Palaeozoic Palaeobotany of Great Britain

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Chapter 7

Permian

Permian vegetation

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,

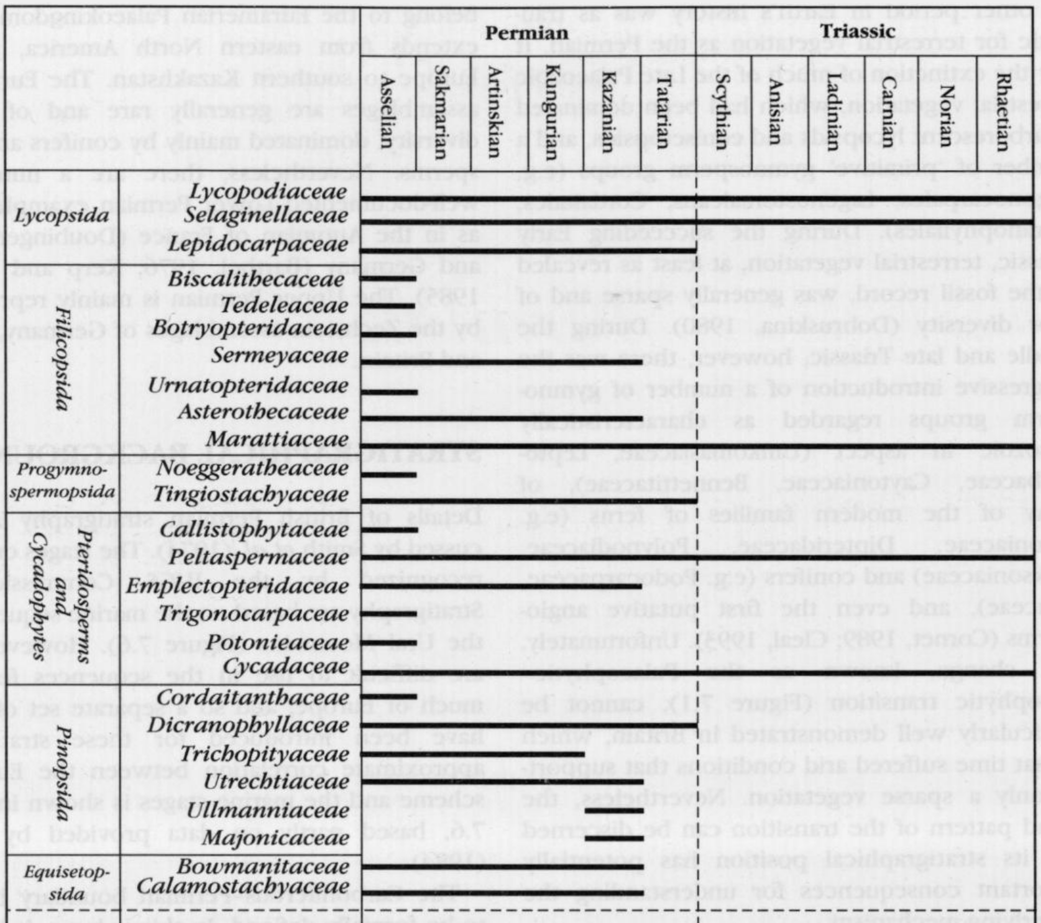

Figure 7.1 The distribution of the principal families of vascular plants in the Permian and Triassic. Based on data from Cleal (1993).

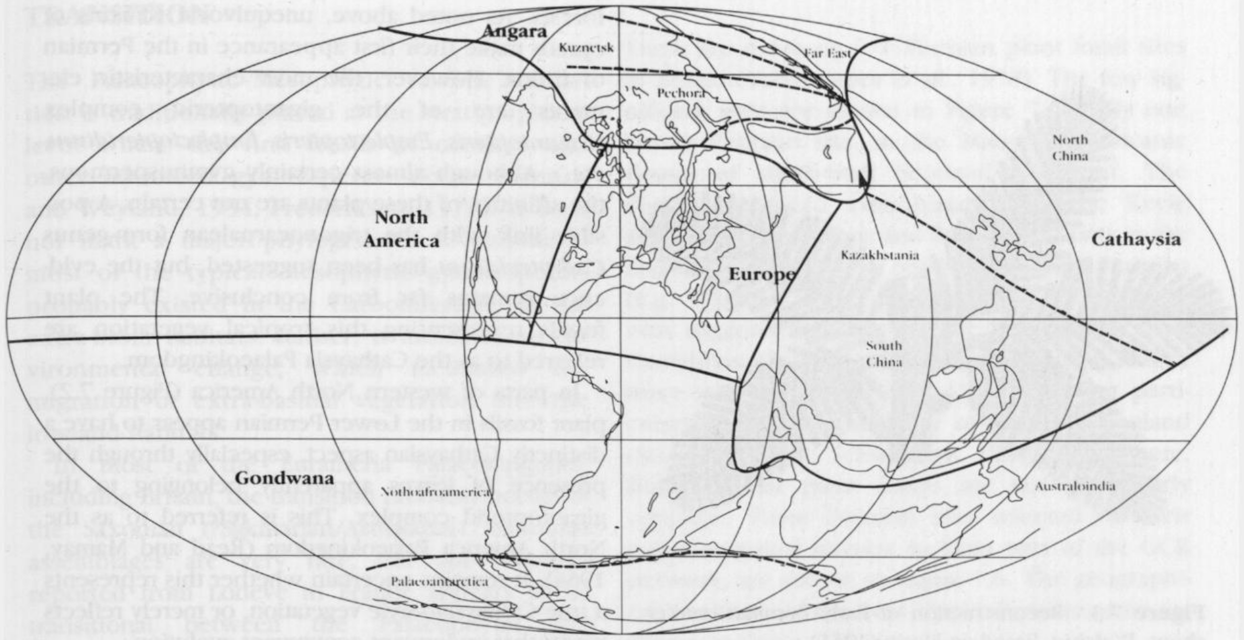

Figure 7.2 The palaeogeography of the Permian, showing the distribution of the major floristic zones (phytochoria). Based on Scotese and McKerrow (1990) and Cleal and Thomas *in* Cleal (1991).

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 pteridosperms 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. Kerp (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 ginkgophyte 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 (Figures 7.3 and 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

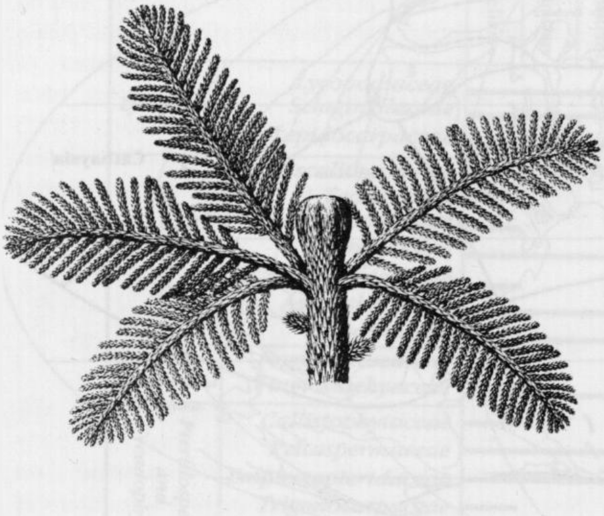

Figure 7.3 Reconstruction of Early Permian conifer shoot, *Walchia*. Based on Florin (1951).

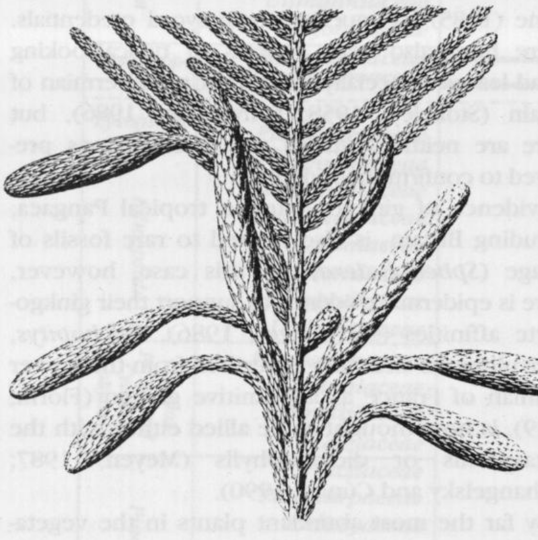

Figure 7.4 Reconstruction of Early Permian conifer cones. Based on Florin (1951).

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, Emplectopteridium,* etc.). Although almost certainly gymnospermous, the affinities of these plants are not certain. A possible link with the trigonocarpalean form-genus *Callipteridium* 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 cordaitanthids of the Carboniferous tropical forests, and referred to the families Rufloriaceae and Vojnovskyaceae (Meyen, 1966, 1988). There were also endemic equisetopsids (Tchernoviaceae) 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.

STAIRHILL

Highlights

Stairhill has yielded the only known plant fossil assemblage from the Lower Permian of Britain, and is comparable to coeval assemblages from continental Europe.

Introduction

Permian sandstones are exposed in the bed of the River Ayr near Stairhill, Strathclyde Region (NS 452243) (see Figure 7.7). Plant fossils were first reported by Mykura (1960, 1965), and preliminary identifications provided by Chaloner (*in* Mykura, 1965). Some of these identifications were subsequently challenged by Wagner (1966; Wagner *in* Smith *et al.*, 1974), and a full systematic analysis of the assemblage was given by Wagner (1983).

Description

Stratigraphy

The plant fossils occur in a one metre thick tuffaceous interval of mudstones and sandstones within the Mauchline Sandstones, and thus

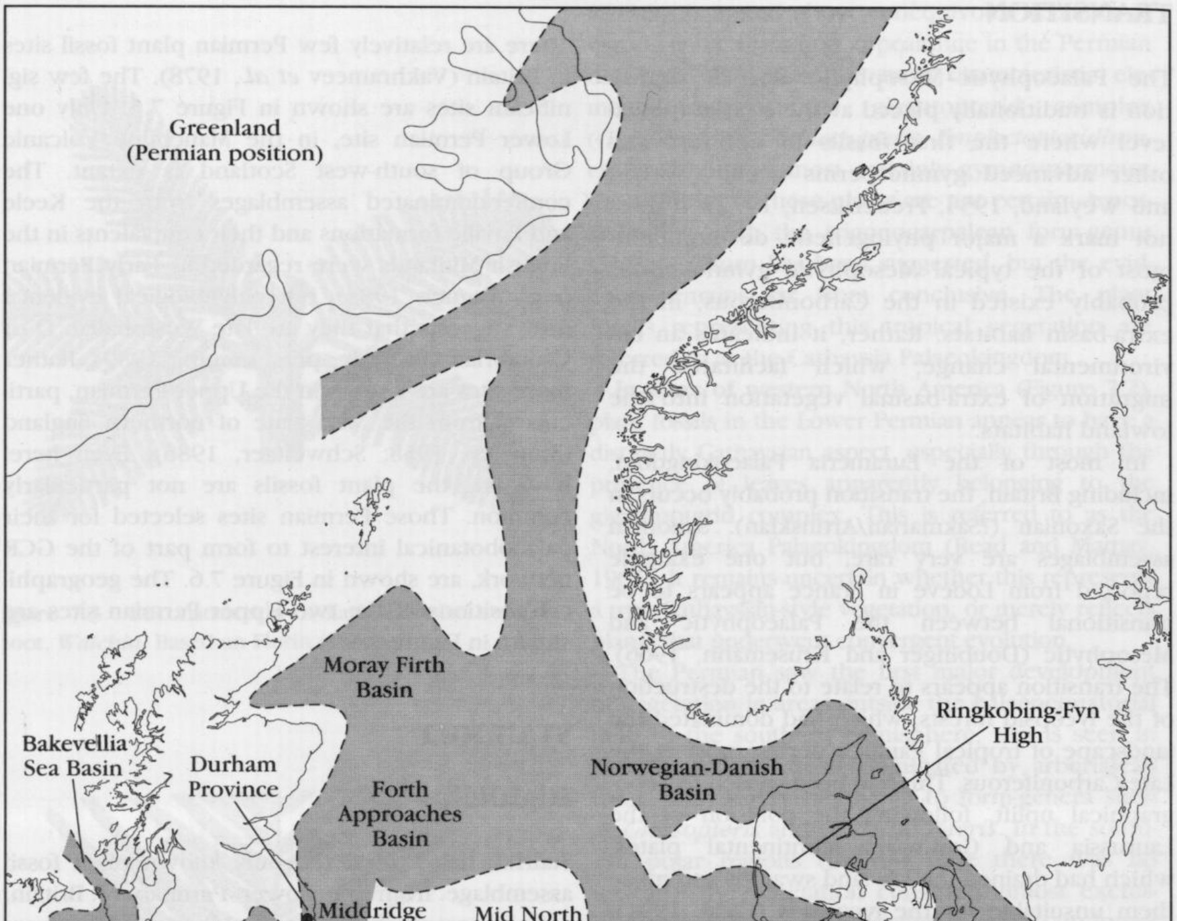

Figure 7.5 Main areas of Late Permian sedimentation in north-west Europe, showing principal palaeobotanical sites including the two GCR sites (Kimberley and Middridge). Based on Schweitzer (1986, figure 1).

Stairhill

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.

comprise part of the New Red Sandstone of the Mauchline Basin. Their chronostratigraphical position has been the matter of some debate, but the plant fossils suggest a probable early Autunian (Asselian) age (Wagner, 1983).

Palaeobotany

The plant fossils are preserved as impressions. The following species are known:

Equisetopsida:
Annularia stellata (Sternberg) Wood
A. cf. *spicata* Gutbier
Asterophyllites equisetiformis Brongniart

Filicopsida:
Lobatopteris geinitzii (Gutbier) Wagner
Remia pinnatifida (Gutbier) Knight
Pecopteris cf. *monyii* Zeiller

Cycadopsida:
Odontopteris subcrenulata var. *gallica* Doubinger and Remy

Interpretation

A variety of equisetopsid foliage was reported from Stairhill by Wagner (1983), who assigned most of that identified to the wide-ranging species *Annularia stellata* and *Asterophyllites equisetiformis*. A single specimen with smaller and stiffer-looking leaves was assigned to *Annularia* cf. *spicata*. However, these identifications may have to be revised in the light of the work of Kerp (1984b), who described rather similar foliage from the Lower Permian of Germany as *Annularia carinata* (Gutbier) Schimper. In the absence of any evidence of fructifications, or even of the morphology of the stem that bore the leaves, the status of these Stairhill leaves is difficult to judge.

The dominant fern in the assemblage is *Lobatopteris geinitzii*. Wagner (1983) gave a detailed systematic discussion of this species, particularly as to its position relative to the very similar *Lobatopteris polypodioides* (Sternberg) Knight, from which it differs by having somewhat larger, squatter pinnules. The Stairhill specimens provide no evidence of fertile structures, but German material (Göppert, 1864) shows *Cyathocarpus*-like sporangia. Together with the predominance of pinnatifid pinnules in the frond, this supports Wagner's inclusion of this species within the form-genus *Lobatopteris*.

Wagner (1983) described some other fern fragments with pinnatifid pinnules similar to those of

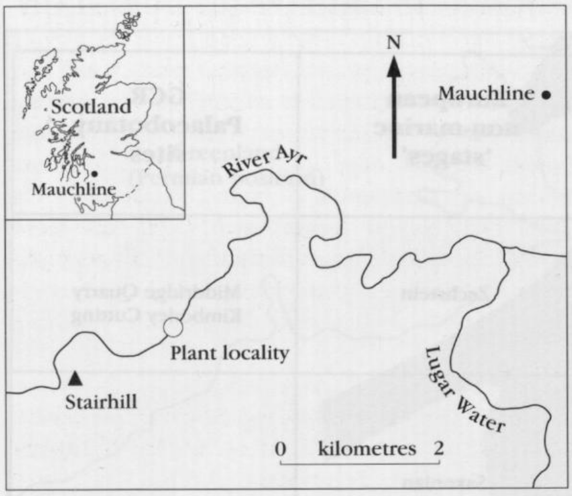

Figure 7.7 Location map for Stairhill. Based on Wagner (1983).

L. geinitzii. However, these have a denser venation with a different forking pattern, and so Wagner identified them as *Pecopteris pinnatifida*. No fertile specimens have so far been found at Stairhill. They are clearly similar, however, to the frond fragments from Spain, which bear sporangia known as *Remia* (Knight, 1985). Knight proposed that the species should be transferred to *Remia*, a view which is followed here.

A single, near-terminal pinna fragment from Stairhill has been compared with *Pecopteris monyii* by Wagner (1983), although he also pointed out that there was a possible comparison with *Pecopteris densifolia* Göppert. The Stairhill specimen has rather tapered pinnules, and so Wagner made the main comparison with *P. monyii*. A definite identification awaits the discovery of more specimens.

Pteridosperm remains all appear to belong to the medullosan frond species *Odontopteris subcrenulata*. Wagner (1983) assigned this species to the form-genus *Mixoneura*. The distinction between *Odontopteris* and *Mixoneura* is far from clear, however, and needs to be confirmed by additional evidence, such as epidermal structures. The traditional view is therefore accepted here, and the species retained in *Odontopteris*. The Stairhill specimens of *O. subcrenulata* have more or less 'square' lateral pinnules with a short midvein, and large apical pinnules. Wagner therefore assigned them to *O. subcrenulata* var. *gallica*, following the classification of Doubinger and Remy (1958).

Stairhill has yielded the only known Early Permian plant fossils from Britain. Assemblages from the Keele Formation of the English Midlands have been thought to be of similar age (Howell, 1859; Vernon, 1912; Dix, 1935), but recent palynological evidence suggests that at least part of the Keele Formation is late Westphalian D or Cantabrian (B. Besly pers. comm., 1989).

The Stairhill assemblage is in many ways typical of the Eurameria Palaeokingdom (i.e. semi-arid palaeoequatorial) in the Lower Permian. In continental Europe, comparable assemblages have been reported from the uppermost Stephanian and Autunian of both France and Germany (reviewed by Doubinger, 1956; Barthel, 1976; Kerp and Fichter, 1985). In particular, the occurrence of *Lobatopteris geinitzii* and *Odontopteris subcrenulata* var. *gallica* supports this comparison. In some ways, the Stairhill assemblage may be regarded as a remnant of the vegetation that flourished on the river levée-banks in the Carboniferous tropical forests, although the lycopsid-dominated swamp vegetation itself had already disappeared (except in China – see Li, 1980). In contrast, many of the coeval assemblages from continental Europe are dominated by conifers (e.g. *Walchia*) and peltasperms (e.g. *Autunia*), suggesting markedly drier edaphic conditions (Bouroz and Doubinger, 1977).

There is also some comparison with assemblages from the basal Permian of eastern North America, as reviewed by Read and Mamay (1964), although many of these have not been fully documented. The American assemblages share species of *Annularia*, *Odontopteris* and various pecopteroids with Stairhill. However, unlike Stairhill, they often have abundant peltasperms ('callipterids') and conifers. Further west, in Texas, Arizona and New Mexico, fossils are of plants belonging to the North America Palaeokingdom and are quite different from anything seen in Europe, with the occurrence of leaves resembling the gigantopterids of China. Elsewhere, the Lower Permian fossil floras are totally different from what is seen at Stairhill, with the gigantopteroid assemblages of the Cathaysia Palaeokingdom, the *Cordaites/Rufloria* assemblages of the Angara Palaeokingdom and the arberialean assemblages of the Gondwana Palaeokingdom (Vakhrameev *et al.*, 1978; Meyen, 1987; Allen and Dineley, 1988; Cleal and Thomas *in* Cleal, 1991).

Conclusion

Stairhill has yielded the only plant fossils of indisputably Early Permian age (about 295 million years old) in Britain. They can be compared with some of the floras from continental Europe, such as from southern France and Saarland, which are also dominated by horsetails, ferns and a group of seed plants known as the Trigonocarpales. However, most European floras of this age were growing in rather drier habitats, and as a consequence tended to be dominated by other types of seed plants, particularly conifers and the now extinct peltasperms. Plants at Stairhill represent the last, poor remnants of the luxurious tropical swamp-forests that were at their maximum development in the Late Carboniferous (see previous chapter).

MIDDRIDGE QUARRY

Highlights

Middridge Quarry has yielded the most diverse assemblage of plant fossils from the Upper Permian of Britain. It includes the best British examples of the conifer families Ullmanniaceae and Majonicaceae, and what may be the earliest British example of cycad foliage.

Introduction

The Upper Permian exposures near Bishop Auckland, County Durham, have long been famous for their plant fossils (Sedgwick, 1829; King, 1850; Kirkby and Duff, 1872; Howse, 1890; Stoneley, 1958; Mills and Hull, 1976). Most of the specimens were collected during the nineteenth century from localities which are no longer available. In 1977, however, a new exposure was made at Middridge Quarry, between Bishop Auckland and Newton Aycliffe (NZ 249252), which allowed Late Permian fossils to be collected in this area for the first time in nearly 100 years (Bell *et al.*, 1979). A useful summary of the palaeobotany of this site is provided by Schweitzer (1986).

Description

Stratigraphy

The geology of this site is described by Bell *et al.* (1979). The 'Basal' Permian Breccia lies unconformably on Langsettian (Upper Carboniferous) sandstones and shales, and is overlain by about 2.5 metres of mainly calcareous siltstones known as the Marl Slate. These are in turn overlain by massive dolomitic limestones of the Lower Magnesian Limestone. The plant fossils occur in the Marl Slate, which here represents a shallow water deposit formed near the margin of the Zechstein Sea. The plant remains were presumably transported into the sea by rivers. The Marl Slate has been interpreted as a lateral equivalent of the Kupferschiefer Formation of Germany, and thus probably belongs to the Kazanian Stage.

Palaeobotany

The plant fossils are preserved as adpressions, often with cuticles still present. The following species have been described to date:

Algae:
Algites virgatus (Munster) Stoneley

Equisetopsida:
Neocalamites mansfeldicus Weigelt

Peltaspermales:
Peltaspermum martinsii (Germar) Poort and Kerp

Cycadopsida(?):
Pseudoctenis middridgensis Stoneley

Pinopsida (?Ginkgoales):
Sphenobaiera digitata (Brongniart) Florin

Pinopsida:
Pseudovoltzia liebeana (Geinitz) Florin
Ullmannia frumentaria (Brongniart) Göppert
U. bronnii Göppert

Uncertain affinities:
'*Neuropteris' huttoniana* King
Psygmophyllum cuneifolium (Kutorga) Schimper
Lesleya eckhardtii (Kurtze) Remy and Remy
Plagiozamites middridgensis Schweitzer

Interpretation

A single Middridge specimen was described briefly by Stoneley (1958) as *Algites virgatus*. It shows slender, forking axes originating from a basal patch of carbonized tissue (?holdfast). Two of the axes bear a terminal 'plume-like' structure, although no details were preserved. Similar, albeit smaller, bodies are present in the holotype specimen of the species figured by Munster (1842).

Stems and foliage of the equisetopsid *Neocalamites mansfeldicus* were first recorded from Middridge by Bell *et al.* (1979). Stoneley (1958) recorded examples of similar stems from other localities in north-east England as *Paracalamites kutorgai* (Geinitz) Zalessky, which she regarded as an earlier synonym of *N. mansfeldicus*. However, *P. kutorgai* probably belongs to the equisete family Tchernoviaceae, which is restricted to Angaran assemblages (Meyen, 1971) and would thus not be expected to occur in Britain. As the fructifications of *N. mansfeldicus* are unknown, there seems little justification at this stage for combining it in synonymy with this Angaran species.

Both King (1850) and Bell *et al.* (1979) record '*Neuropteris' huttoniana* from Middridge, but the specimens have not been illustrated. Stoneley (1958) referred to this taxon as *Mixoneura* sp., but it does not have the broadly attached pinnules seen in the type-species of this form-genus (*Odontopteris subcrenulata* (Rost) Zeiller). Equally, however, it is unlikely to belong to *Neuropteris* (as originally assigned by King, 1850) as interpreted by Cleal *et al.* (1991), since this is mainly restricted to Westphalian assemblages. Stoneley suggested a comparison with *Neurocallipteris neuropteroides* (Göppert) Cleal *et al.*, but that species has never previously been reported from higher than the Lower Permian. Establishing the taxonomic position of this Middridge species will have to wait until larger specimens become available to determine the frond architecture, and also preferably with cuticles preserved.

Although neither Stoneley (1958) nor Townrow (1960) record *Peltaspermum martinsii* from Middridge, it is listed (but not figured) by Bell *et al.* (1979), Schweitzer (1986) and Poort and Kerp (1990).

Another type of foliage was described by Stoneley (1958) as ?*Psygmophyllum cuneifolium*, a species belonging to the pteridosperm order Peltaspermales. Although showing some similarities to fragments of cycad frond, they have a more complex architecture, consisting of both sub-dichotomous and pinnate branching. Fragments of cuticles prepared from the Middridge specimens show sunken, cyclocytic stomata not arranged in distinct bands, and thus quite compatible with the epidermal structure usually associated with *Psygmophyllum* (Meyen, 1987). Whether the comparison with *P. cuneifolium*, a species more usually associated with Angaran assemblages, is valid will have to await the discovery of more complete material.

Stoneley (1958) based her description of *Pseudoctenis middridgensis* on a single fragment from Middridge, although Bell *et al.* (1979) report that they have since found additional material. Small fragments of adaxial cuticle prepared from the Stoneley specimen showed simple intercellular flanges (anticlinal walls), which preclude the assignment of the frond fragment to the Bennettitales, and Schweitzer (1986) argued that it probably belonged to the cycads. However, no evidence of abaxial cuticle was found. Consequently the stomatal structure, which is a key feature for recognizing *Pseudoctenis* (Harris, 1964), is unknown. If correctly assigned, it would be the only cycad frond found below the Mesozoic in Britain, although cycad remains have been reported from the Lower Permian of China (Gao and Thomas, 1989).

Sphenobaiera digitata is also listed, but not figured, from here by Stoneley (1958) and Bell *et al.* (1979). None of the Middridge specimens were found to yield cuticles, but Stoneley figures examples from Hilton Beck with sunken stomata surrounded by prominent papillae, of a type normally associated with this species. Stoneley (1958) and Schweitzer (1986) referred the species to the Ginkgoales, following Florin (1936), which would have made it the earliest example of the order known from Britain. In the absence of evidence of its fructifications, its taxonomic position must be regarded as provisional (the 'capsule' from Hilton Beck described by Stoneley is neither attached to *Sphenobaiera* foliage nor does it show any structure).

By far the most abundant plant fossils found at Middridge are conifer twigs, belonging to *Ullmannia* (Ullmanniaceae) and *Pseudovoltzia* (Majonicaceae). These two form-genera are best distinguished by their fertile structures, the epidermal structures being essentially indistinguishable. The naming of the Middridge conifers has relied on the leaf morphology, which must clearly raise some doubt as to the reliability of the identifications.

Pseudovoltzia shoots tend to be extremely heterophyllous, with needle-like leaves anything up to 20 mm long. Although not reported to date from Middridge, the characteristic lobed cone-scales of this group of conifers has been found at other Marl Slate localities, such as Kimberley Railway Cutting (see below). Stoneley (1958) identified all the Marl Slate specimens as *P. liebeana*, the best known species of the form-genus.

The leaves of *Ullmannia frumentaria* (Figure 7.8) are very similar to the above, except that they tend to be laxer and lie more parallel to the stem. Attached to one such shoot, Stoneley (1958) described what may be a female cone, similar in shape to *U. frumentaria* cones reported from Germany (Florin, 1938–1945), although no structure is preserved.

A specimen with smaller, broader leaves was described by Stoneley (1958) as *Ullmannia bronnii*, and further specimens as *Hiltonia rivulii* Stoneley. They were distinguished from *U. bronnii* by the leaves having a rounder apex, a decurrent base and no clearly marked vein. Also mentioned were differences in the thickness of the walls of the subsidiary cells surrounding the stomata. However, Schweitzer (1962) has shown that these differences are not sufficient to justify the separation of the two species, and that they should be regarded as synonymous.

A single problematic specimen was described by Stoneley (1958) as *Taeniopteris eckhardtii* Kurtze. Although fragmentary and without cuticles preserved, it shows a thick mid-vein and simple, straight lateral veins, very similar to the specimens from the Kupferschiefer of Mansfeld in Germany, the type area of this species (Schweitzer, 1968, fig. 4). Remy and Remy (1977) have argued that this type of nervation pattern is more characteristic of the form-genus *Lesleya*, to which they transferred Kurtze's species. The taxonomic position of this species is totally unclear. Schweitzer (1986) argued that it was most likely cycad foliage, but Meyen (1987) regarded at least some *Lesleya* leaves as belonging to the Dicranophyllales, a primitive order of conifer-like plants, that became extinct at the end of the Permian.

Plagiozamites bellii, for which Middridge is the type locality, has been interpreted as shoots with helically arranged leaves up to 90 mm long (Schweitzer, 1986). Although some details of the epidermal structure are known, including stomata, the affinities of the shoots are unclear beyond that they are almost certainly gymnospermous.

Plant fossils are known from a number of exposures of the Marl Slate and its lateral equivalents in northern England (evidence reviewed by Stoneley, 1958). Of these, Middridge Quarry has yielded the most diverse assemblage of abundant plant remains. The nearest comparison is with the Hilton Beck Plant Bed in Cumbria (Murchison and Harkness, 1864; Stoneley, 1958), but that locality has not yielded the *Pseudoctenis*, *Lesleya*, *Psygmophyllum*, *Plagiozamites* or '*Neuropteris*' species found at Middridge. The assemblage from Kimberley Railway Cutting in Nottinghamshire (see below) is also not as diverse as that from Middridge, although it has yielded rather better examples of the peltasperm *Peltaspermum*.

The Marl Slate assemblage belongs to the Atlantic Palaeoarea of Vakhrameev *et al.* (1978) (also called the Zechstein 'flora' by Meyen, 1987), which probably extended throughout present-day Europe, although the fossil evidence is relatively sparse. This is a subdivision of the Europe Palaeokingdom of Cleal and Thomas (*in* Cleal, 1991; see also Figure 7.2). The closest comparison outside of Britain is with the flora from the Kupferschiefer of the Lower Rhine, Saxony and Thuringia in Germany (Schweitzer, 1962, 1968, 1986), and Pec (formerly Funfkirchen) in Hungary (Heer, 1876). These continental localities yield

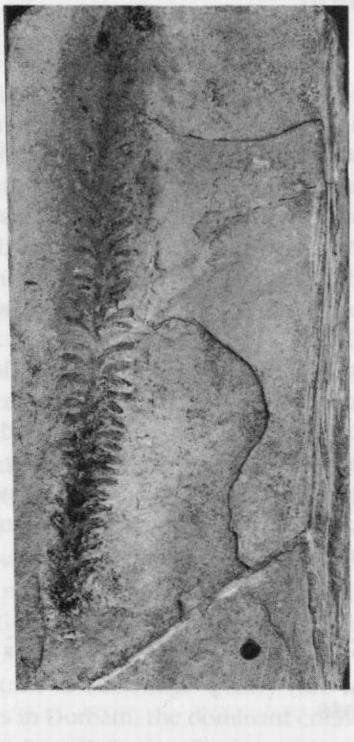

Figure 7.8 *Ullmannia frumentaria* (Brongniart) Göppert. Conifer shoot; Natural History Museum, London, specimen V.35130. Marl Slate (Upper Permian), Middridge Quarry. × 0.5. (Photo: Photographic Studio, Natural History Museum, London.)

most of the species contained in the British assemblages. However, they also include a number of species not found in Britain, such as the conifers *Quadrocladus*, *Culmitzischia* and *Rhenania*.

The vegetation represented by the Atlantic Palaeoarea is thought to reflect the relatively sparse vegetation growing in semi-arid conditions around the hypersaline Zechstein Sea. It contrasts markedly with the situation further east in the palaeoequatorial belt, such as in China, where the vegetation was dominated by lush, lycopsid-dominated swamp-forests (Li, 1980). This difference in vegetation was probably the result of the collision between the Gondwana and Laurussia continental plates during the very late Carboniferous. The collision would have had its maximum effect in Europe and North America, and the resulting topographical changes there would have caused a marked lowering of the water-table, making conditions unsuitable for the growth of the swamp-forests. China escaped the effects of this orogenic event, however, thus allowing the lycopsid-dominated swamp-forests to persist there.

Conclusion

Middridge Quarry is the best site in Britain for fossils of Late Permian plants, about 270 million years old. Similar fossil floras have been reported from Germany and Hungary, and are thought to represent the vegetation surrounding a large, inland sea that covered parts of northern and central Europe – the Zechstein Sea. Conifers are the dominant plants in the flora, mainly preserved as fragments of leafy shoot, but occasionally with reproductive cones. They belong to two families (Ullmanniaceae and Majonicaceae) that flourished in the Late Permian, but then became extinct at the end of the period. Far less abundant, but nevertheless of considerable evolutionary interest, are fragments that may represent early cycads and ginkgos that later, in the Mesozoic, became major components of the vegetation in Britain.

KIMBERLEY RAILWAY CUTTING

Highlights

Kimberley Railway Cutting is the best British locality for the Late Permian *Peltaspermum martinsii*, the only good example of the Peltaspermaceae known from this country.

Introduction

There are a number of early records of plant remains from the now disused railway cutting (SK 500452) in the village of Kimberley, Nottinghamshire (Wilson, 1876, 1881; Smith, 1913; Carr, 1914) and Carruthers (*in* Wilson, 1881) compared them with the Permian floras of continental Europe. The first species list was not, however, published until Stoneley's (1958) monograph on the British Permian plant fossils. Most recently, Townrow (1960) described specimens from here in his study on the pteridosperm family Peltaspermaceae.

Description

Stratigraphy

About 10 metres of Upper Permian strata are exposed, lying unconformably on Westphalian (Upper Carboniferous) shales. A thin 'Basal' Permian Breccia is overlain by Marl Slate (the Lower Permian Marls of some authors), which in turn is overlain by Lower Magnesian Limestone. Plant fragments occur throughout the Marl Slate part of the sequence, but the most abundant and well-preserved material occurs in clay bands just below the junction with the Lower Magnesian Limestone. As at Middridge Quarry (see above), the Marl Slate here probably belongs to the Kazanian Stage, and was deposited in a shallow marine environment.

Palaeobotany

The plant fossils are preserved here as adpressions, sometimes with cuticles preserved. The following species have been reported so far:

Peltaspermales:
- *Peltaspermum martinsii* (Germar) Poort and Kerp

Pinopsida:
- *Pseudovoltzia liebeana* (Geinitz) Florin
- *Ullmannia bronnii* Göppert
- *Samaropsis triangularis* (Geinitz) Seward

Interpretation

P. martinsii is now taken as a 'natural, whole-plant' species (Poort and Kerp, 1990). This is based on the presumed connection between fronds previously known as *Lepidopteris martinsii* (Germar) Townrow and ovulate structures identified as *Strobilites bronnii* Solms-Laubach. So far, a connection between these organs has not been proved, but there is a consistent association between them, including at Kimberley Cutting, and a close similarity in their epidermal structure. The ovulate structures were initially regarded as fragments of conifer male-cone (Florin, 1938–1945). However, Poort and Kerp (1990) demonstrated that they have ovules attached to small, peltate discs, similar to those of *Peltaspermum ottonis* (Harris) Poort and Kerp from the Rhaetian of Greenland.

Fragments of *P. martinsii* foliage described by Stoneley (1958) and Townrow (1960) have yielded details of the frond architecture, particularly the presence of intercalated pinnules on the main rachis. They have also yielded cuticles, showing that stomata occur on both abaxial and adaxial surfaces of the leaf. Stoneley argued that the British specimens differed from those from Germany described by Gothan and Nagalhard (1922) in not having a papilla on each of the epidermal cells, but, by staining the cuticles with safranin, Townrow was able to demonstrate that epidermal papillae are present in at least some of the British specimens. The taxonomic significance of these epidermal papillae is thus doubtful (Townrow suggested that their presence or absence might be controlled by pinnule shape), and the German and British specimens are almost certainly specifically identical.

Figure 7.9 *Samaropsis triangularis* (Geinitz) Seward. Conifer seed; Natural History Museum, London, V.6209. Marl Slate (Upper Permian), Kimberley Railway Cutting. × 3. (Photo: Photographic Studio, Natural History Museum, London.)

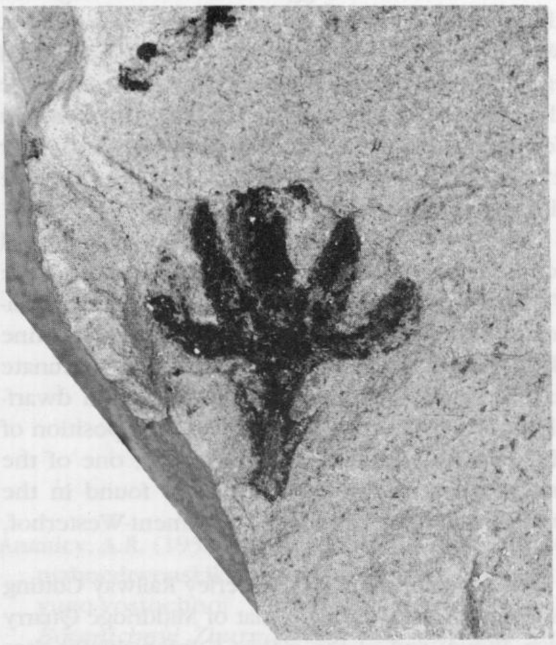

Figure 7.10 *Pseudovoltzia liebeana* (Geinitz) Florin. Cone scale from a conifer; Natural History Museum, London, specimen V.35128. Marl Slate (Upper Permian), Kimberley Railway Cutting. × 3. (Photo: Photographic Studio, Natural History Museum, London.)

In contrast to Middridge Quarry (see above) and other sites in Durham, the dominant conifer remains at Kimberley Railway Cutting are shoots of *Ullmannia bronnii* (synonym *Hiltonia rivulii* Stoneley, 1956). *U. frumentaria*, the dominant form at Middridge, has not so far been reported here.

Small, winged seeds were identified by Stoneley (1958) as *Samaropsis triangularis* (Figure 7.9).

Some authors have suggested that these might be the seeds of *Ullmannia frumentaria* (e.g. Weigelt, 1928), but Florin (1938–1945) reported rather differently shaped seeds attached to the dwarf shoot of that species. That *U. frumentaria* foliage has yet to be found at Kimberley is further evidence against this suggestion. It is instead more likely that they are the seeds of *U. bronnii*.

Stoneley (1958) reported examples of the lobed 'cone scales' of *Pseudovoltzia liebeana* (Figure 7.10), but she illustrated them by only a diagrammatic silhouette, revealing nothing of their fine detail (if any was preserved). This is unfortunate as the detailed structure of the bract and dwarf-shoot is a key feature for justifying the position of this species within the Majonicaceae, one of the most important families of conifer found in the palaeoequatorial Permian (Clement-Westerhof, 1987, 1988).

The assemblage from Kimberley Railway Cutting is meagre compared with that of Middridge Quarry (see above) and of the classic Kupferschiefer sites in Germany (Schweitzer, 1962, 1968). It is of significance, however, as the best British locality for *Peltaspermum martinsii*. This species is the only well-documented British representative of the Peltaspermaceae, one of the very few families of land plants that survived the Palaeophytic–Mesophytic floral transition, discussed in the introduction to the present chapter.

Conclusion

Kimberley Railway Cutting is the best British locality for the group of seed plants with fern-like fronds, known as the Peltaspermaceae. The family is now extinct, but during the Permian and the succeeding Triassic Period (290–205 Ma) it was an important element of the equatorial vegetation. These British examples are about 270 million years old. It was one of the very few families of land plant to have survived the large-scale vegetational change that occurred between the Palaeozoic and Mesozoic eras, around 250 million years ago, as discussed earlier in this chapter.