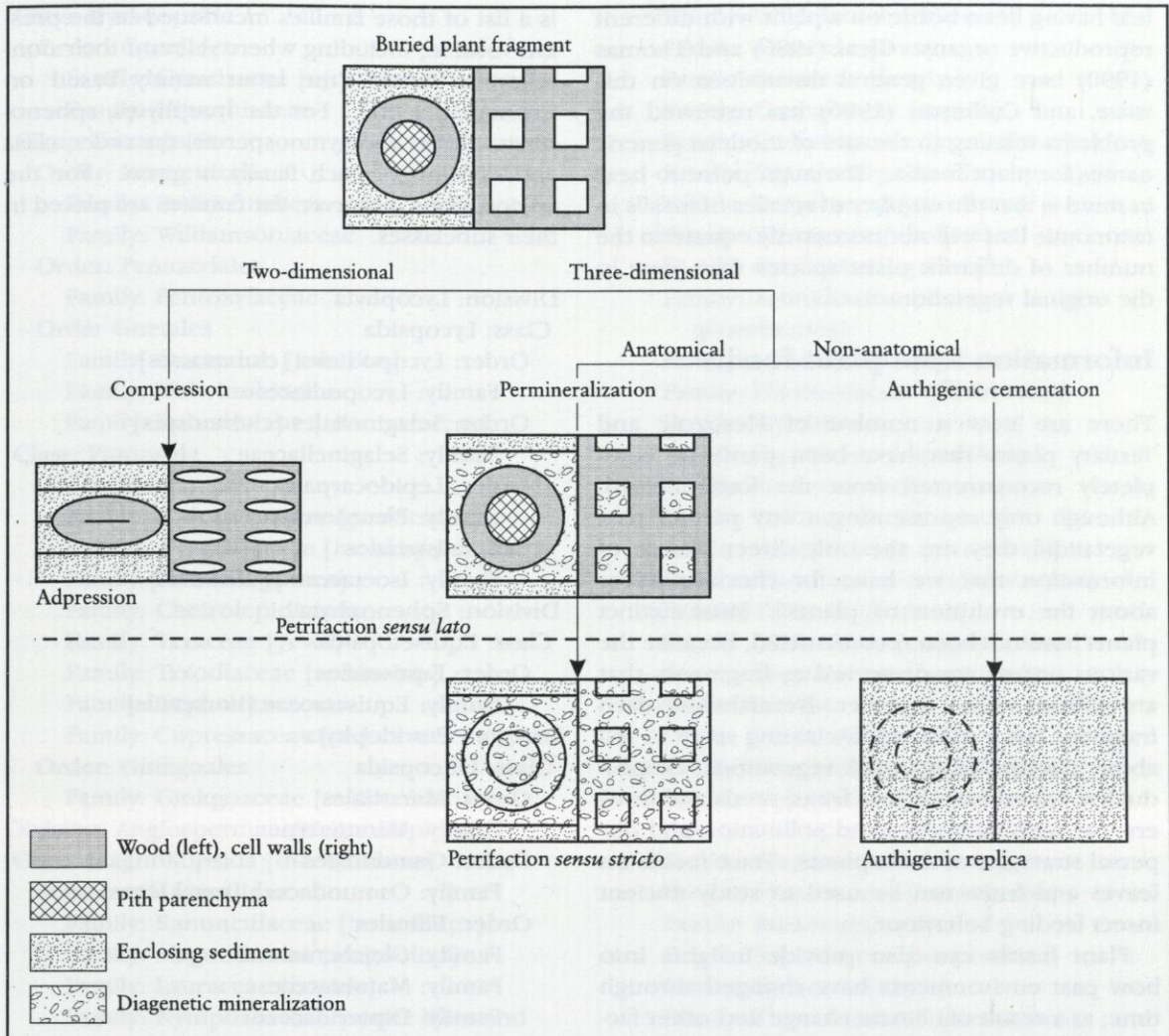
If the plant tissue is relatively robust, such as wood, it may be preserved with little compression. Especially in Tertiary strata, the wood may still be preserved partly intact, such as the lignite deposits at Bovey Tracey in Devon (Chandler, 1957) and at Bees Nest in Derbyshire (see Chapter 8). Sometimes fragments of burnt, charcoaled wood can be found in Jurassic rocks (see Chapter 3). More commonly, however, the plant tissue is lost, leaving a three-dimensional cavity in the rock, known as a mould. This mould may subsequently become filled with sediment or mineralization, resulting in a cast. Even soft tissue can be preserved in this way if it is quickly encapsulated by mineralization. One of the best British localities for this is Runswick Bay in Yorkshire, where the plant remains including fructifications are preserved in ironstone nodules (see Chapter 3). There are also the pyritized fruits and seeds in the London Clay at Sheppey (see Chapter 7).

The best-preserved fossils are known as petrifications, where mineralization has impregnated the plant tissue to preserve details of the cell structure. Unlike in the Palaeozoic Era (Cleal and Thomas, 1995), petrifications are not especially common in the British Mesozoic or Tertiary strata. The best-documented Mesozoic petrifications are from the Jurassic rocks of the Rajmahal Hills in India (reviewed by Agashe, 1995). The most notable British Mesozoic petrifications are in the Purbeckian rocks of the Isle of Portland, although the floras here are relatively low in diversity. Some of the pyritized fossils in the London Clay also show evidence of preserved cell structure.

### Naming plant fossils

It is clearly vital to have a consistent means of naming plant fossils, especially when comparisons are to be made between floras from





**Figure 1.2** 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 stylized rectangular cells. (After Bateman, 1991, fig. 2.2.)

different localities. The problem is that a fossil cannot be named in exactly the same way as a living plant, because it only represents a fragment of the original living organism. We may have a well-preserved fossil leaf, but we often do not know what reproductive organs would have been borne on the same plant or what the anatomy of its stems was. 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. The scheme is broadly similar to that used for living plants and laid out in the *International Code of Botanical Nomenclature* (Greuter *et al.*, 2000),

but provides for different parts of the same plant to be assigned to different morphogenera and morphospecies. For example, a plant of the Caytoniales that has been reconstructed from Jurassic fossils of Yorkshire, has leaves that are called *Sagenopteris phillipsii* (Brongniart) Presl, pollen organs that are called *Caytonanthus arberi* (Thomas) Harris, and fruits that are called *Caytonia nathorstii* (Thomas) Harris. Although there is good anatomical evidence that these types of organ originated from the same natural species of plant (Harris, 1964), they are almost invariably found isolated and so it is more convenient to assign them to different names. There is also the possibility of a similar type of



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leaf having been borne on a plant with different reproductive organs. Cleal (1986) and Thomas (1990) have given general discussions on this issue, and Collinson (1986) has reviewed the problems relating to the use of modern generic names for plant fossils. The main point to bear in mind is that the number of species of fossils in taxonomic lists will not necessarily equate to the number of different plant species that grew in the original vegetation.

### Information from plant fossils

There are now a number of Mesozoic and Tertiary plants that have been partly or completely reconstructed from the fossil record. Although only representing a tiny part of past vegetation, they are the only direct source of information that we have for checking ideas about the evolution of plants. Most extinct plants have not been reconstructed, because the various organs are preserved as fragments that are difficult to link together. Nevertheless, each fragment has a different fascinating story to tell about ancient plants and vegetation. Reproductive structures, such as fruits, seeds and flowers, can help us understand pollination and dispersal strategies of these plants. Trace fossils on leaves and fruits can be used to study ancient insect feeding behaviour.

Plant fossils can also provide insights into how past environments have changed through time, as a result of climate change and other factors. There have been numerous examples of this sort of palaeoecological study, such as those by Spicer and Hill (1979) on the Yorkshire Jurassic succession and Collinson (1983b) on the Tertiary deposits of the Isle of Wight. From such work, it is possible to gain a better understanding of how the structure and biodiversity of vegetational habitats have changed through time. Such work can be extended to an interpretation of regional floras (e.g. Vakhrameev, 1991; Dobruskina, 1994; Collinson, 2000b), palaeoclimates (Allen et al., 1994) 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 but the one used here is essentially that of Cleal and Thomas (1999). The following

is a list of those families mentioned in the present volume, including where relevant their non-scientific names (the latter mainly based on Cronquist, 1981). For the lycophytes, sphenophytes, ferns and gymnosperms, the order, class and division of each family is given. For the angiosperms, however, the families are placed in their subclasses.

Division: Lycophyta

Class: Lycopsidea

Order: Lycopodiales [clubmosses]

Family: Lycopodiaceae

Order: Selaginellales [clubmosses]

Family: Selaginellaceae

Order: Lepidocarpaceae

Family: Pleuromeiaceae

Order: Isoetales

Family: Isoetaceae [quillworts]

Division: Sphenophyta

Class: Equisetopsida

Order: Equisetales

Family: Equisetaceae [horsetails]

Division: Pteridophyta

Class: Filicopsida

Order: Marattiales

Family: Marattiaceae

Order: Osmundales

Family: Osmundaceae [royal ferns]

Order: Filicales

Family: Gleicheniaceae

Family: Matoniaceae

Family: Dipteridaceae

Family: Polypodiaceae

Family: Dicksoniaceae

Family: Schizaeaceae

Family: Cyatheaceae

Family: Tempskyaceae

Family: Dennstaedtiaceae

Family: Aspidaceae

Order: Marsileales

Family: Marsileaceae

Order: Salviniales

Family: Salviniaceae

Family: Azollaceae

Division: Gymnospermophyta

Class: unnamed

Order: Peltaspermales

Family: Peltaspermeaceae

Family: Corystospermeaceae

Order: Czekanowskiales

Family: Czekanowskiaceae

Order: Glossopteridales

Family: Caytoniaceae



## *The systematics of the Plant Kingdom*

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Class: Cycadopsida

Order: Cycadales

Family: Cycadaceae [cycads]

Family: Nilssoniaceae

Class: Gnetopsida

Order: Bennettitales

Family: Bennettitaceae

Family: Williamsoniaceae

Order: Pentoxylales

Family: Pentoxylaceae

Order Gnetales

Family: Gnetaceae [joint-firs]

Family: Welwitschiaceae

Family: Ephedraceae [mormon teas]

Class: Pinopsida

Order: Pinales

Family: Podocarpaceae [podocarps]

Family: Araucariaceae [monkey puzzles]

Family: Pinaceae [pines]

Family: Cheirolepidiaceae

Family: Taxaceae [yews]

Family: Taxodiaceae [redwoods]

Family: Cephalotaxaceae

Family: Cupressaceae [cedars and junipers]

Order: Ginkgoales

Family: Ginkgoaceae [maidenhair trees]

Division: Angiospermae (Magnoliophyta)

Class: Magnoliopsida [dicotyledons]

Subclass: Magnoliidae

Family: Ranunculaceae [buttercups]

Family: Magnoliaceae [magnolias]

Family: Lauraceae [laurels]

Family: Nymphaeaceae [water lilies and water shields] (includes Cabombaceae of some authors)

Family: Papaveraceae [poppies]

Family: Menispermaceae [moonseeds]

Family: Sabiaceae [sabras]

Family: Annonaceae [custard apples]

Subclass: Hamamelidae

Family: Platanaceae [plane trees]

Family: Cercidiphyllaceae [katsura trees]

Family: Fagaceae [beeches]

Family: Hamamelidaceae [witch hazels]

Family: Ulmaceae [elms]

Family: Juglandaceae [walnuts]

Family: Trochodendraceae [yama-kuruma]

Family: Moraceae [mulberries]

Family: Myricaceae [bayberries]

Family: Urticaceae [nettles]

Family: Betulaceae [birches]

Subclass: Caryophyllidae

Family: Caryophyllaceae [pinks]

Subclass: Dilleniidae

Family: Dilleniaceae [dilleniads]

Family: Theaceae [teas]

Family: Ericaceae [heaths]

Family: Capparaceae [capers]

Family: Cucurbitaceae [cucumbers]

Family: Dipterocarpaceae [merantis]

Family: Droseraceae [sundews]

Family: Ebenaceae [ebonies]

Family: Cyrillaceae [cyrillas]

Family: Actinidiaceae [chinese gooseberries]

Family: Epacridaceae [epacris]

Family: Flacourtiaceae [flacourtias]

Family: Myrsinaceae [myrsines]

Family: Sapotaceae [sapodillas]

Family: Sterculiaceae [cacaos]

Family: Styracaceae [storaxes]

Family: Symplocaceae [sweetleafs]

Family: Elaeocarpaceae [elaecarpus]

Family: Tiliaceae [lindens]

Family: Clethraceae [pepperbushes]

Family: Begoniaceae [begonias]

Subclass: Rosidae

Order: Fabales [legumes]

Family: Staphyleaceae [bladdernuts]

Family: Celastraceae [bittersweets]

Family: Cornaceae [dogwoods]

Family: Icacinaceae [icacinas]

Family: Rhamnaceae [buckthorns]

Family: Rutaceae [rues]

Family: Sapindaceae [soapberries]

Family: Rosaceae [roses]

Family: Thymelaeaceae [mezerums]

Family: Vitaceae [grapes]

Family: Anacardiaceae [sumac]

Family: Burseraceae [frankincenses]

Family: Euphorbiaceae [spurges]

Family: Linaceae [flaxes]

Family: Lythraceae [loosestrifes]

Family: Meliaceae [mahoganies]

Family: Nyssaceae [sorghums]

Family: Olacaceae [olaxes]

Family: Onagraceae [evening primroses]

Family: Rhizophoraceae [red mangroves]

Family: Aquifoliaceae [hollies]

Family: Haloragaceae [wild milfoils]

Family: Myrtaceae [myrtles]

Family: Alangiaceae [alangiums]

Subclass: Asteridae

Family: Asteraceae [asters]

Family: Oleaceae [olives]

Family: Apocynaceae [dogbanes]

Family: Asclepiadaceae [milkweeds]

Family: Boraginaceae [borages]



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Family: Caprifoliaceae [honeysuckles]  
Family: Bigoniaceae [trumpet-creepers]  
Family: Solanaceae [nightshades]  
Class: Liliopsida [monocotyledons]  
Subclass: Arecidae  
Family: Araceae [arums]  
Family: Arecaceae [palms]  
Subclass: Commelinidae  
Family: Musaceae [bananas]  
Family: Typhaceae [bullrushes]  
Family: Zingiberaceae [gingers]  
Family: Cyperaceae [sedges]  
Family: Juncaceae [rushes]  
Family: Sparganiaceae [bur-reeds]  
Subclass: Alismatidae  
Family: Hydrocharitaceae [water soldiers]  
Family: Alismataceae [water plantains]  
Family: Potamogetonaceae [pondweeds]  
Family: Najadaceae [water nymphs]  
Family: Posidoniaceae [posidonias]  
Family: Ruppiaceae [ditch grasses]

### THE SELECTION OF MESOZOIC-TERTIARY PALAEOBOTANY GCR SITES

This volume describes 51 sites that were selected for the Geological Conservation Review because of their special significance in the study and understanding of Mesozoic to Tertiary palaeobotany in Britain. The general principles guiding GCR site selection are described in the introductory GCR volume (Ellis *et al.*, 1996), but can be encapsulated in three broad components:

- **International** geological importance (e.g. palaeontological 'type' sites and other sites that have achieved informal, but widely held, international recognition).
- Presence of 'classic' or **exceptional** features that are scientifically important (e.g. 'text-book' examples of particular palaeobotanical features or exceptionally rare occurrences).
- Presence of **representative** geological features (e.g. characteristic or typical British palaeobotanical assemblages) that are essential in comprehensively portraying the fossil plant record of Britain.

However, in order to ensure true national importance in the selected *representative* sites, site selection was underpinned by the premise

that the particular 'GCR Block' (site selection category; of which two are relevant here, Mesozoic Palaeobotany and Tertiary Palaeobotany) should be represented by the *minimum number* of sites. Only those sites absolutely necessary to represent the most important aspects of Britain's Mesozoic to Tertiary palaeobotany were therefore selected.

On an entirely practical level, all selected sites must be conservable, meaning in essence: (a) that development planning consents do not exist or else amendments can be negotiated; and (b) that sites are physically viable, for example, in terms of the long-term stability of exposures.

To compile the ultimate site list for the Mesozoic Palaeobotany and Tertiary Palaeobotany GCR Blocks, extensive consultations were carried out with appropriate palaeobotanists, and a large number of sites were assessed before the final listing was produced. There are many problems inherent in producing a truly representative list of nationally important sites that merit conservation. In order to help provide a framework for selecting sites within a GCR Block, the concept of *GCR networks* is applied.

### GCR Networks

GCR Networks are the themes for site selection that link clusters of representative sites within a GCR Block. Five Mesozoic and five Tertiary GCR palaeobotany networks were devised.

#### *Mesozoic palaeobotany GCR networks*

The Mesozoic Era was a time of relatively high sea levels, due to the lack of significant polar ice, and therefore much of the British Mesozoic stratigraphical record is in marine facies that contain few or no plant remains. A notable exception is the Triassic strata, but these consist largely of deposits laid down in arid conditions and so again contain few plant fossils.

Most British sites for Mesozoic palaeobotany can be grouped into the following five GCR networks, representing times when terrestrial conditions became more widespread over these islands:

1. **Rhaetian Stage.** The Rhaetian Stage represents a time of transition between the arid conditions that had persisted throughout most of the Triassic Period,



## The selection of GCR sites

- and the shallow marine conditions of the Early Jurassic Epoch. See Chapter 2.
2. Lower and Middle Jurassic Series of Yorkshire, where extensive river deltas became established, allowing the development of a lush vegetation. See Chapter 3.
  3. Middle and Upper Jurassic Series of southern England, where shallow marine deposits contain remains of a coastal vegetation. See Chapter 4.
  4. Middle and Upper Jurassic Series of Scotland, where evidence of a somewhat different type of vegetation developed than in England. See Chapter 5.
  5. Lower Cretaceous Series. The fluvio-deltaic Wealden deposits have yielded the best British Cretaceous floras. These are supplemented by a single locality in the Upper Greensand. See Chapter 6.

### *Tertiary palaeobotany GCR Networks*

The Palaeogene sites are, with one exception, in the upper Palaeocene to lower Oligocene strata of southern England. There are three classic floras within the succession, each of which has a long history of investigation: the London Clay (early Eocene) flora, the Lower Headon Hill Formation (late Eocene) flora and the Bembridge Marls (Eocene/Oligocene transition) flora. Sites representing these classic floras are complemented by a number of other sites that, although not yielding such diverse floras, are important in providing evidence that helps 'fill in the gaps' between the three classic floras to

provide a more complete palaeobotanical history of Britain. The result is that southern Britain has an unrivalled series of sites showing a transition between tropical forest vegetation and more temperate marsh vegetation. For the purposes of this volume, the Palaeogene palaeobotany GCR sites have been selected for three principal networks:

- Palaeocene Palaeobotany GCR Network, including the Palaeocene–Eocene transition interval (Chapter 7),
- Ypresian–Lutetian Palaeobotany GCR Network (Chapter 8),
- Bartonian–Rupelian Palaeobotany GCR Network (Chapter 9).

The Palaeogene site in the Hebrides, Ardtun, does not easily fit into the division of the three principal Palaeogene GCR networks given above, and it preserves quite different vegetation to that found in England. It has nevertheless been included in Chapter 7 as sole representative of a complementary 'Hebridean Province' Palaeobotany GCR Network.

Very little is known about the Neogene vegetation of Britain, there being only one significant locality for plant macrofossils, Bees Nest in Derbyshire. This site, the sole representative of the Neogene Palaeobotany GCR Network, is dealt with at the end of Chapter 9.

The full list of the Mesozoic and Tertiary palaeobotany GCR sites is given in Table 1.1 and the geographical distribution is summarized in Figure 1.3, overleaf on pages 14 and 15.

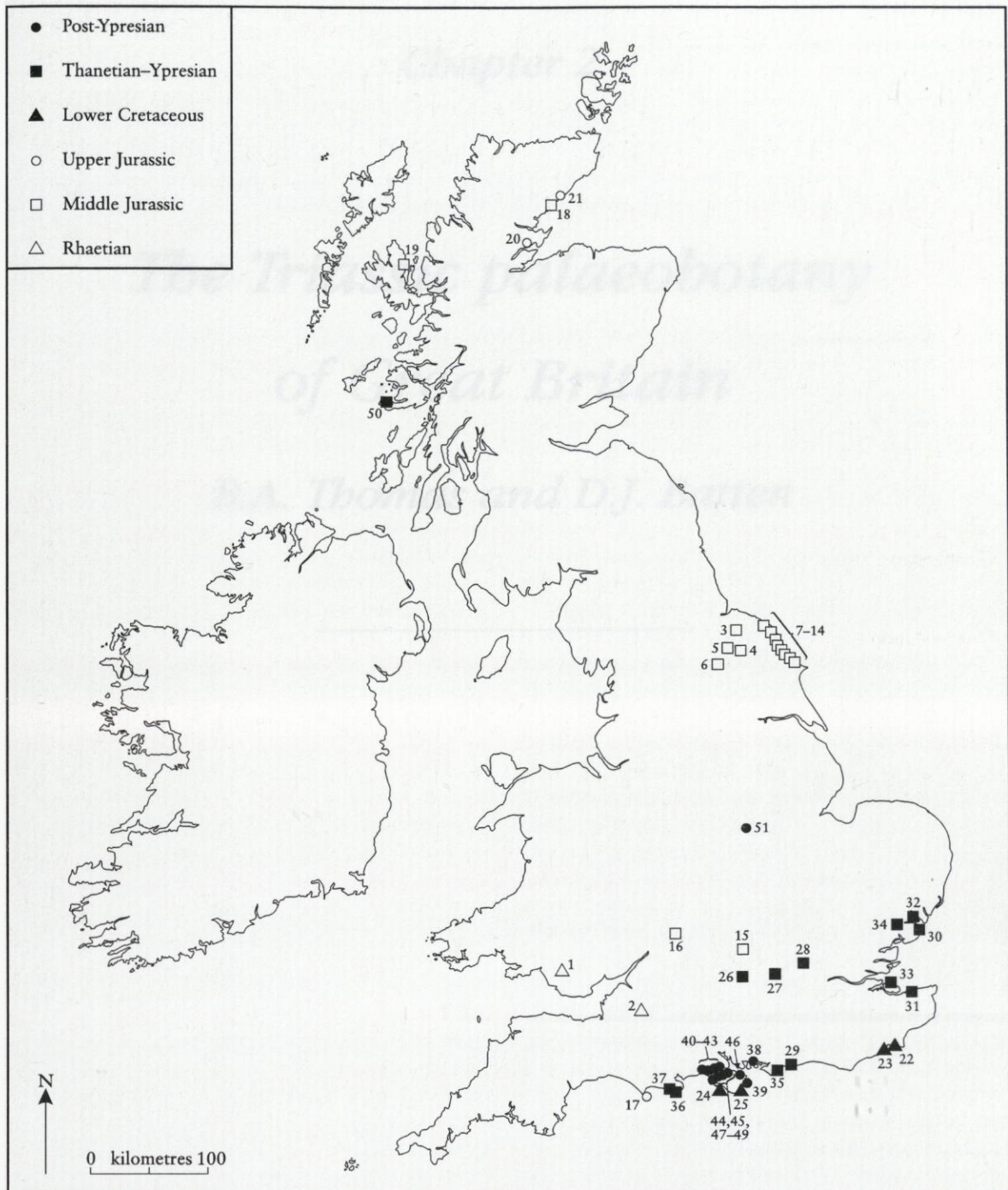


**Table 1.1** Mesozoic and Tertiary Palaeobotany GCR sites

GCR network	Site name	Site number
Rhaetian (Chapter 2)	Cnap Twt	1
	Hapsford Bridge	2
Lower and Middle Jurassic of Yorkshire (Chapter 3)	Roseberry Topping	3
	Botton Head	4
	Broughton Bank (Hasty Bank)	5
	Hillhouse Nab	6
	Hayburn Wyke	7
	Cloughton Wyke	8
	Maw Wyke	9
	Red Cliff (Gristhorpe Bay)	10
	Beast Cliff	11
	Scalby Ness	12
	Whitby–Saltwick	13
	Runswick Bay	14
Middle and Upper Jurassic of southern England (Chapter 4)	Stonesfield	15
	Huntsman's Quarry	16
	Maggot, Kingbarrow and Waycroft quarries	17
	Brora	18
Middle and Upper Jurassic of Scotland (Chapter 5)	Bearrerig River	19
	Eathie Fishing Station	20
	Culgower	21
	Covehurst	22
Lower Cretaceous (Chapter 6)	Cliff End	23
	Hanover Point	24
	Luccombe Chine	25
	Cold Ash	26
Palaeocene and Palaeocene–Eocene Transition (Chapter 7)	Pincent's Kiln	27
	Harefield	28
	Felpham	29
	Walton-on-the-Naze	30
	Herne Bay <sup>1</sup>	31
	Harwich	32
	Sheppey	33
	Wrabness	34
Ypresian–Lutetian ('early and middle Eocene', Chapter 8)	Bognor Regis	35
	Lake	36
	Arne	37
	Bracklesham	38
	Whitecliffe Bay	39
	Highcliffe	40
	Barton	41
	Hordle Cliffs	42
	Paddy's Gap	43
	Headon Hill and Totland Bay	44
Bartonian–Rupelian ('upper Eocene–early Oligocene' (Chapter 9)	Colwell Bay	45
	Chapel Corner	46
	Thorness Bay	47
	Hamstead Ledge	48
	Bouldnor Cliff	49
	Ardtun	50
	Bees Nest	51

<sup>1</sup> Herne Bay is also described in Chapter 8

## The selection of GCR sites



**Figure 1.3** The distribution of the Mesozoic and Tertiary palaeobotany GCR sites. See Table 1.1 for site names.