Chapter 6 Upper Carboniferous

The productivity of terrestrial vegetation during the Late Carboniferous was greater than at any other time during the Palaeozoic. This is most clearly seen in the development of thick, coal-forming peats in the tropical lowland habitats the result of dense forests, dominated by lycopsids, ferns and in some cases cordaites (see (Figure 6.3)). However, there is also evidence of extensive vegetation in the tropical extra-basinal areas, as well as in parts of the high latitudes, in Angara and Gondwana (Figure 6.1).

Conditions at this time were clearly favourable for plant life in the tropics (e.g. high levels of precipitation). Probably because of this, there were relatively few major evolutionary innovations in these floras; most major events seem to have occurred in other habitats, such as the tropical extra-basinal habitats (e.g. the appearance of conifers) and at higher latitudes (e.g. the appearance of glossopterids). Nevertheless, the plant fossils found in the Upper Carboniferous tropical deposits are of considerable interest, as they represent the acme of palaeophytic vegetation. They also have a major economic importance, through the hydrocarbon fuels (coals, oil and gas) that they generated. Consequently, the palaeobotany of these strata has been more intensely studied over the years than any other part of the geological column.

Palaeogeographical setting

At the start of the Late Carboniferous, Britain was on the southern margins of the Laurussian continent, positioned near the equator (Figure 6.1). Probably sometime in the late Westphalian or early Stephanian, however, the Gondwanan continent collided with Laurussia to form the Pangaean 'super-continent' that stretched from the south pole to high northern latitudes. During much of the subperiod, a series of major fluvial deltas pro-graded over large areas of present-day northern Europe and eastern North America. The resulting delta-plains provided the substrate for the growth of extensive forests — the very first major tropical rain-forests.

The forests were at their peak during the Westphalian Epoch, and the peat deposits that they produced have resulted in extensive coals. Economically significant Upper Carboniferous coalfields occur throughout the palaeoequatorial belt, from central North America (Arkansas, Kansas), through much of Europe to the Ukraine, as well as in China. The British coalfields belong to what is often called the Paralic Belt, which was a trough or 'valley' that extended from Poland in the east, through northern Germany, the Netherlands, Belgium, northern France to the British Isles and the Maritime Provinces of Canada.

Although largely formed under non-marine conditions, the trough was periodically flooded by eustatic rises in sea level. Coal formation in the Paralic Belt eventually ceased towards the end of the Westphalian or very early Stephanian; the youngest British coals are in the basal Cantabrian (Cleal, 1978, 1984b, 1986c).

During the Namurian and most of the Westphalian, Britain was subject to a hot and wet tropical climate. However, the formation of Pangaea disrupted the oceanic and atmospheric currents, and was at least partially responsible for a change to a significantly arid climate in the tropical regions towards the end of the Carboniferous (Rowley *et al.,* 1985). The collision between Laurussia and Gondwana also caused a degree of topographical uplift of the tropical regions. This in turn made the area less suitable for the growth of the lycopsid-dominated forests, which were physiologically constrained to lowland swamps. The lycopsids in the tropical forests of Pangaea were initially replaced by tree-ferns and pteridosperms, which were still capable of generating considerable peat accumulations. Eventually, in the Permian, the latter were in turn largely replaced by tracts of conifers, better adapted to the drier habitats. However, it is unlikely that these were anywhere near as aerially extensive as the lycopsid forests, and certainly never resulted in any significant peat accumulations. It is interesting to postulate that the reduction in the tropical plant biomass towards the end of the Carboniferous may itself have been a factor causing climatic change, through a 'greenhouse effect'.

There is a marked provincialism in plant fossil distribution in the Upper Carboniferous (Chaloner and Lacey, 1973; Chaloner and Meyen, 1973; Vakhrameev *et al.,* 1978; Meyen, 1987; Chaloner and Creber, 1988; Allen and Dineley,

1988). Four palaeokingdoms are usually recognized (Figure 6.1), each having its own discrete set of plant fossil assemblages. The tropical part of Pangaea, including Britain, belongs to the Euramerian Palaeokingdom, which extended from central North America, through Europe and North Africa, to the Caucasus.

Stratigraphical background

As pointed out in the introduction to the previous chapter, it is convenient to divide this part of the discussion on British palaeobotanical sites into Upper and Lower Carboniferous chapters. This corresponds both to a natural division of the plant fossil assemblages, and to the sub-systemal division currently accepted by the RUGS Subcommission on Carboniferous Stratigraphy.

The marked provincialism of both fossil faunas and floras in the Upper Carboniferous has made it impossible to establish a chronostratigraphy for use throughout the world. Even within the equatorial belt, problems of detailed correlation have prevented agreement on a unified classification; the outline scheme proposed by Bouroz *et al.* (1978) still requires considerable refinement before it becomes a practical stratigraphical tool.

The British Upper Carboniferous is classified according to a modified form of the 'Heerlen Classification', named after the conferences on Carboniferous stratigraphy held at Heerlen between 1928 and 1958 (Wagner, 1974). The part of this chronostratigraphy relevant to the following discussion is summarized in (Figure 6.11), including the revised stage nomenclature outlined by Engel (1989).

Wagner (1984) proposed eleven plant fossil zones for the Upper Carboniferous Eurameria Palaeokingdom, and a twelfth was added by Cleal (1984b). Of these, the top four (Barmen= to Stephanian C in age) are not found in Britain. The remaining eight are shown in (Figure 6.11), with the GCR palaeobotanical sites plotted against them.

Late Carboniferous vegetation

There was a significant change in tropical vegetation between the early and late Carboniferous (the latter represented in (Figure 6.3)), probably due to climatic changes triggered by the growth in the southern polar ice-cap. A number of groups declined or became extinct, such as the archaeocalamites and the callamopityalean pteridosperms, whilst others underwent a major radiation, such as the true ferns (especially the marattialeans), the trigonocarpalean pteridosperms, and the cordaites (Figure 6.2).

As in the Early Carboniferous, lycopsids were the most important component of this vegetation. If the adpression record is viewed in isolation, this is not immediately apparent, as the dominant fossils preserved there tend to be pteridosperms, ferns and equisetes. However, if the coal-forming peat deposits are examined, either by looking at coal-balls (e.g. Phillips, 1980; Phillips and DiMichele, 1992) or palynology (A.H.V. Smith, 1962), it is found that (at least through most of the Westphalian) they are dominated by lycopsid remains. A number of herbaceous forms have been found, which are strikingly similar to the Recent *Selaginella* (Thomas, 1992). However, the best documented Late Carboniferous lycopsids were the arborescent forms (e.g. Flemingitaceae, Lepidocarpaceae, Sigillariostrobaceae — Thomas, 1978a; (Figure 6.4)). They dominated many of the tropical forests and, although they suffered a major decline in Pangaea towards the end of the Westphalian, they continued to be important in Cathaysia through to the end of the Permian Period (Li, 1980). Much of the primary work on the Upper Carboniferous lycopsids was done on fossils from British coal-balls (reviewed by Scott, 1920–1923), and later supplemented by work on adpressions (e.g. Thomas, 1967a, b, 1970, 1974, 1977, 1978a, b). In more recent years, however, work on American fossils has come to the fore, resulting in significant progress in understanding the diversity, reproductive strategies and population dynamics of these arborescent lycopsids (e.g. Phillips, 1979; DiMichele and DeMaris, 1987). It is now clear that the forests were extremely heterogeneous, their composition controlled largely by substrate conditions.

Two orders of equisetopsids are known from the forests: the arborescent Calamostachyales and the herbaceous Bowmanitales. Fossils of the former are particularly common, especially pith casts of the stems (*Calamites*) and foliage (*Annularia, Asterophyllites*). They represent plants that were superficially very similar to the Recent Equisetales, except in

size, reaching heights of ten metres or more (Figure 6.5). However, there are marked differences in their reproductive organs, the calamostachyalean strobili having bracts separating the sporangiophores. Also, the larger stems of the Calamostachyales developed a zone of secondary wood, not seen in the living forms. They are generally thought to have grown along the margins of standing water or on sand bars within streams (Scott, 1977, 1978).

Fossilized foliage of the Bowmanitales (*Sphenophyllum*) is also extremely common. They were exclusively herbaceous, and were probably creeping, ground-cover plants (Batenburg, 1977; (Figure 6.6)) that were early colonizers of disturbed land within the swamp.

The Coenopteridales persisted into the Late Carboniferous, represented mainly by the form-genus *Corynepteris,* but they were never common (Scott and Galtier, 1985). True ferns, however, became much more common, especially in the tropical forests. Kidston's (1923–25) studies on the British Upper Carboniferous ferns have proved of fundamental importance in understanding their palaeobiology, and have proved the foundation for the more recent studies, such as by Danzé (1956) and Brousmiche (1983). Most of the herbaceous ferns belong to three orders, the Botryopteridales, Urnatopteridales and Crossothecales (Brousmiche, 1983; Meyen, 1987). It was once though that the extant family Gleicheniaceae was present at this time, in the form of *Oligocarpia,* but these fossils are now assigned to the extinct family Sermeyaceae within the Botryopteridales. Evidence as to the habitat of these ferns is still very limited but they probably grew in open areas or in some cases as under-storey within the main parts of the forests.

Tree-ferns also became common at this time (Figure 6.7); particularly after the decline of the lycopsids in the Stephanian, they were dominant components of the tropical lowland forests (DiMichele *et al.,* 1985). The most abundant belong to the order Marattiales, which appears to have had a global distribution. Their foliage (*Pecopteris sensu lato* — Kidston, 1923–1925; Dalinval, 1960) and trunks (*Psaronius, Caulopteris, Megaphyton, Artisophyton* — Crookall, 1955; Morgan, 1959; Pfefferkorn, 1976; Mickle, 1984) are extremely common fossils, especially in the upper part of the Upper Carboniferous. A second group known from the tropical forests (e.g. *Senftenbergia),* was originally thought to belong to the extant family Schizaeaceae but is now assigned to the extinct Tedelaceae (Eggert and Taylor, 1966).

The progymnosperms had declined significantly by the Upper Carboniferous. In the equatorial belt, foliage assigned to the form-genus *Noeggerathia* occurs sporadically, and bears a close similarity to the Lower Carboniferous *Rhacopteris* and *Archaeopteris* fronds. However, their fructifications (known as *Discinites*) are in the form of discrete cones (Hirmer, 1941; Danzé 1957), quite different from the loose clusters of sporangia of the more typical Early Carboniferous progymnosperms.

Of the gymnosperms, the pteridospermous groups were the commonest in the tropical forests. The traditional concept of pteridosperms was of a group of plants with complex, fern-like fronds, but which reproduced by seeds. However, the current view is that the pteridosperms were a heterogeneous group of only distantly related plants, which independently developed such complex fronds (e.g. Crane, 1985).

The trigonocarpalean pteridosperms (Medullosales *auct.*) originated in the Early Carboniferous and persisted into the very early Permian, but they are regarded as a characteristically Late Carboniferous group. Adpressions of their foliage (e.g. *Neuropteris, Alethopteris* — Laveine, 1967; Wagner, 1968; Cleal and Shute, 1991, 1992; Cleal *et al,* 1991) are extremely common in the Upper Carboniferous, and their stems are major components of some of the coals (e.g. Delevoryas, 1955), particularly those representing drier habitats. The trigonocarpaleans developed a variety of growth habits, including lianas, ground-creepers, shrubs and trees, although the latter two were probably the commonest (e.g. (Figure 6.8)). Some (e.g. *Alethopteris*) had very large fronds (up to seven metres long according to Laveine, 1986), although others (e.g. *Callipteridium, Odontopteris*) were much smaller. The seeds, which were attached directly to the fronds, also tended to be large. The Trigonocarpales seem to have been mainly restricted to the equatorial belt; records of *Neuropteris* foliage from the northern high latitudes (e.g. Gorelova *et al.,* 1973) are all extremely doubtful.

The Lagenostomales were the second major group of pteridosperms of the tropical forests (Taylor and Millay, 1981). Unlike most of the Early Carboniferous members of the order, they appear to have been relatively small plants. The *Lyginopteris*-bearingplants were probably shrubs, that favoured the wetter habitats in Namurian and early Westphalian swamps. Most of the others, however, such as the *Eusphenopteris/Heterangium* and the *Mariopteris/Schopfiastrum*

plants, had a creeping or vinose habit. Most lagenostomalean fronds were consequently rather smaller than those of the Trigonocarpales. The only unequivocal records of this order are from the equatorial belt.

A third pteridosperm order known from the tropical forests was the Callistophytales (Rothwell, 1975, 1981). It first appears both as adpressions and coal-ball petrifactions in the middle Westphalian D, and occurs consistently through the rest of the Carboniferous. The few known species assigned to the order probably represent creeping plants (Figure 6.9), with fronds bearing lobed pinnules (*Dicksonites*), and there is therefore some superficial comparison with the Lagenostomales. However, in just about every other character (e.g. stem and rachial anatomy, seed structure, pollen) they are quite different, and suggest possible affinities with the peltasperms (e.g. *Callipteris auct.*) that occur commonly in the Permian.

In addition to the pteridosperms, the other major group of Late Carboniferous gymnosperms was the cordaites (Rothwell, 1988). They were mostly trees (although some herbaceous forms are also known) with long, strap-like leaves with a parallel nervation (Figure 6.10). There were separate male and female fructifications, each consisting of clusters of cones attached to a central rachis. In the tropical areas such as Britain, cordaites were probably most abundant in the drier, extra-basinal habitats, although some also seem to have grown within the swamp-forests, perhaps on the raised levee banks. During the somewhat drier interval in the mid-Westphalian, they even formed major components of the forest, particularly in coastal areas where they were similar to Recent mangroves (DiMichele *et al,* 1985).

From the detailed structure of the fructifications, the cordaites seem to have been closely related to the early conifers. The conifers themselves were already in existence in the Late Carboniferous (records from North America and Britain), although they mainly grew in the extra-basinal habitats and are thus rarely found in the fossil record (A.C. Scott and Chaloner, 1983; Lyons and Darrah, 1989).

Outside the tropical belt, vegetation was not particularly lush during the Late Carboniferous. In the southern continents of Gondwana, the polar ice-cap had a severely limiting effect on the vegetation, restricting it largely to herbaceous lycopsids and shrubby progymnosperms. This has been described by Retallack (1980) as the *Botrychiopsis* tundra. Only at the very end of the Carboniferous did the ice-cap contract, allowing forests of arberialean ('glossopterid') trees to develop. In the northern continent of Angara there was no significant ice-cover, but vegetation was still very restricted, consisting mainly of shrubby lycopsids; Meyen (1972) described it as a 'cheerless and monotonous "brush" of fairly short straight sticks'. As in Gondwana, conditions seem to have become more favourable to vegetation towards the end of the Carboniferous, and the variety of plants present started to increase, probably as a result of migration from the tropical forests. However, it was not until the Permian that the Angaran vegetation became as lush and diverse as that seen in the Late Carboniferous tropical forests of Eurameria.

Upper Carboniferous plant fossils in Britain

During the Namurian, extensive fluvial deltas in Britain produced sandstone bodies, belonging to the Millstone Grit. There is some evidence of the vegetation growing on these deltas (e.g. Lacey, 1952c), but the preservation of the fossils is often poor and they have not been studied to the same extent as elsewhere in Europe (e.g. Stockman and Williere, 1952–1953; Josten, 1983). British Namurian vegetation is thus somewhat of an unknown quantity and no GCR sites have been selected for the palaeobotany of this series.

In the Westphalian, the sedimentary regime in Britain changed to mainly middle and then upper delta-plain deposits. The resulting strata, known as the Coal Measures (Figure 6.3), are particularly suited to the preservation of plant fossils. In the South Wales and Bristol–Somerset coalfields, plant fossils can be found throughout the sequence, from the basal Langsettian to the basal Cantabrian (Dix, 1933, 1934; Moore and Trueman, 1942; Cleal, 1978; Cleal and Thomas, 1991). In the Forest of Dean, they are restricted to the upper Westphalian D and Cantabrian (Wagner and Spinner, 1972). In the English Midlands and Pennines coalfields, plant fossils are mainly restricted to the Langsettian and Duckmantian parts of the sequence (e.g. Arber, 1914, 1916; Kidston 1923–1925), as much of the Bolsovian and Westphalian D is represented by red-beds (the Etruria Formation — Besly and Turner, 1983) in which the plant fragments have been mostly removed by oxidation. There is a short interval in the upper Westphalian D of these coalfields where plants are found (the Halesowen Formation and its lateral equivalents — e.g. Arber, 1914). This in turn is succeeded by more red-beds (the

Keele Formation — probably upper Westphalian D and Cantabrian) in which they are extremely uncommon and consist mainly of conifer fragments. In northernmost England and Scotland, plant fossils are known mainly from the upper Langsettian to lower Bolsovian, but few sites have been studied in any detail (for an exception see Thomas and Cleal, 1993).

Britain has a number of 'classic' assemblages, such as the Duckmantian Barnsley Seam 'flora' of Yorkshire and the Westphalian D Radstock 'flora' of Somerset (Kidston, 1923–1925; Crookall, 1955–1975; Thomas and Cleal, 1994). Unfortunately, in neither case has it proved possible to find conservable sites to represent these assemblages. Attempts have been made to conserve parts of the tips at Kilmersdon and Writhlington to represent the Radstock assemblage (Cleal, 1985; Jarzembowski, 1989), but the life expectancy of these sites was considered too short to justify selection as GCR sites. In fact, this was a problem found throughout this part of the GCR; despite the extremely widespread distribution of the Upper Carboniferous plant fossils, the majority of work that has been done on them was based on material from underground workings or spoil-tips, which was unsuitable for long-term conservation. Those sites which were eventually selected are shown in (Figure 6.11).

Other than some poorly preserved examples from the upper Westphalian Pennant Measures of the South Wales and Bristol-Somerset coalfields, Upper Carboniferous petrifactions are known from the only coal-ball horizon in Britain, known as the Halifax Hard Bed and Union Seam amongst other names (Phillips, 1980). It proved impossible to select a GCR site for coal-balls, however, as they nearly all originated from defunct and now sealed mine workings. One spoil tip was, until recently, still available for collecting coal-balls (Rowley Tip, Burnley) although the quality of the petrifaction was rather poor; this has now been landscaped for recreational use.

Stephanian plant fossils are very poorly represented in Britain. There are records of the basal *Odontopteris cantabrica* Zone from the Forest of Dean (Wagner and Spinner, 1972; Cleal, 1986c) and South Wales (Cleal, 1978), although no conservable outcrops yielding the fossils are known. The zone may also occur in the Keele Formation of the English Midlands. The species list given by Dix (1935) from these strata refers to *Odontopteris* cf. *schlotheimii* Brongniart, a name which has often been given in error for specimens of *O. cantabrica* Wagner (see Wagner *in* Wagner *et al,* 1969). She also mentions *Pecopteris miltoni* (Artis) Brongniart, which could in fact refer to *Lobatopteris vestita* (Lesquereux) Wagner. Dix's material is in clear need of taxonomic revision.

The best available review of the literature pertaining to British Upper Carboniferous plant fossils was that provided by Jongmans (1940).

References

(Figure 6.3) Diorama of a Late Carboniferous (Coal Measures) tropical swamp forest. Taken from the 'Evolution of Wales' exhibition, National Museum of Wales, Cardiff.
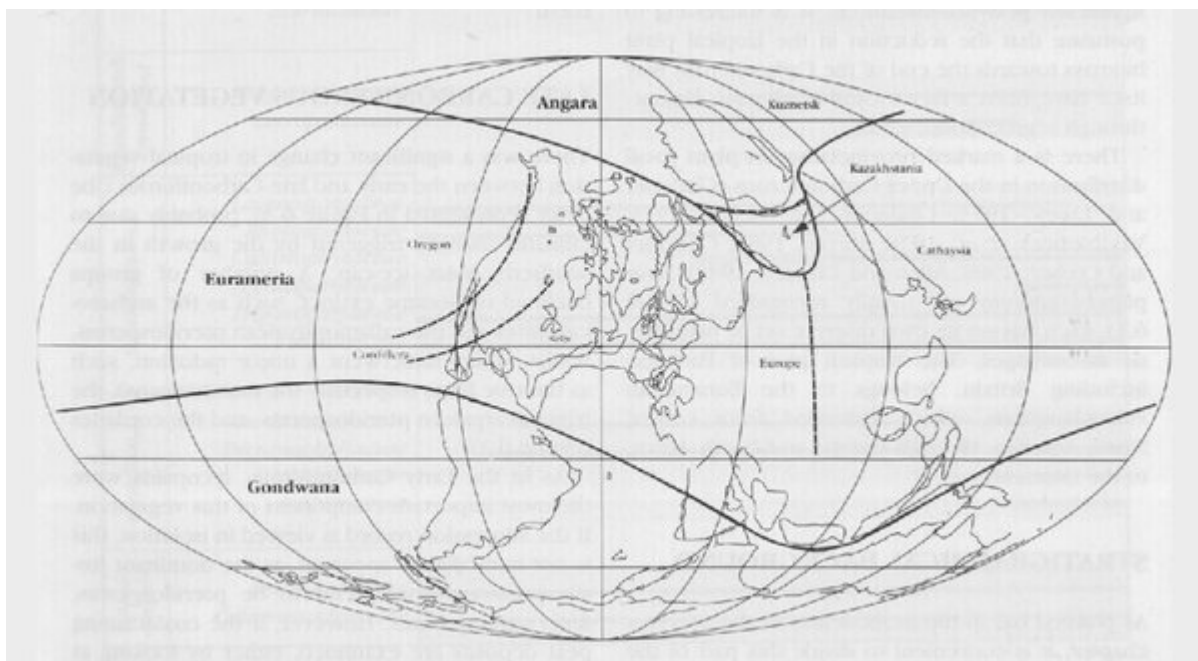
(Figure 6.1) The palaeogeography of the Late Carboniferous, showing the distribution of the major floristic zones (phytochoria). Based on Scotese and McKerrow (1990) and Cleal and Thomas in Cleal (1991).

Chronostratigraphy		Biostratigraphy	GCR palaeobotany Sites
Series	**Stage**		
Stephanian	Cantabrian	*Odontopteris cantabrica*	
Westphalian	'Westphalian D'	*Lobatopteris vestita*	
		Lobatopteris micromiltoni	Jockie's Syke
		Linopteris bunburii	Llanbradach Quarry
	Bolsovian ('Westphalian C')	*Paripteris linguaefolia*	Nostell Priory
	Duckmantian ('Westphalian B')	*Lonchopteris rugosa/ Alethopteris urophylla*	
	Langsettian ('Westphalian A')	*Lyginopteris hoeninghausii/ Neuralethopteris schlehanii*	Cattybrook Claypit Wadsley Fossil Forest Nant Llech
Namurian	Yeadonian	*Neuralethopteris larischii/Pecopteris aspera*	
	Chokierian		

(Figure 6.11) Chronostratigraphical and biostratigraphical classification of the Upper Carboniferous, and the positions of the GCR palaeobotany sites.
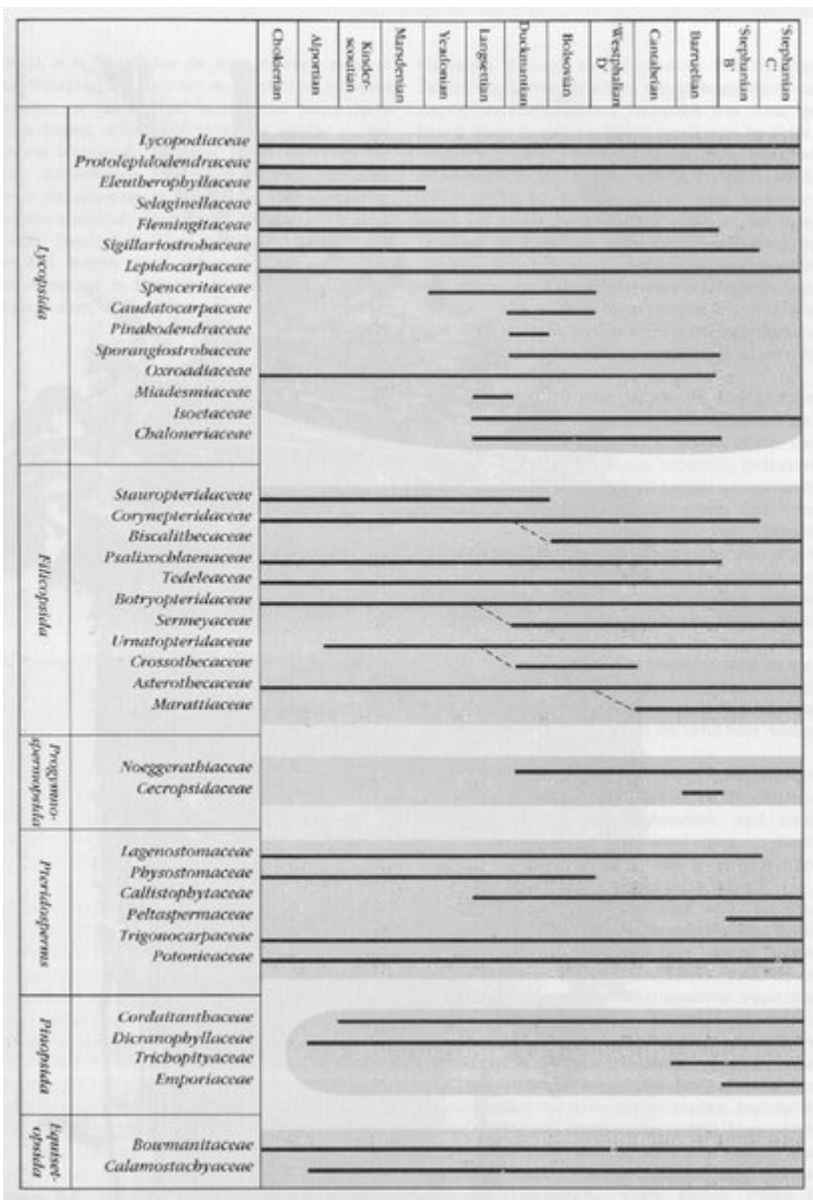
(Figure 6.2) The distribution of the principal families of vascular plants in the Late Carboniferous. Based on data from Cleal (1993).
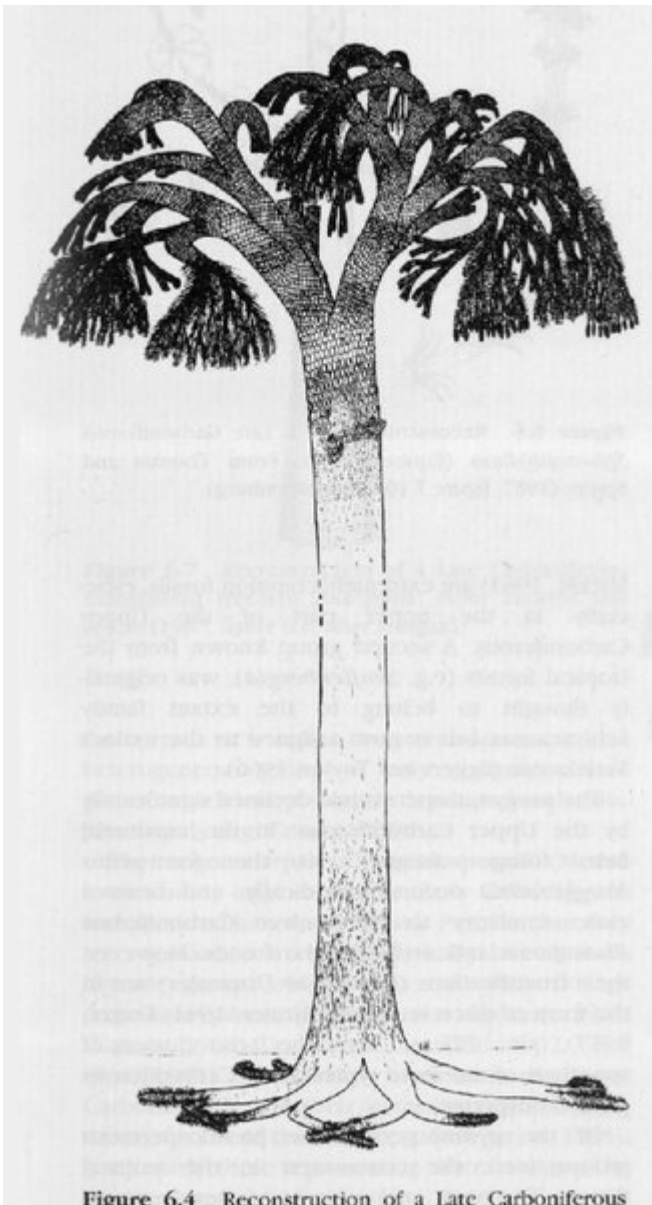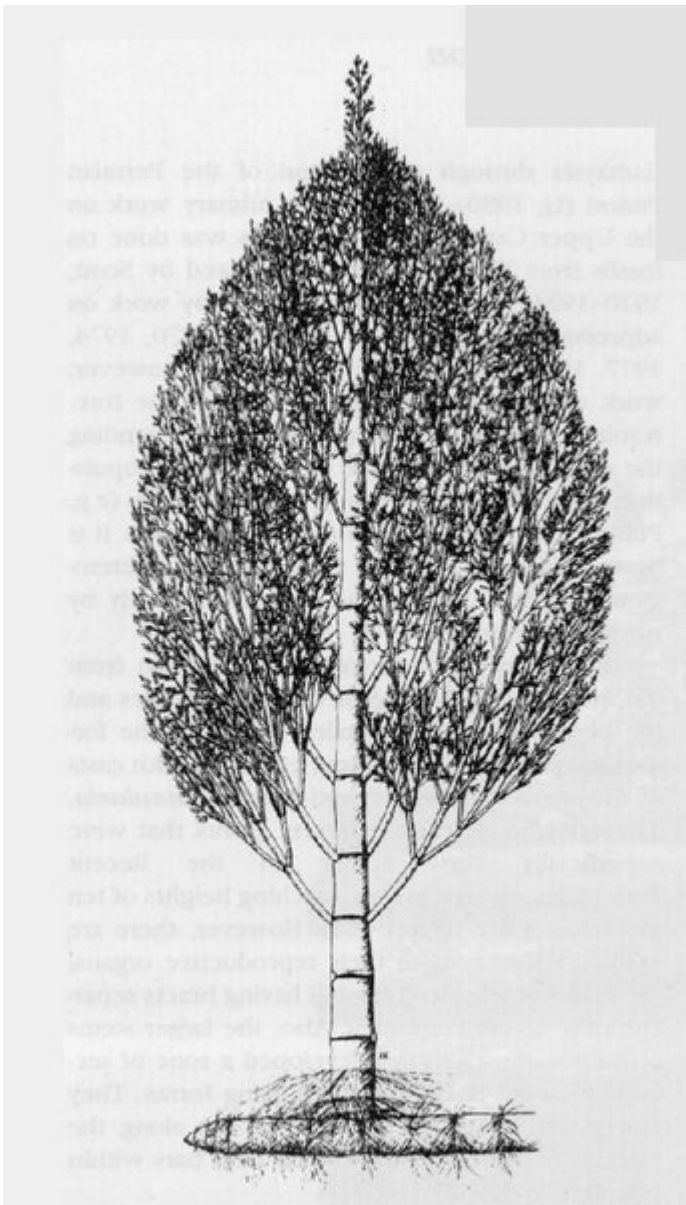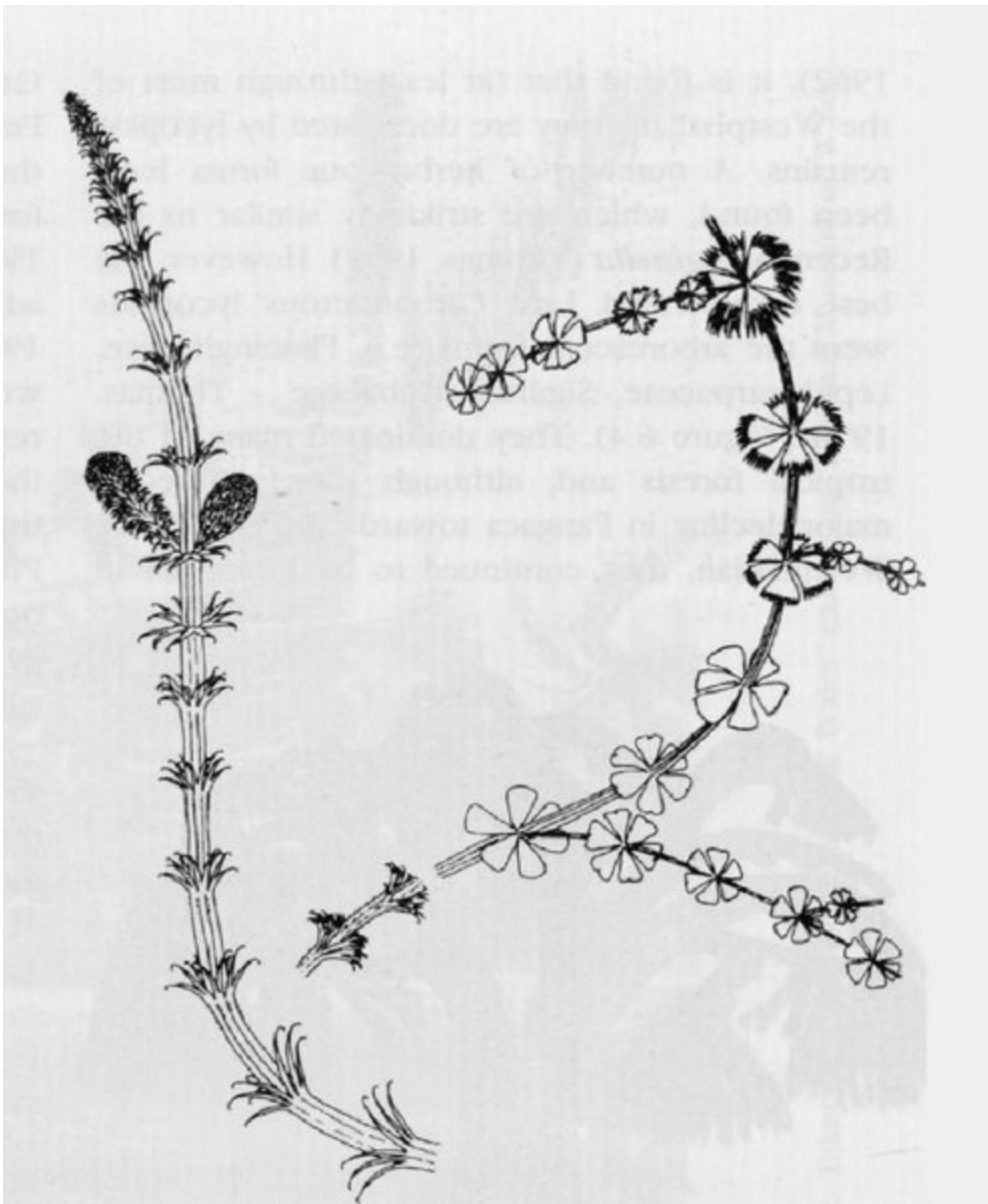
(Figure 6.4) Reconstruction of a Late Carboniferous giant lycopsid, Lepidodendron. From Thomas and Spicer (1987, figure 7.5).

(Figure 6.5) Reconstruction of a Late Carboniferous giant equisetopsid Calamites. From Thomas and Spicer (1987, figure 7.11; after Hirmer).

(Figure 6.6) Reconstruction of a Late Carboniferous Sphenophyllum (Equisetopsida). From Thomas and Spicer (1987, figure 7.10; after Battenburg).
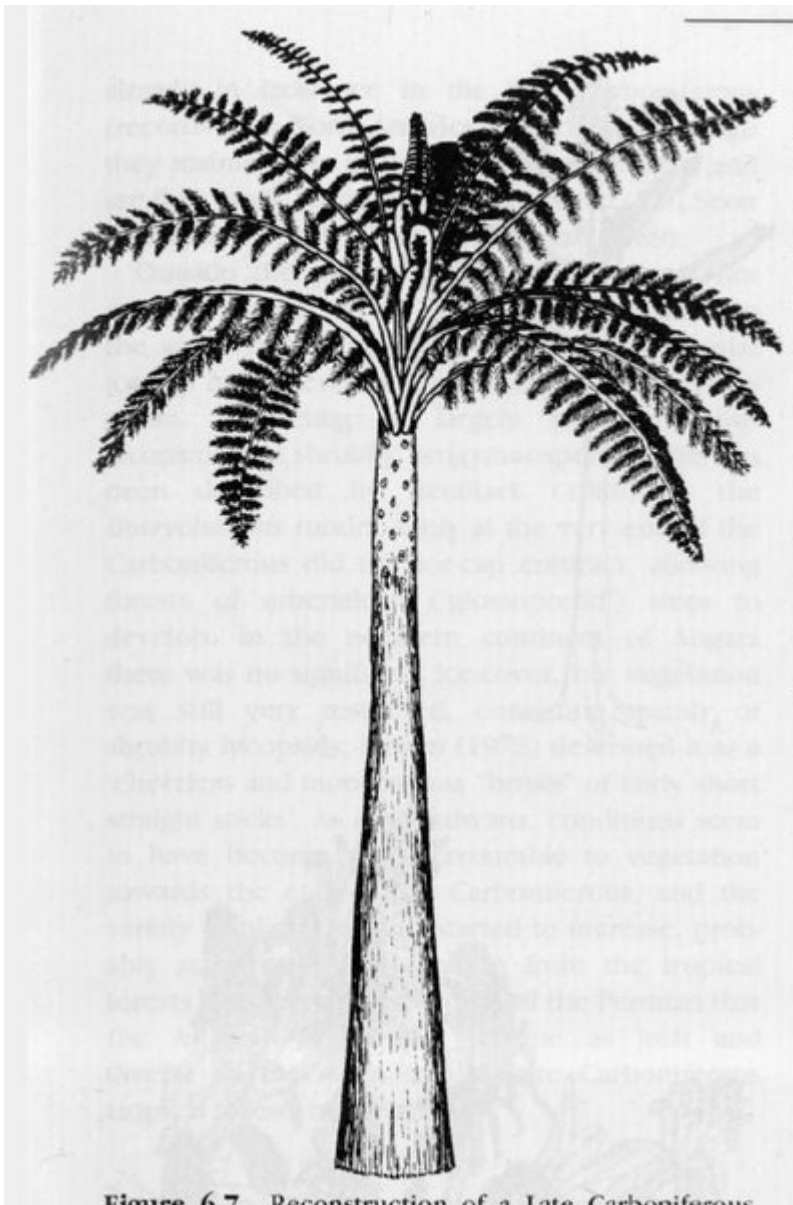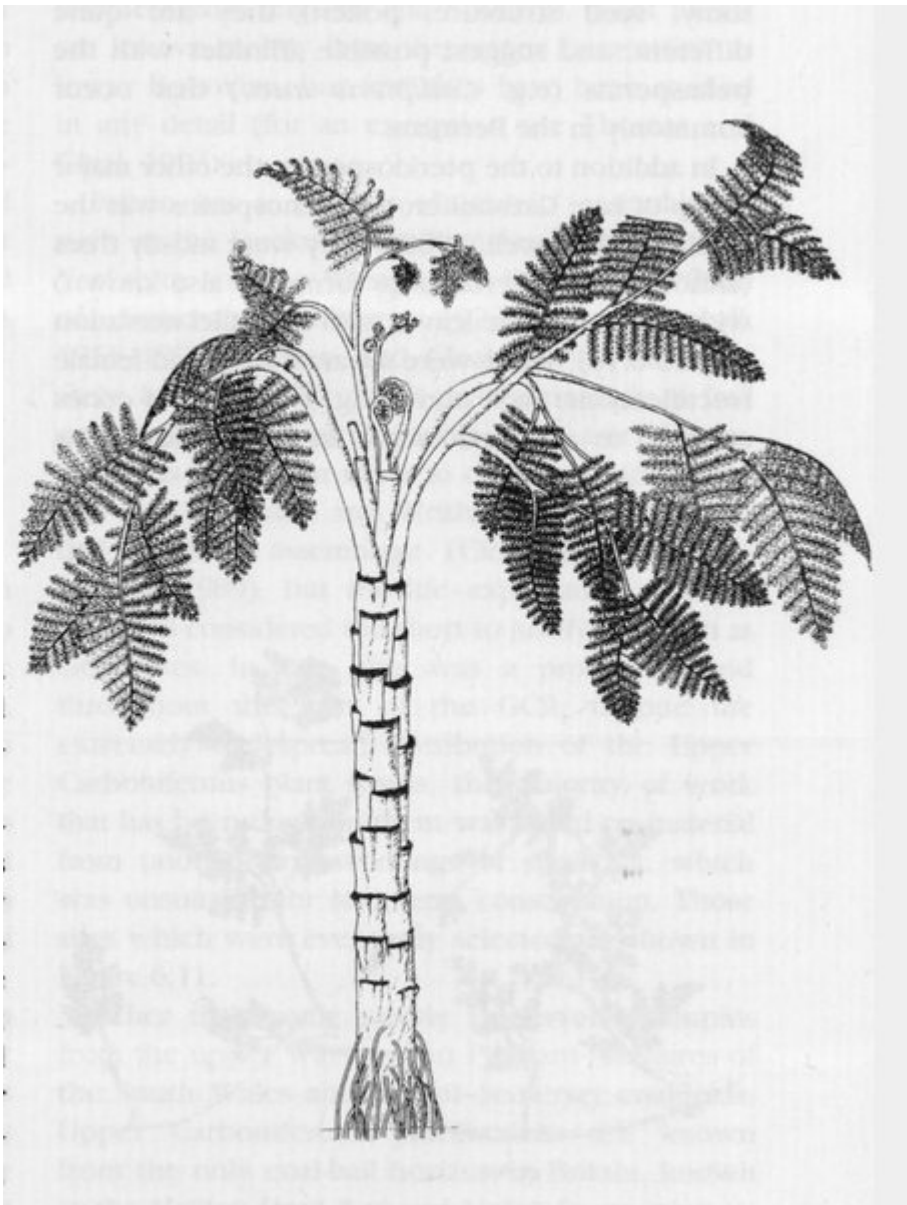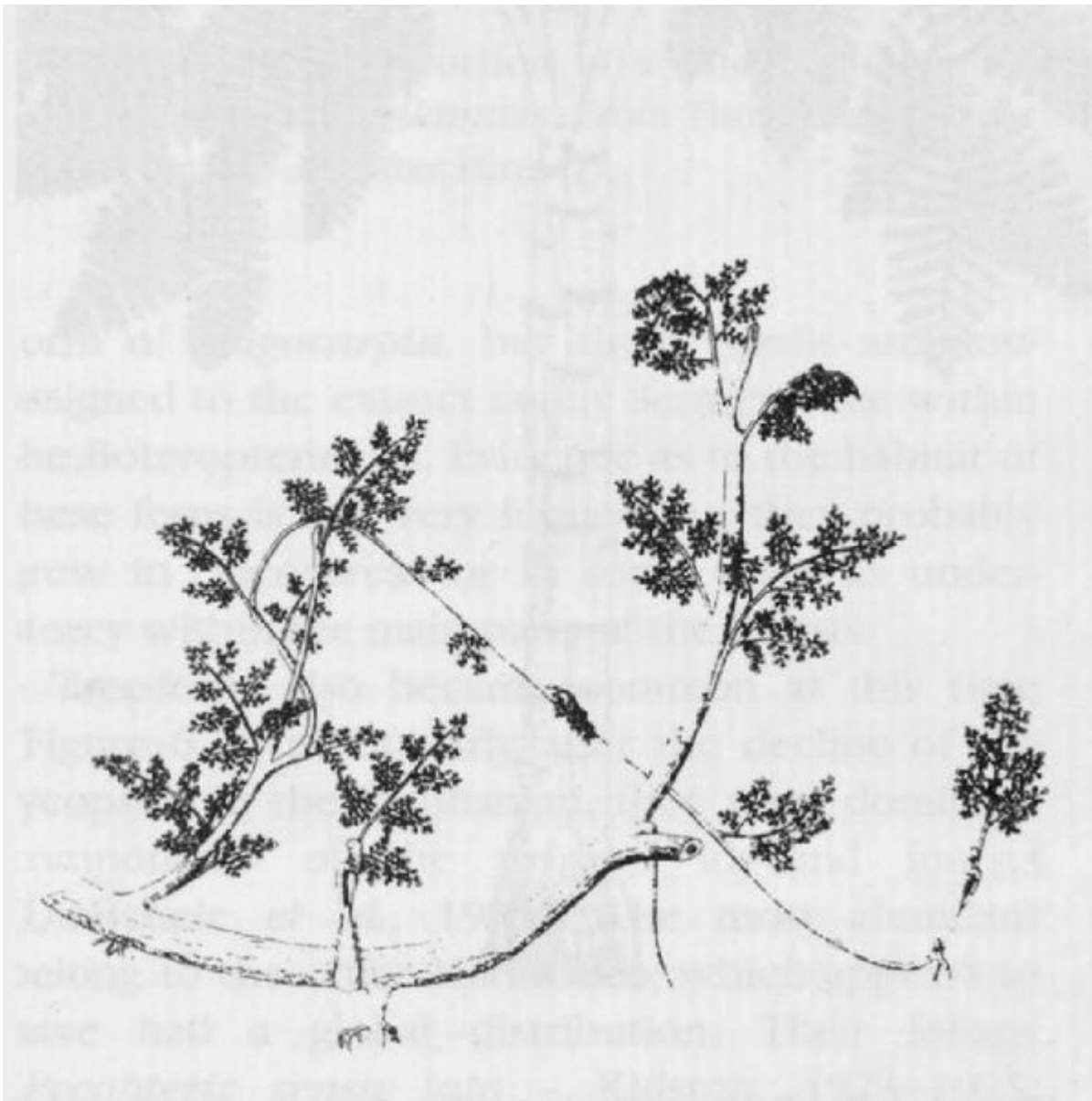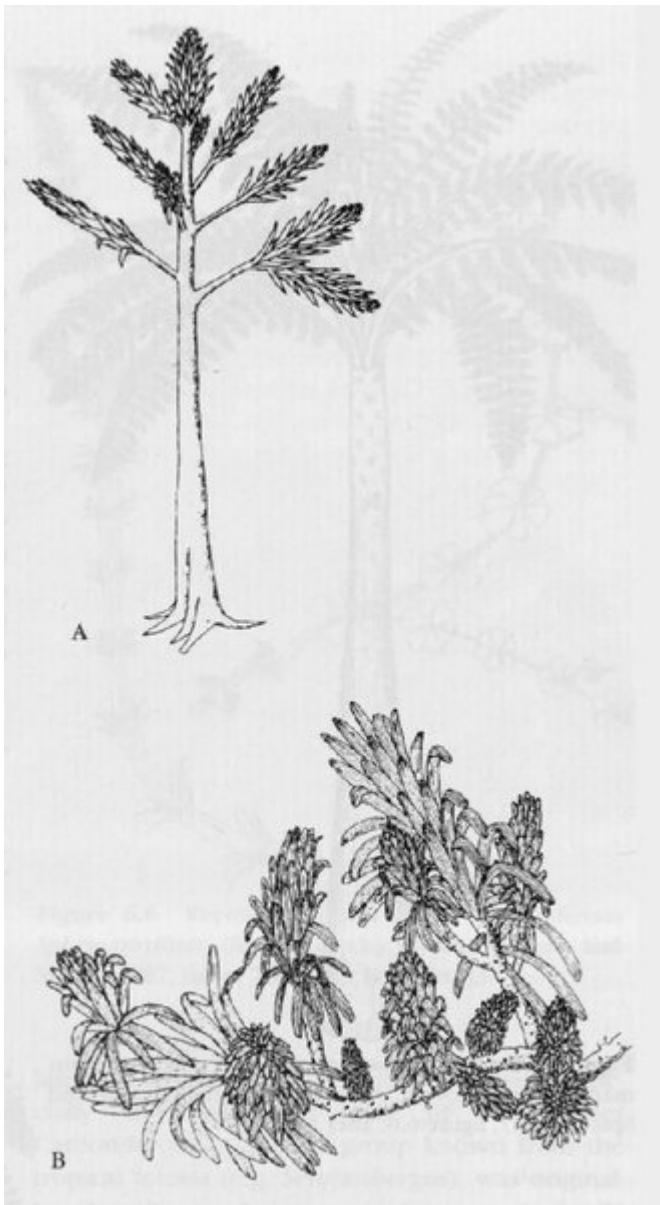
(Figure 6.7) Reconstruction of a Late Carboniferous marattialean tree-fern *Psaronius*. From Thomas and Spicer (1987, figure 6.6; after Morgan).

(Figure 6.8) Reconstruction of a Late Carboniferous trigonocarpalean pteridosperm, Alethopteris. From Thomas and Spicer (1987, figure 10.2; after Stewart and Delevoryas).

(Figure 6.9) Reconstruction of a Late Carboniferous callistophyte liana. From Thomas and Spicer (1987, figure 10.6; after Rothwell).

(Figure 6.10) Reconstruction of Late Carboniferous cordaitaleans: (A) an arborescent form found in the palaeoequatorial swamp-forests; (B) a smaller form. From Thomas and Spicer (1987, figure 11.1; after D.H. Scott, and Rothwell and Warner).