# Chapter 5 Lower Carboniferous

The Early Carboniferous saw few really significant phylogenetic changes in terrestrial plants; rather it was a time of consolidation of the developments that had occurred in the Devonian (Figure 5.1). In particular, there was the diversification of early ferns and fern-like plants (Galtier and Scott, 1985), lycopsids (Thomas, 1978a), equisetopsids (Thomas and Spicer, 1987) and gymnosperms (Rothwell, 1986; Rothwell and Scheckler, 1988). The development of the latter was a major advance in the evolution of terrestrial vegetation, as they were the first plants that were not constrained by their reproductive biology to moist habitats, and could thus take advantage of the extra-basinal or 'upland' areas. The Early Carboniferous also saw the development of the earliest extensive forests, first in equatorial latitudes (Long, 1979a), and then in northern high latitudes (Meyen, 1982); forests did not develop in the southern high latitudes until the end of the Late Carboniferous, probably due to the influence of a polar ice-cap (Retallack, 1980).

There are marked differences in the plant fossils from the Lower and the Upper Carboniferous. This not just at the rank of species or even form-genus: taxa such as the Calamopityales and Archaeocalamitaceae have not been identified with certainty from above the Lower Carboniferous (although see Mamay and Bateman, 1991 for a possible exception); whereas the Trigonocarpales, the Callistophytales and the Cordaitanthales are more or less restricted to the Upper Carboniferous (Cleal, 1993). For this reason, the palaeobotany of the two subsystems of the Carboniferous are treated separately in this volume.

## Palaeogeographical setting

As in the Devonian, Britain in the Early Carboniferous was on the southern margins of the Laurussian continent and was very close to the equator (Figure 5.2). The Gondwanan continent was progressively drifting north and eventually, in the Late Carboniferous, collided with Laurussia to form the Pangaea 'super-continent', which extended from the south pole to high northern latitudes; but, in the Early Carboniferous, the two landmasses were still separate.

It was once thought that Lower Carboniferous plant fossils indicated a globally uniform *Lepidodendropsis-Rhacopteris-Triphyllopteris* flora for that time (Jongmans, 1952). Subsequent work by Raymond (1985) and Raymond and Parrish (1985) has revealed some evidence of provincialism. The extent of floristic differentiation was exaggerated in these studies, because most of the southern latitude (Gondwanan) assemblages used by Raymond and her co-workers are in fact from the Upper Carboniferous (Wagner *et al.,* 1985). It is nevertheless possible to recognize two discrete palaeokingdoms: the Angaran Palaeokingdom, representing northern high latitude vegetation, and the Euramerian Palaeokingdom for equatorial and southern high latitude vegetation (Figure 5.2). The British assemblages belong to the latter.

Much of Britain at this time was covered by shallow seas, which resulted in extensive carbonate deposits that contain few well-preserved terrestrial plant fossils. There were also some areas of land, however, such as the St George's island extending over much of Wales and the English Midlands, and the Caledonian landmass in northern Scotland. Deltaic, lagoonal and shallow marine deposits on the margins of these land areas have yielded a variety of plant fossil assemblages. The Scottish deposits are particularly significant, as they were influenced by contemporaneous volcanic activity, resulting in the extensive suite of petrifaction sites in this region.

## Stratigraphical background

Kidston (1894a) and Gothan (1913, 1952) argued that there is a sharp Floral Break or 'Florensprung' between the Lower and Upper Carboniferous. Subsequently, there have been disagreements as to exactly how sharp the change really is and at what stratigraphical level it occurs (see, for instance, papers by Havlena, Wagner, and Pfefferkorn and Gillespie in Ramsbottom *et al.,* 1982). That there is at least a broad distinction between Lower and Upper Carboniferous plant fossil assemblages is, however, undeniable and provides a convenient division for the discussion of the palaeobotany of this period. In this volume the boundary has been drawn at the Arnsbergian-Chokierian ($E_2$–$H_1$) stage boundary. It thus corresponds approximately with the mid-Carboniferous boundary currently being investigated by the IUGS

Subcommission on Carboniferous Stratigraphy (Lane *et al.,* 1985), rather than with the European Dinantian–Silesian subsystem boundary, which cannot be correlated with any significant palaeobotanical change.

The series and stages referred to in this work (see (Figure 5.3) and (Figure 5.4)) are based on the European chronostratigraphy, and are discussed in detail by George *et al* (1976) and Ramsbottom *et al.* (1978). These references also provide details of the lithostratigraphy of the British Lower Carboniferous.

(Figure 5.3) shows the relationship between this chronostratigraphy and the plant fossil biostratigraphy established by Wagner (1984) for use throughout the equatorial belt (see also Cleal, 1991). Unlike the biostratigraphy used in the Devonian (see Chapter 4), Wagner's scheme is based exclusively on assemblage biozones, established on the ranges of the plant taxa. It nevertheless provides a useful framework for the discussion of changes in plant fossil assemblages through time.

## Early Carboniferous vegetation

There is little evidence of an abrupt change in terrestrial vegetation between the Late Devonian and Early Carboniferous; the fossil record of most of the orders of terrestrial plants that lived in the Early Carboniferous extend back at least to the Upper Devonian (Figure 4.1) and (Figure 5.1). There appears, however, to have been a steady increase in abundance of the vegetation, particularly in the equatorial latitudes. The reason for this is not clear. At the beginning of the Carboniferous, there was a rise in sea-level, which flooded many of the extensive deltas that had developed during the Devonian. This would have reduced the area of swampy lowlands, which were probably still the habitat occupied by most terrestrial vegetation. However, the increased area of sea could also have helped increase precipitation, which would favour more lush vegetation. Another factor may simply have been that vascular plants had become better adapted to a wider range of terrestrial habitats.

Lycopsids were probably the most abundant land plants in the Early Carboniferous (Thomas, 1978a). They are represented in the fossil record by a variety of morphologies, including arbores-cent (Flemingitaceae, Sigillariostrobaceae) and herbaceous (Lycopodiaceae, *Oxroadia* — (Figure 5.5)) forms. The Lepidocarpaceae also show the development of a 'seed-like' reproductive structure, in which each female sporangium contained just a single functional megaspore (Thomas, 1981b). The arborescent forms, in particular, were restricted to swampy habitats, due to limitations in the efficiency of their rooting structures. Within these habitats, however, they appear to have formed extensive forests, although they rarely developed thick peat deposits, as in the Upper Carboniferous coal-forming environments. For taphonomic reasons, lycopsid remains are not particularly abundant in the British Lower Carboniferous record, although there are exceptions such as at Glenarbuck, near Glasgow in Scotland, where there is also, at Victoria Park, the best preserved example of an in *situ* lycopsid fossil forest floor.

The progymnosperms also remained important in the Early Carboniferous, and had a fairly uniform global distribution (Beck, 1976; Stewart, 1981). In contrast to the lycopsids, they seem to have favoured somewhat drier habitats, which they shared with the fern-like plants and pterido-spennous groups (see below). Arborescent forms were common, such as the Archaeopteridaceae and Protopityaceae, the latter being best known from Britain. However, one of the commonest types of fossil foliage found in the British Lower Carboniferous (*Rhacopteris*) may well represent small progymnosperms.

The abundance of *Archaeocalamites* stems and pith casts in Lower Carboniferous rocks suggests that the equisetopsids were common at that time (Crookall, 1969). They were not a particularly diverse group, however, consisting almost exclusively of the Archaeocalamitaceae; the Bowmanitaceae (e.g. *Sphenophyllum*) and Calamostachyaceae (e.g. *Calamites*) are found in the Lower Carboniferous, but only rarely. The archaeocalamitids appear to have been shrubby plants, probably forming thickets around areas of standing water (this may partly explain their abundance in the fossil record). There have been few studies on their fructifications, and as a consequence the position of the family within the Equisetopsida is still a matter of debate, but most of what is known has been determined from British fossil material, both adpression and petrifaction.

The so-called 'pre-ferns' reached their acme in the Early Carboniferous. Their fossil remains are best known from the equatorial latitudes, particularly of Britain and France (Galtier and Scott, 1985; Scott and Galtier, 1985). However, they can only be reliably distinguished from true ferns and some pteridosperms if evidence of the stem and fructification anatomy is available. Since virtually no Lower Carboniferous petrifactions have been reported from Gondwana or Angara, their presence there cannot be entirely ruled out. They seem to have been exclusively herbaceous or possibly shrubby plants. Their foliage approached the form of discrete fronds, but did not develop a fully laminate form as in true ferns.

The earliest occurring order of true ferns, the Botryopteridales, make their first rare appearances in the Early Carboniferous, although did not become important elements of terrestrial vegetation until the Late Carboniferous (Galtier and Scott, 1985; Scott and Galtier, 1985). Most of these early ferns were small, rambling plants. Although their fronds were small, they had started to develop a clearly laminate form. Towards the top of the Lower Carboniferous, the first evidence of arborescent marattialean ferns is found (Pfefferkorn, 1976, although see also Meyer-Berthaud and Galtier, 1986b). These are the oldest known ferns to have developed the arborescent habit, which they achieved by adopting a polystelic strategy to build thick trunks, rather than by the development of thick zones of secondary wood, as in the progymnosperms and gymnosperms. The marattialeans are also the oldest known order of ferns still living today (Cleal, 1993).

Although seed plants first appear in the Late Devonian (Chapter 4), it was not until the Early Carboniferous that they underwent a significant phylogenetic radiation and became important components of terrestrial vegetation (Niklas *et al.,* 1980; Rothwell and Scheckler, 1988). The plant fossils from the Scottish Cementstone Group have been particularly important in demonstrating this radiation, and have shown that a number of families had already appeared by the late Tournaisian. The Early Carboniferous gymnosperms appear to have been mostly of the type traditionally known as pteridosperms (Figure 5.6), (Figure 5.7) and (Figure 5.8). The concept of pteridosperms is now thought to be polyphyletic (e.g. Crane, 1985; Meyen, 1987), but it nevertheless provides a convenient descriptive term for the early gymnosperms with large, fernlike fronds. In the Lower Carboniferous, two orders have been identified, the Lagenostomales and Calamopityales, both of which included arbo-rescent and herbaceous plants (see reconstructions by Retallack and Dilcher, 1988, based mainly on British material).

## Lower Carboniferous plant fossils in Britain

Plant fragments occur sporadically throughout the Lower Carboniferous of Britain, but identifiable assemblages are mainly restricted to sites in Scotland, Wales and the Welsh Borders. These sites fall into two broad categories: those that yield petrifactions sometimes in conjunction with adpressions, and those that yield adpressions alone.

Petrifaction sites can themselves be divided into two main types: those in fluviolacustrine and those in volcanogenic facies (Scott *et al.,* 1984; Scott and Rex, 1987). The former are best represented in Britain by the Cementstone Group of Scotland, which has yielded some of the best known Tournaisian fructifications from anywhere in the world. The volcanogenic sites are also mainly restricted to Scotland (Figure 5.9). By the nature of their genesis, such deposits tend to be of restricted extent. Nevertheless, they include some of the most important Lower Carboniferous palaeobotanical sites in the world, such as the Pettycur Limestone in Fife, the Oxroad Bay Tuff in the Lothians, and the Clyde Plateau Volcanic Formation in Strathclyde.

Very few adpressions have been described from the Tournaisian of Britain. Only one lower Tournaisian site has been recorded, in the Avon Gorge near Bristol (Utting and Neves, 1970), but the material from here has yet to be described in detail. In the Upper Tournaisian, adpressions are known sporadically from the Scottish Cementstone Group, but again there are few published descriptions, other than from Foulden (Scott and Meyer-Berthaud, 1985).

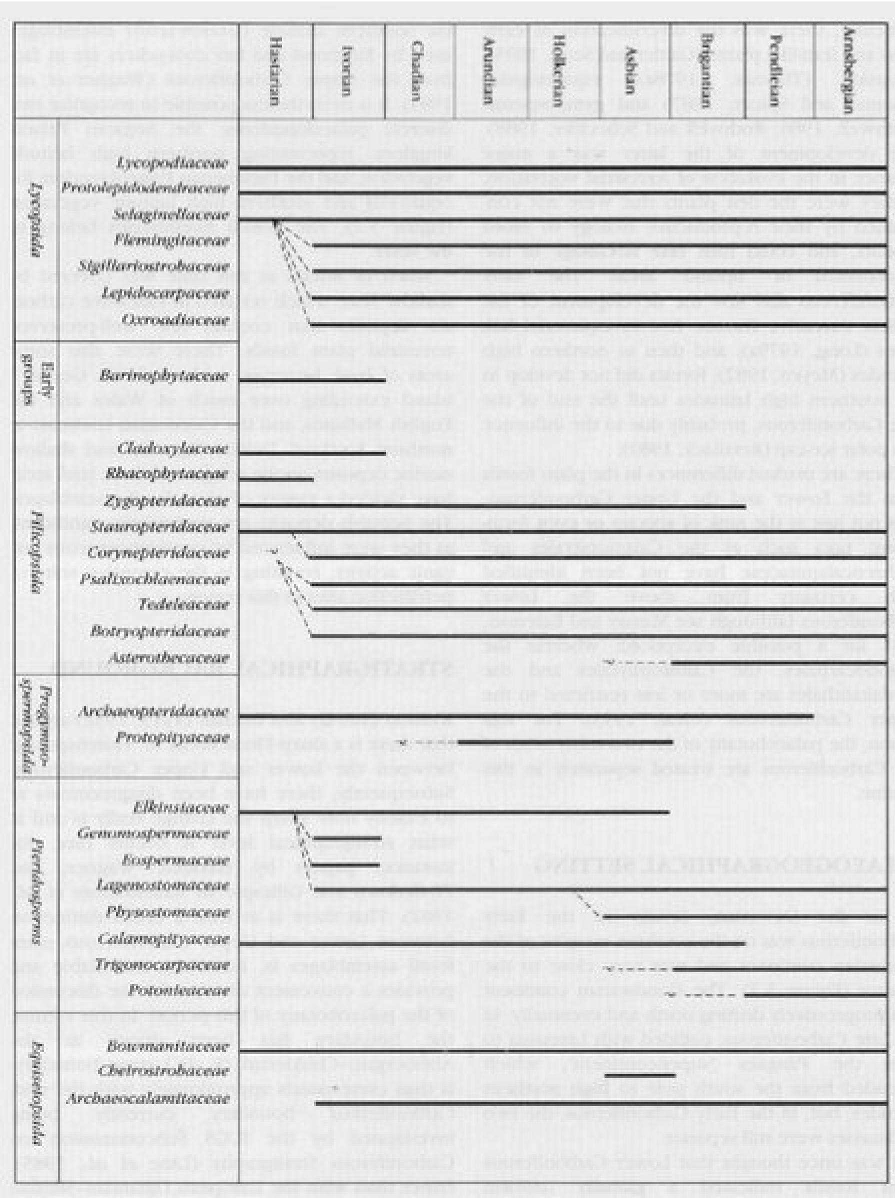
Visean adpressions occur more widely in Britain. In Scotland, some of the best material originated from the Burdiehouse Limestone in the middle Oil Shale Group, but there are no longer any exposures of this horizon that yield plant fossils. However, adpressions can still be found in other parts of the Oil Shale Group, such as the Wardie Shales (Scott, 1985). The Visean strata in the Borders Region of Scotland have also yielded adpressions. On the whole, assemblages from the Borders Region tend to be of restricted composition, although there are exceptions, such as in the Glencartholm Volcanic

Group.

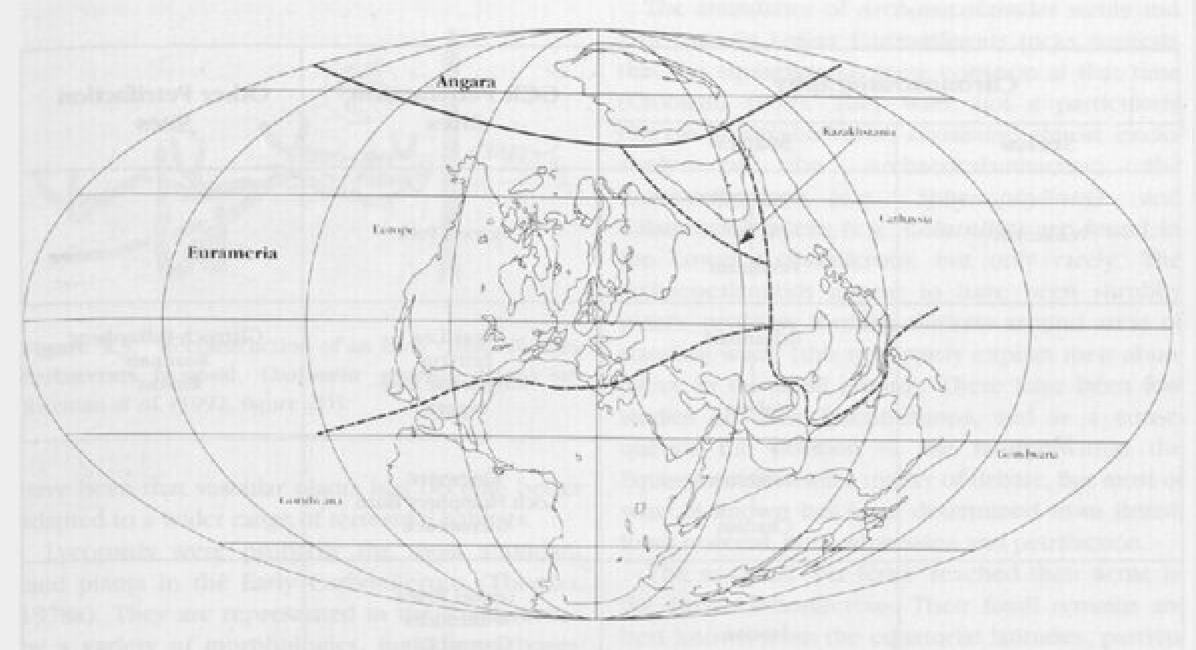
Elsewhere in Britain, Visean plant fossils are best known from North Wales, in particular from the Lower Brown Limestone and Upper Black Limestone groups. There is also the well-known Drybrook Sandstone 'flora' from the Forest of Dean.

Basal Namurian (i.e. Pendleian and Arnsbergian) adpressions are known from southern Scotland (e.g. Walton *et al.,* 1938), Avon (Moore, 1941) and South Wales (Dix, 1934). These assemblages are on the whole restricted in composition, and full descriptions of the material have yet to be published.

**References**




*(Figure 5.1) The distribution of families of vascular plants in the Early Carboniferous. Based on data from Cleal (1993).*




(Figure 5.2) The palaeogeography of the Early Carboniferous, showing the distribution of the major floristic zones (phytochoria). Based on Scotese and McKerrow (1990) and Cleal and Thomas in Cleal (1991).

| Chronostratigraphy: Series | Chronostratigraphy: Stages | Plant Fossil Biostratigraphy | GCR Adpression sites | Other significant Adpression sites (Palaeoequatorial Belt) |
|---|---|---|---|---|
| Namurian | Arnsbergian | *Lyginopteris larischii* | | South Wales[6] Belgium Upper Silesia[5] Zonguldak[7] |
| | Pendleian | *Lyginopteris bermudensiformis/ Lyginopteris stangeri* | | Upper Limestone Group[6] Belgium Upper Silesia[5] Zonguldak[7] |
| Visean | Brigantian | *Lyginopteris bermudensiformis/ Neuropteris antecedens* | Puddlebrook Quarry Moel Hiraddug Teilia Quarry Wardie Shore Glencartholm Loch Humphrey Burn | Horton Group[4] Upper Silesia[5] |
| | Arundian | | | |
| | Chadian | | | |
| Tournaisian | Ivorian | *Triphyllopteris* | | Pocono Formation[1] Geigen near Hof[2] Doberlug-Kirchhain[2] Valdeinfierno[3] Horton Group[4] |
| | Hastarian | *'Adiantites'* | | Pocono Formation[1] Geigen near Hof[2] |

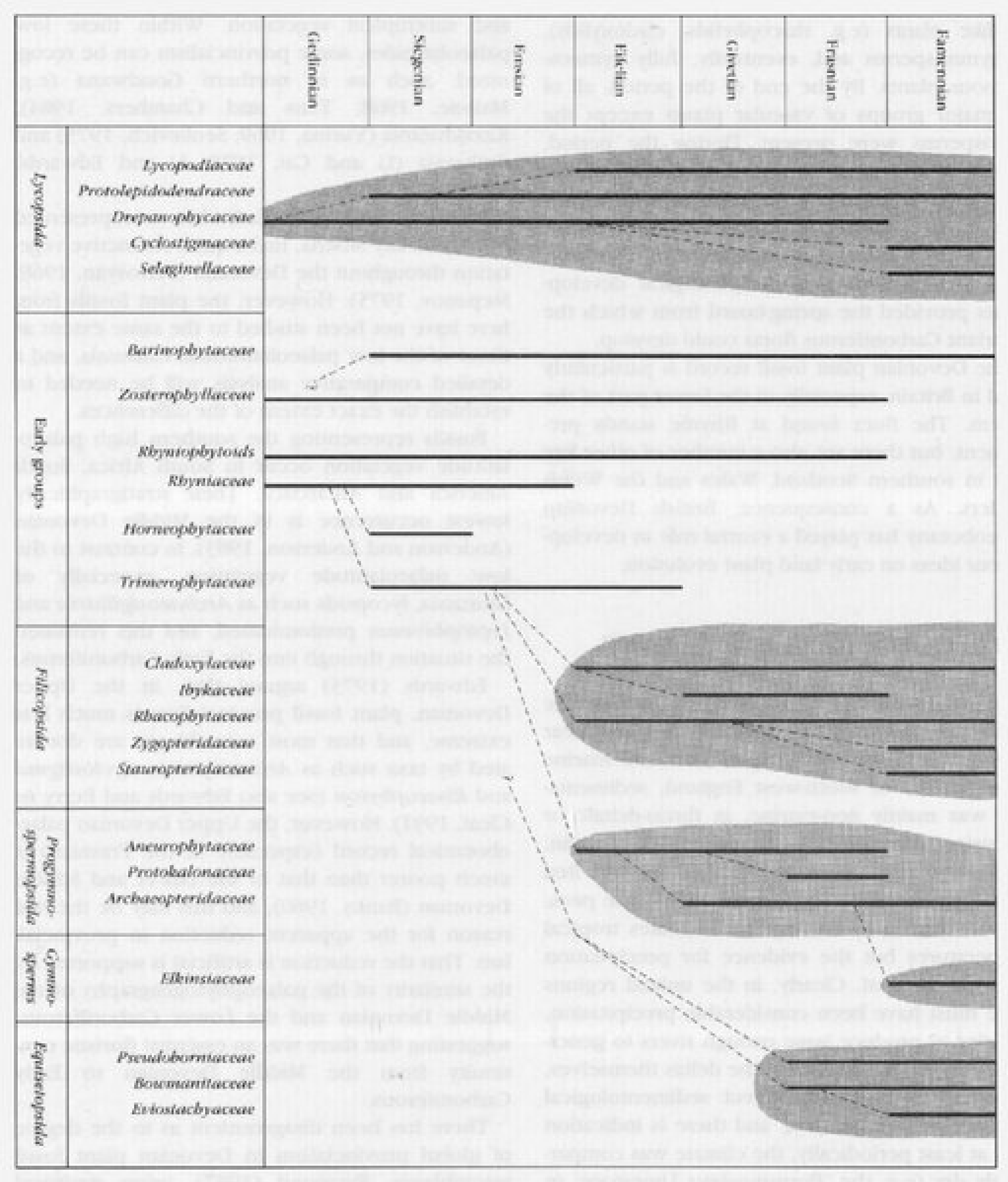
[1] USA [2] Germany [3] Spain [4] Nova Scotia, Canada [5] Poland and Moravia [6] UK [7] Turkey

(Figure 5.3) Chronostratigraphical and biostratigraphical classification of the Lower Carboniferous, and the positions of the GCR and other major palaeobotanical sites in this subsystem (adpressions).

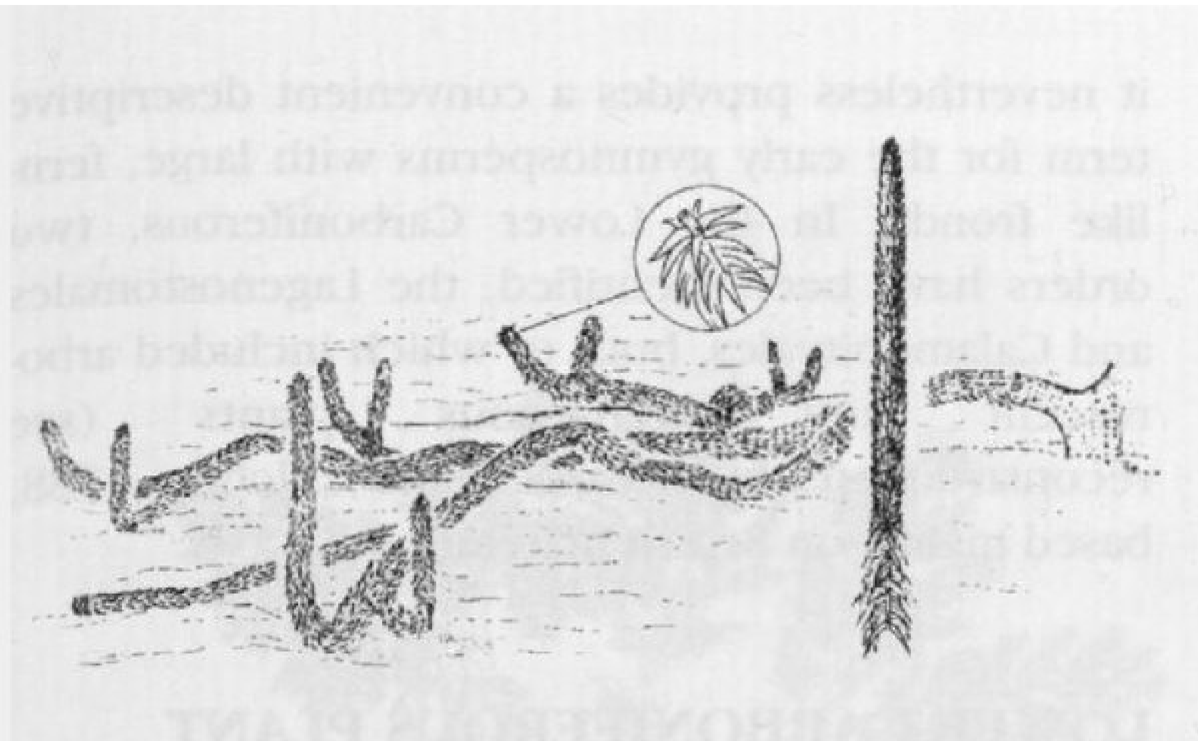
| Chronostratigraphy | | GCR Petrifaction Sites | Other Petrifaction Sites |
|---|---|---|---|
| Series | Stages | | |
| Namurian | Arnsbergian – Pendleian | Victoria Park | |
| Visean | Brigantian – Asbian | Weak Law<br>Pettycur<br>Kingswood End<br>Laggan | Glätzisch-Falkenberg[2]<br>Roannais[1]<br>Esnost[1] |
| Visean | Holkerian – Chadian | Kingwater<br>Loch Humphrey Burn<br>Glenarbuck | |
| Tournaisian | Ivorian | Lennel Braes<br>Whiteadder<br>Oxroad Bay<br>Loch Humphrey Burn | |
| Tournaisian | Hastarian | | New Albany Shale[3]<br>Saalfeld[2]<br>Montagne Noire[1] |

[1] France
[2] Germany
[3] USA

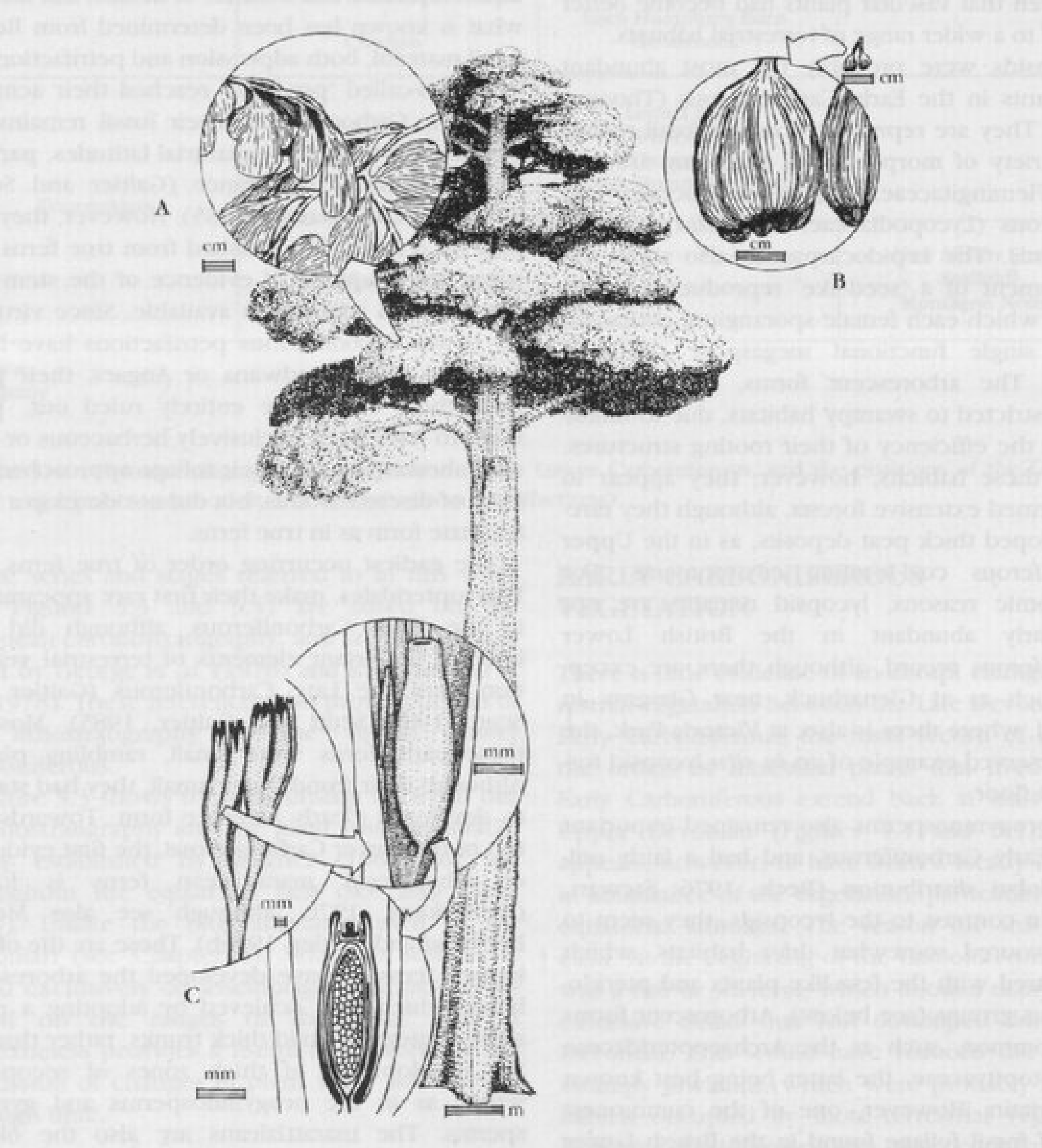
*(Figure 5.4) Chronostratigraphical classification of the Lower Carboniferous, and the positions of the GCR and other major palaeobotanical sites in this subsystem (petrifactions).*



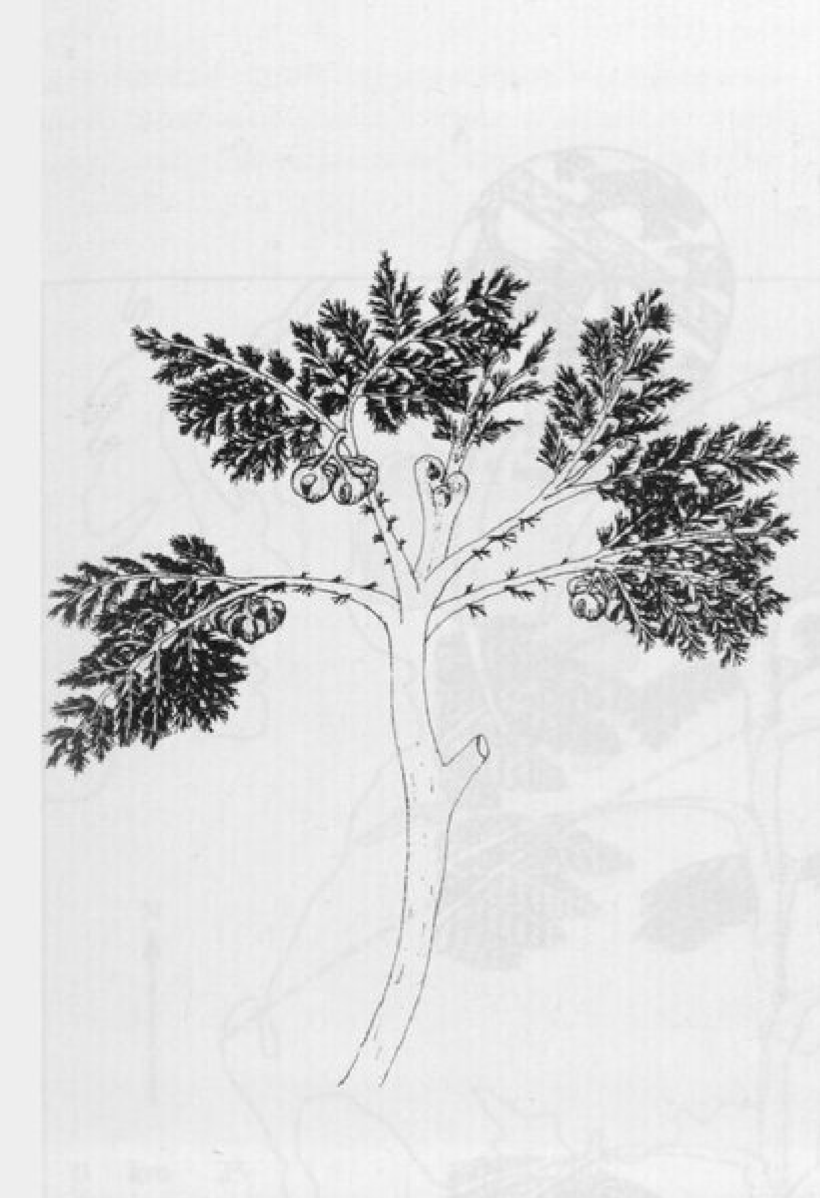

*(Figure 4.1) The distribution of families of vascular plants in the Devonian. Based on data from Cleal (1993).*



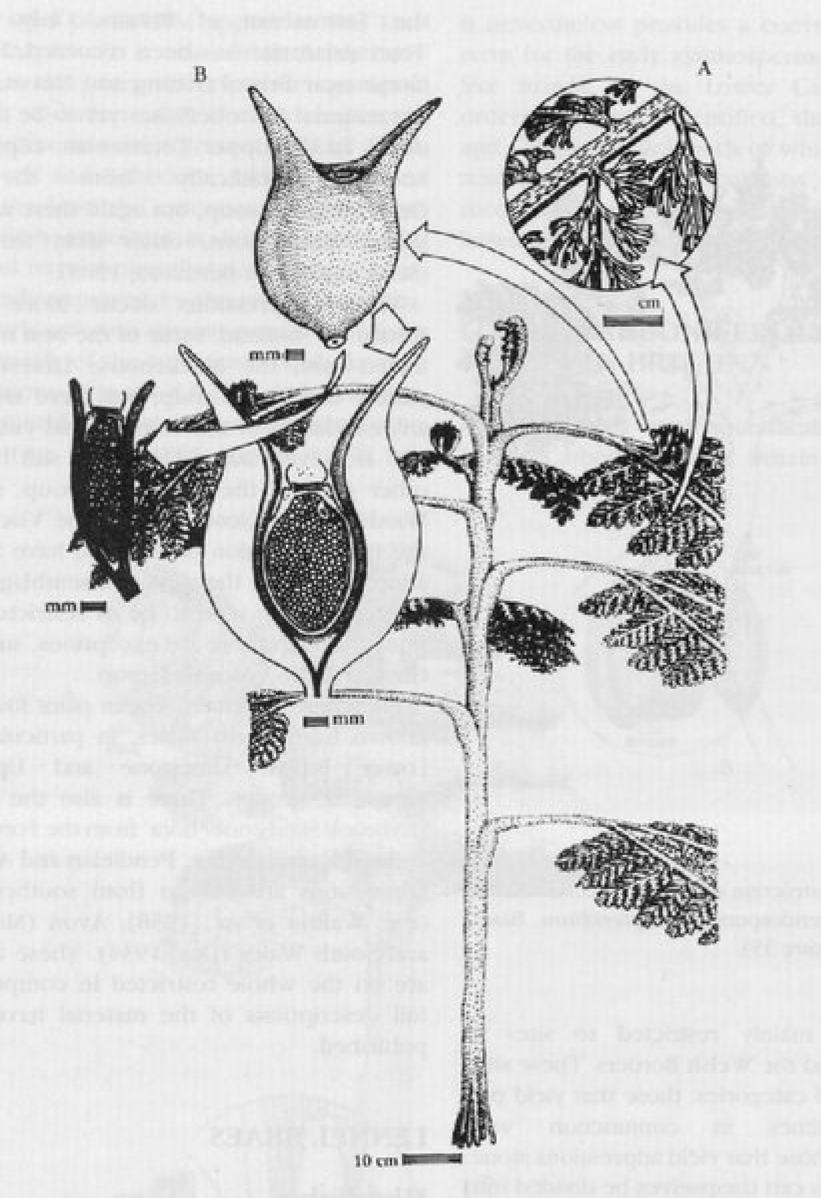
(Figure 5.5) Reconstruction of an Early Carboniferous herbaceous lycopsid, Oxroadia gracilis. Based on Bateman et al. (1992, figure 2D).



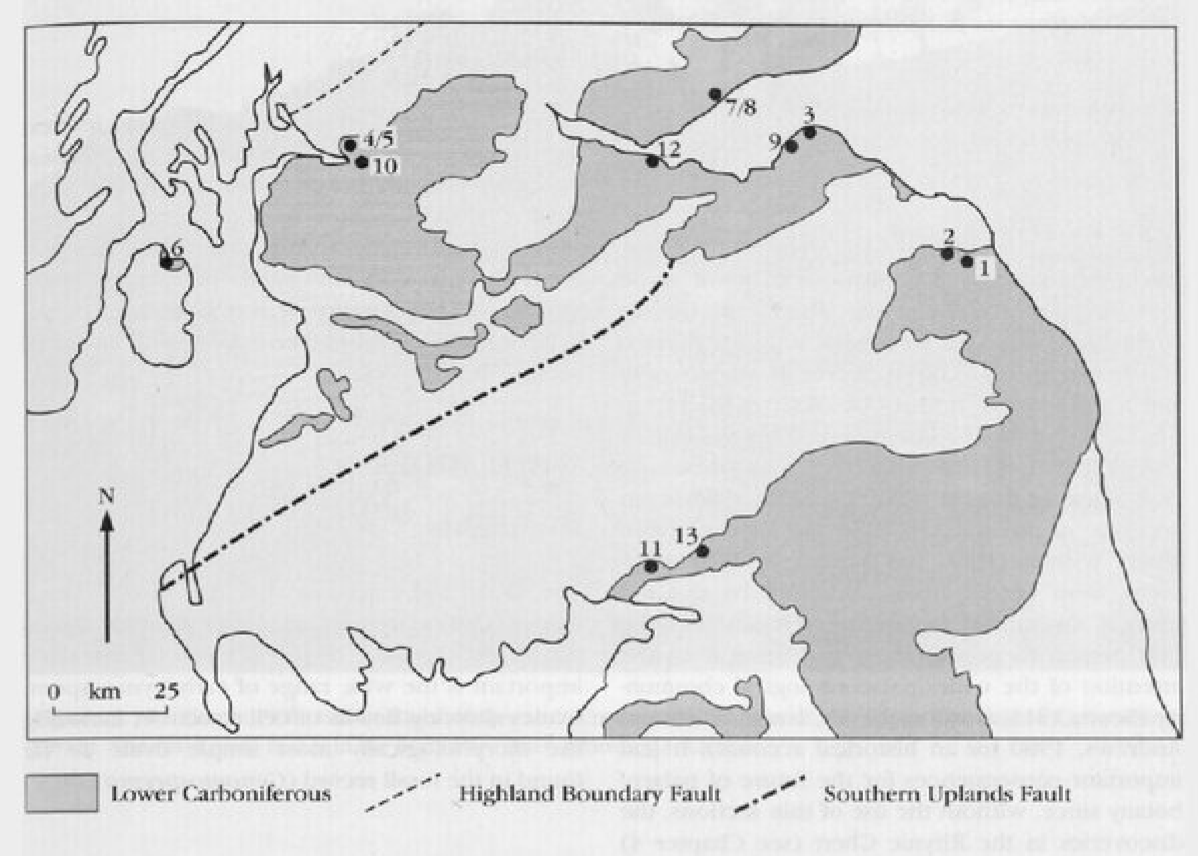

(Figure 5.6) Reconstruction of the Early Carboniferous lagenostomalean pteridosperm tree Stamnostoma, with insets showing details of foliage (A), pollen organs (B) and seeds (C). Based on Retallack and Dilcher (1988).



*(Figure 5.7) Reconstruction of the Early Carboniferous lagenostomalean pteridosperm Diplopteridium. Based on Rowe (1988b, figure 35).*




*(Figure 5.8) Reconstruction of the Early Carboniferous calamopityalean pteridosperm Lyrasperma, with insets showing details of foliage (A) and seeds (B). Based on Retallack and Dilcher (1988).*




*(Figure 5.9) Distribution of Lower Carboniferous rocks in Scotland, showing location of GCR palaeobotany sites. 1 — Lennel Braes; 2 — Whiteadder; 3 — Weak Law; 4 — Loch Humphrey Burn; 5 — Glenarbuck; 6 — Laggan; 7 — Pettycur; 8 — Kingswood End; 9 — Oxroad Bay; 10 — Victoria Park; 11 — Glencartholm; 12 — Wardie Shore; 13 — Kingwater.*