Chapter 7 Permian

No other period in Earth's history was as traumatic for terrestrial vegetation as the Permian. It saw the extinction of much of the Late Palaeozoic terrestrial vegetation, which had been dominated by arborescent lycopsids and equisetopsids, and a number of 'primitive' gymnosperm groups (e.g. Trigonocarpales, Lagenostomaleans, Cordaitales, Dicranophyllales). During the succeeding Early Triassic, terrestrial vegetation, at least as revealed by the fossil record, was generally sparse and of poor diversity (Dobruskina, 1980). During the middle and late Triassic, however, there was the progressive introduction of a number of gymnosperm groups regarded as characteristically Mesozoic in aspect (Umkomasiaceae, Leptostrobaceae, Caytoniaceae, Bennettitaceae), of many of the modern families of ferns (e.g. Matoniaceae, Dipteridaceae, Polypodiaceae, Dicksoniaceae) and conifers (e.g. Podocarpaceae, Pinaceae), and even the first putative angiosperms (Cornet, 1989; Cleal, 1993). Unfortunately, this change, known as the Palaeophytic-Mesophytic transition (Figure 7.1), cannot be particularly well demonstrated in Britain, which at that time suffered arid conditions that supported only a sparse vegetation. Nevertheless, the broad pattern of the transition can be discerned and its stratigraphical position has potentially important consequences for understanding the underlying mechanism.

Palaeogeographical setting

By the Early Permian, the Laurussia and Gondwana continental plates had fused to form part of the Pangaea 'super-continent' (Figure 7.2). Britain lay on the eastern margins of Pangaea and, although it had drifted north relative to its position in the Carboniferous, it was still within tropical latitudes (probably *c.* 20° north by the end of the Permian). The Lower Permian is mainly represented by red-beds, indicating arid climatic conditions, and generally not conducive to the preservation of plant fossils. The Upper Permian consists of carbonate beds deposited in the Zechstein and *Bakevellia* inland seas.

There is greater provincialism in Permian plant fossil distribution than in any other part of the Palaeozoic (Vakhrameev *et al.,* 1978; Meyen, 1987; Allen and Dineley, 1988; Cleal, 1991). Most currently accepted palaeophytogeographical models recognize five discrete palaeokingdoms for the period (Figure 7.2). The British assemblages belong to the Euramerian Palaeokingdom, which extends from eastern North America, through Europe to southern Kazakhstan. The Euramerian assemblages are generally rare and of limited diversity, dominated mainly by conifers and peltasperms. Nevertheless, there are a number of well-documented Lower Permian examples, such as in the Autunian of France (Doubinger, 1956) and Germany (Barthel, 1976; Kerp and Fichter, 1985). The Upper Permian is mainly represented by the Zechstein assemblages of Germany, France and Britain.

Stratigraphical background

Details of British Permian stratigraphy are discussed by Smith *et al.* (1974). The stages currently recognized by the IUGS Commission on Stratigraphy are based on the marine sequences in the Ural Mountains (Figure 7.6). However, they are difficult to use in the sequences found in much of Europe, and so a separate set of stages have been introduced for these strata. The approximate correlation between the European scheme and the marine stages is shown in (Figure 7.6), based partly on data provided by Kozur (1984).

The Carboniferous–Permian boundary has still to be formally defined. In this volume, it is taken to correspond to the Stephanian–Autunian boundary, which appears to correlate broadly with the Gzhelian–Asselian boundary in the standard marine sequences (Doubinger and Bouroz, 1984).

Permian vegetation

The British Permian plant fossils represent the vegetation growing in the equatorial parts of the Pangaean 'super-continent' (Figure 7.2). Pteridophytic plants were on the whole rare in this vegetation. There were remnant populations of arborescent lycopsids and ferns in the Autunian, similar to those found in the Carboniferous, but they had largely disappeared by the Saxonian. There is palynological evidence that osmundacean ferns were present here in the Late Permian (Schweitzer, 1986), but macrofossils have yet to be found.

Equisetopsids similar to those found in the Carboniferous persisted into the Autunian, including the large calamostachyaleans (Kerp, 1984b) and the herbaceous bowmanitaleans (Kerp, 1984a). By the Late Permian, however, only small equisetopsids are found (*Neocalamites*). The latter were similar in general morphology to the recent *Equisetum,* but their affinities remain uncertain in the absence of fructifications.

Some characteristic pteridospermous groups of the Late Carboniferous tropical vegetation (Trigonocarpales, Callistophytales) also continued into the earliest Permian, but became extinct by the end of the Autunian. The dominant ptetidosperms during the rest of the Permian Period were bushes or shrubs of the Peltaspermales. Although so far not reliably identified from Britain, remains of their fronds are common fossils in the Lower Permian of continental Europe, and are known as *Autunia* (*Callipteris auct.*), amongst other names (Kerp, 1986). In the Upper Permian of Britain, on the other hand, peltasperms are well represented, belonging to the form-genus *Peltaspermum* (Townrow, 1960; Poort and Kerp, 1990). They appear most closely related to the Carboniferous pteridosperms, the Callistophytales.

There is unequivocal evidence that cycads were present in Cathaysia (Gao and Thomas, 1989), but their presence in Pangaea is less certain. Kelp (1983) has described fertile leaves of what may be a primitive cycad-like plant (*Sobernheimia*), although Crane (1985) has queried their cycad credentials. There have also been reports of typical-looking cycad leaves, especially from the Upper Permian of Britain (Stoneley, 1958; Schweitzer, 1986), but there are neither cuticles nor fructifications preserved to confirm their identity.

Evidence of ginkgophytes in tropical Pangaea, including Britain, is also limited to rare fossils of foliage (*Sphenobaiera*). In this case, however, there is epidermal evidence to support their ginkgo-phyte affinities (Schweitzer, 1986). *Trichopitys,* an ovuliferous structure described from the Lower Permian of France as a primitive ginkgo (Florin, 1949), is now thought to be allied either with the peltasperms or dicranophylls (Meyen, 1987; Archangelsky and Cúneo, 1990).

By far the most abundant plants in the vegetation of tropical Pangaea were conifers (Figure 7.3) and (Figure 7.4). In the Early Permian they mainly belong to the Walchiaceae, which is the most primitive known conifer family, with a fossil record extending back into the Westphalian (Florin, 1938–1945; Clement-Westerhof, 1988). In the Late Permian, they were largely replaced by the Ullmanniaceae and Majonicaceae, whose ovuliferous cones have a simpler and thus 'more advanced' structure.

Outside Europe, Permian tropical vegetation is best represented in China, which seems to have escaped the dramatic environmental changes that caused the extinction of the swamp-forests of Europe and North America. Arborescent lycopsids, equisetopsids, cordaites and marattialean ferns all persist here into the Late Permian ('Gu and Zhi', 1974; Li, 1980; Asama, 1984), and are the real successors of the Carboniferous tropical forests. As noted above, unequivocal remains of cycads make their first appearance in the Permian of China. However, the most characteristic elements are of the gigantopterid complex (*Gigantopteris, Emplectopteris, Emplectopterielium,* etc.). Although almost certainly gymnospermous, the affinities of these plants are not certain. A possible link with the trigonocarpalean form-genus *Calliptericlium* has been suggested, but the evidence remains far from conclusive. The plant fossils representing this tropical vegetation are referred to as the Cathaysia Palaeokingdom.

In parts of western North America (Figure 7.2), plant fossils in the Lower Permian appear to have a distinctly Cathaysian aspect, especially through the presence of leaves apparently belonging to the gigantopterid complex. This is referred to as the North America Palaeokingdom (Read and Mamay, 1964). It remains uncertain whether this represents a true Cathaysian-style vegetation, or merely reflects plants that underwent convergent evolution.

The Permian saw the first major development of vegetation in areas outside the palaeoequatorial belt. In the southern hemisphere, this is seen in the growth of forests dominated by arberialean trees, with leaves belonging to form-genera such as *Glossopteris* and *Gangamopteris.* In the southern polar regions (by this time there was no ice-cap), the vegetation consisted almost exclusively of these trees (Archangelsky, 1990). In lower latitudes (South Africa and South America), however, they are also associated with a range of other plant groups, including lycopsids, calamostachyalean equisetopsids and marattialean ferns and conifers (Archangelsky and Arrondo, 1969, 1975; Archangelsky *et al.,* 1981; Archangelsky, 1990; Anderson and Anderson, 1985; Clement-Westerhof, 1988).

In the northern hemisphere, temperate conditions produced a diverse range of vegetation in what was Angara (now Siberia). The dominant group consisted of plants related to the cordait-anthids of the Carboniferous tropical forests, and referred to the families Rufloriaceae and Vojnovskyaceae (Meyen, 1966, 1988). There were also endemic equisetopsids (Tchemoviaceae) and pteridosperms (Cardiolepidaceae), as well as a range of ferns, conifers and cycadophytes (Meyen, 1971, 1976, 1982, 1987). Much of the lowland parts of Angara were probably covered by forest, although some areas of more open vegetation also probably existed, including floras dominated by mosses (Fefilova, 1978).

The Palaeophytic–Mesophytic transition

The Palaeophytic–Mesophytic floristic transition is traditionally placed at the stratigraphical level where the first fossils of conifers and other advanced gymnosperms occur (Gothan and Weyland, 1954; Frederiksen, 1972). It does not mark a major phylogenetic development; most of the typical Mesophytic gymnosperms probably existed in the Carboniferous, in the extra-basin habitats. Rather, it indicates an environmental change, which facilitated the migration of extra-basinal vegetation into the lowland habitats.

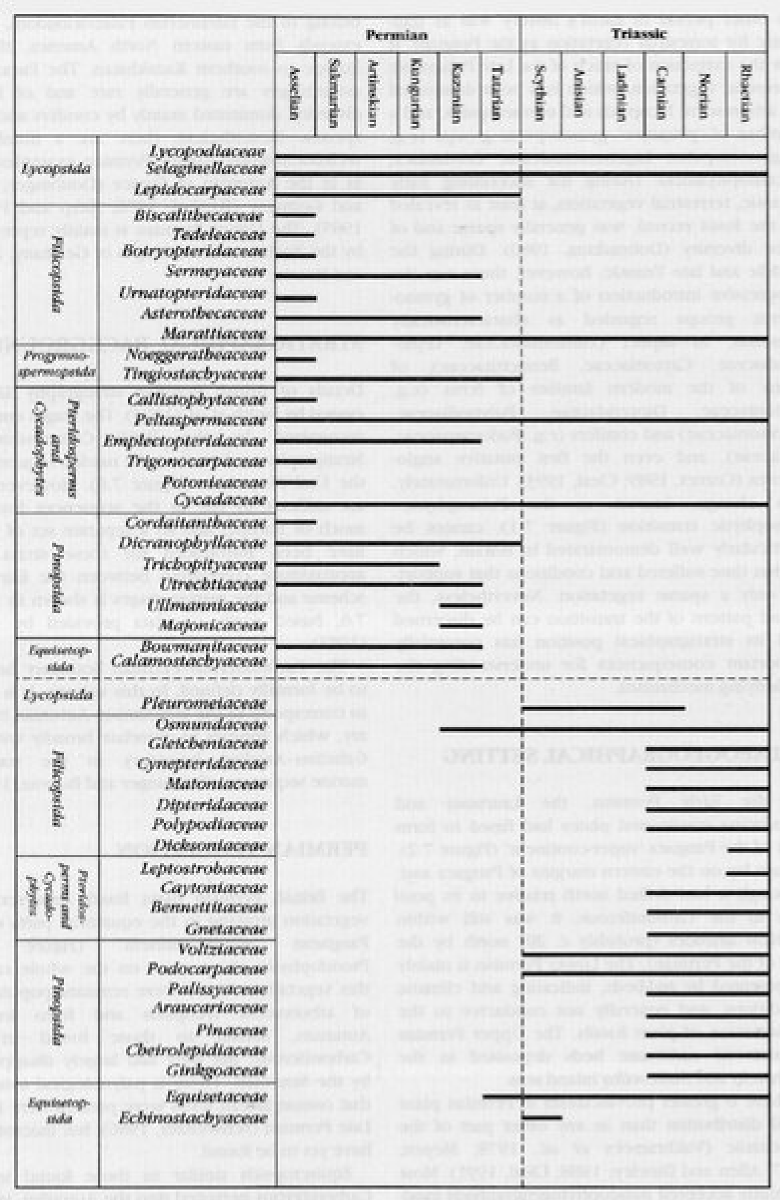
In most of the Eurameria Palaeokingdom, including Britain, the transition probably occurs in the Saxonian (?Sakmarian/Artinskian). Saxonian assemblages are very rare, but one example reported from Lodeve in France appears to be transitional between the Palaeophytic and Mesophytic (Doubinger and Krusemann, 1966). The transition appears to relate to the destruction of the lycopsid forests, which had dominated the landscape of tropical Pangaea during most of the Late Carboniferous. This had been caused by topographical uplift, following the collision of the Laurussia and Gondwana continental plates, which had drained the lowland swamps and made them unsuitable for the lycopsids (Cleal, 1991). They were partially replaced by stands of conifers, but there is no evidence that these were anywhere near as extensive as the earlier lycopsid forests.

Elsewhere in the world, the Palaeophytic–Mesophytic transition occurs at significantly higher stratigraphical levels, at or just above the Permian–Triassic boundary (Roy Chowdhury *et al.,* 1975; Sadovnikov, 1981; Wang, 1989). It coincides with the start of a period of climatic aridity, which influenced much of the globe during the early Triassic. Despite the difference in timing, it is tempting to link the changes in tropical Pangaea with those elsewhere in the world. A significant reduction in the tropical biomass may have instigated a global climatic change through a 'greenhouse effect', which only later had a significant impact on the vegetation of other parts of the world (Cleal, 1991). If this model is correct, it has clear implications for understanding what might follow the further destruction of the present-day tropical forests.

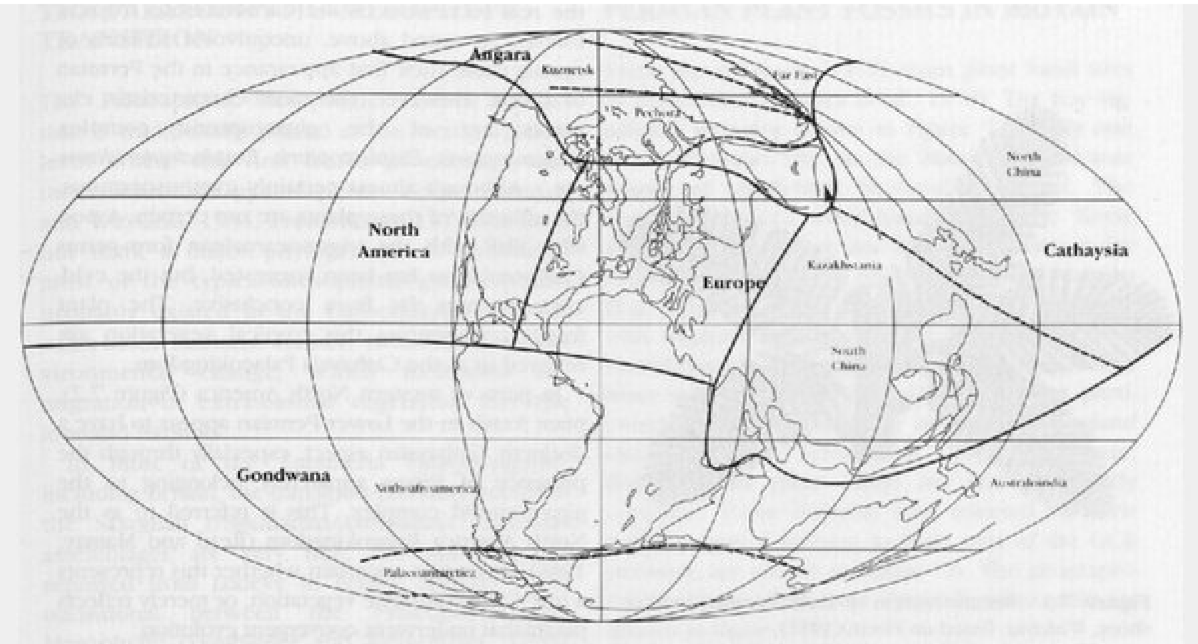
Permian plant fossils in Britain

There are relatively few Permian plant fossil sites in Britain (Vakhrameev *et al.,* 1978). The few significant sites are shown in (Figure 7.5). Only one Lower Permian site, in the Mauchline Volcanic Group of south-west Scotland is extant. The conifer-dominated assemblages from the Keele and Enville formations and their equivalents in the English Midlands were regarded as Early Permian (e.g. Wagner, 1983), but palynological evidence now suggests that they are late Westphalian D or Cantabrian (B. Besly, pers. comm., 1989). Rather more sites are known in the Upper Permian, particularly from the Marl Slate of northern England (Stoneley, 1958; Schweitzer, 1986). Even here, however, the plant fossils are not particularly common. Those Permian sites selected for their palaeobotanical interest to form part of the GCR network, are shown in (Figure 7.6). The geographical positions of the two Upper Permian sites are shown in (Figure 7.5).

References



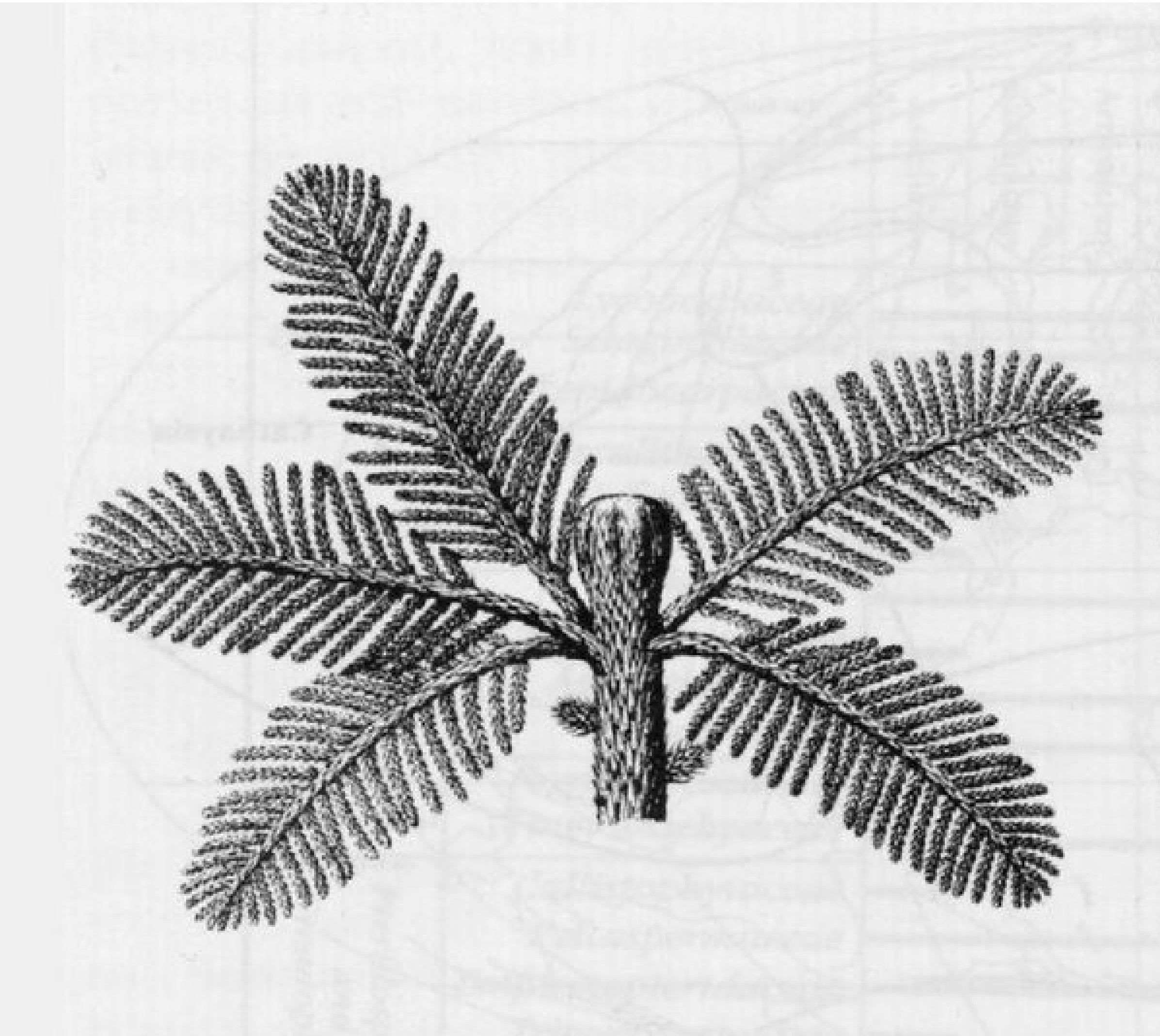
(Figure 7.1) The distribution of the principal families of vascular plants in the Permian and Triassic. Based on data from Cleal (1993).



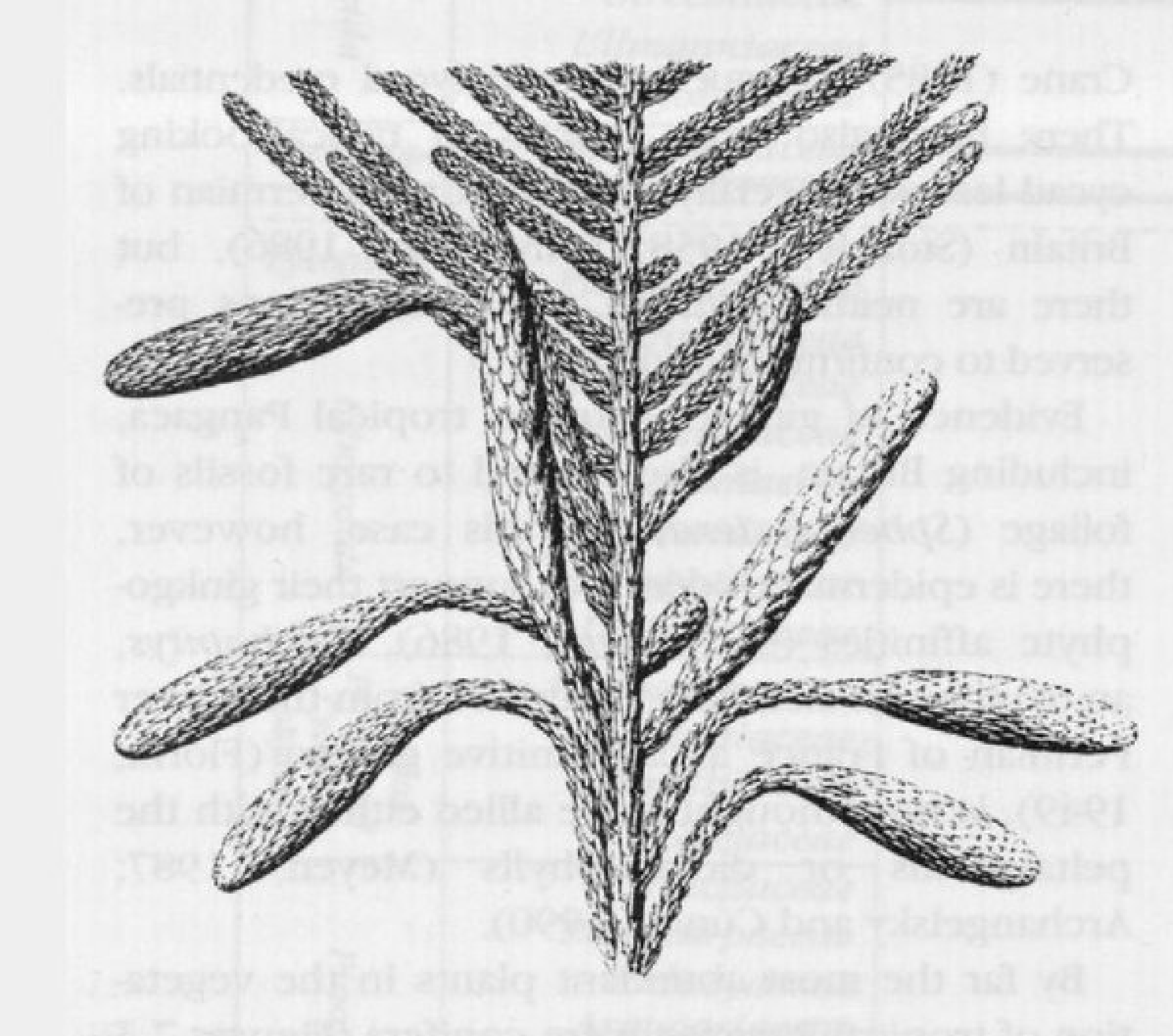
(Figure 7.2) The palaeogeography of the Permian, showing the distribution of the major floristic zones (phytochoria). Based on Scotese and McKerrow (1990) and Cleal and Thomas in Cleal (1991).

International Chronostratigraphy		European non-marine 'stages'	GCR Palaeobotany sites
Series	**Stages**		
Upper Permian	Tatarian	Zechstein	Middridge Quarry Kimberley Cutting
	Kazanian		
Lower Permian	Kungurian	Saxonian	
	Artinskian		
	Sakmarian		
	Asselian	Autunian	Stairhill

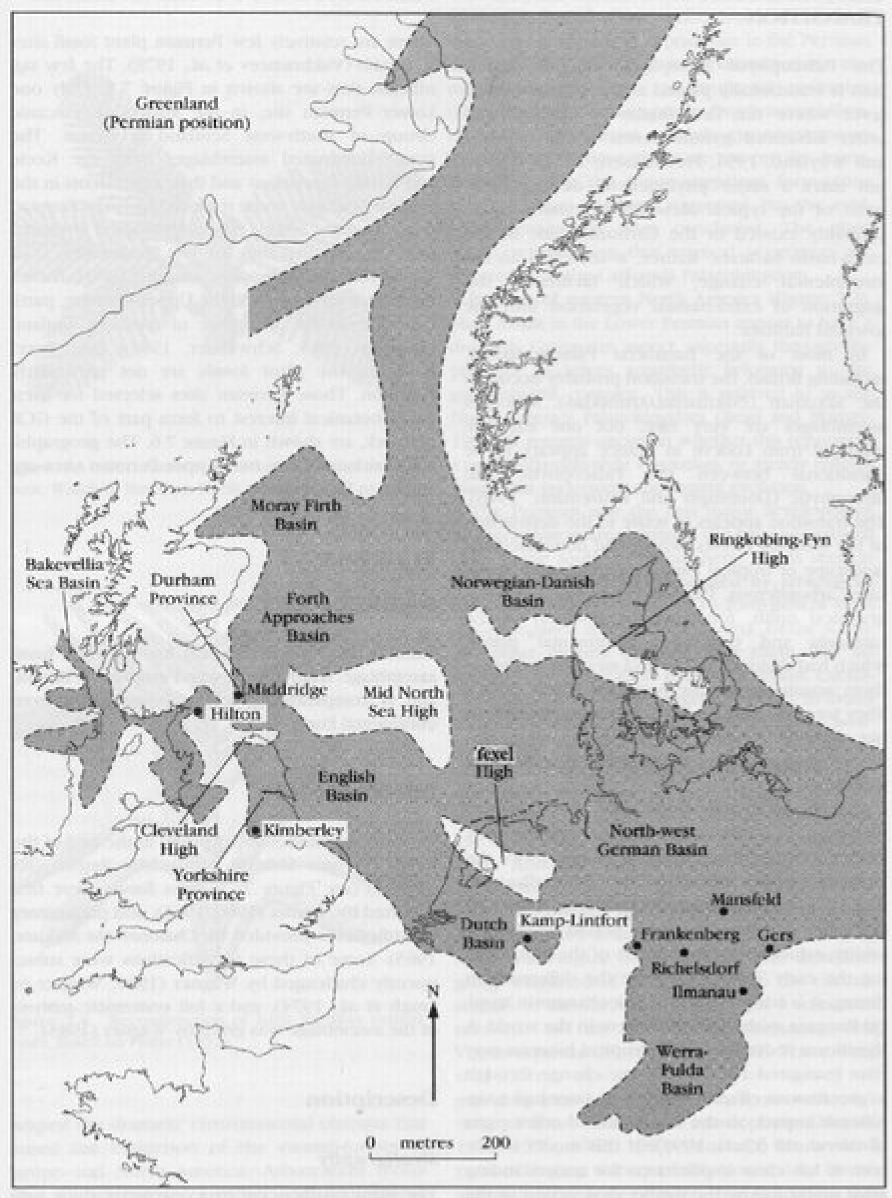
(Figure 7.6) Chronostratigraphical classification of the Permian and the positions of the GCR palaeobotany sites.



(Figure 7.3) Reconstruction of Early Permian conifer shoot, Walchia. Based on Florin (1951).



(Figure 7.4) Reconstruction of Early Permian conifer cones. Based on Florin (1951).



(Figure 7.5) Main areas of Late Permian sedimentation in north-west Europe, showing principal palaeobotanical sites including the two GCR sites (Kimberley and Middridge). Based on Schweitzer (1986, figure 1).