Palaeozoic Palaeobotany of Great Britain

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GCR Editor: W.A. Wimbledon and D. Palmer

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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.

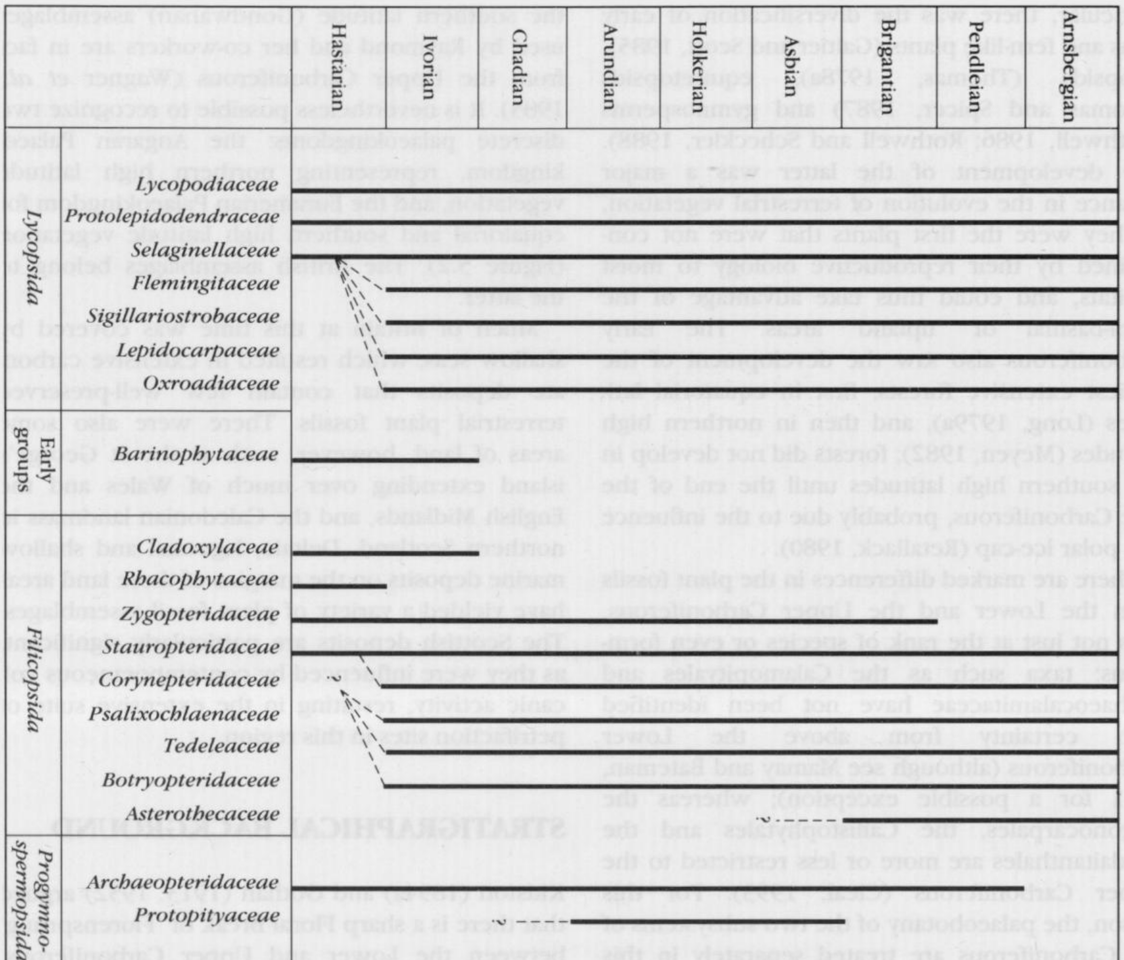

Figure 5.1 The distribution of families of vascular plants in the Early Carboniferous. Based on data from Cleal (1993).

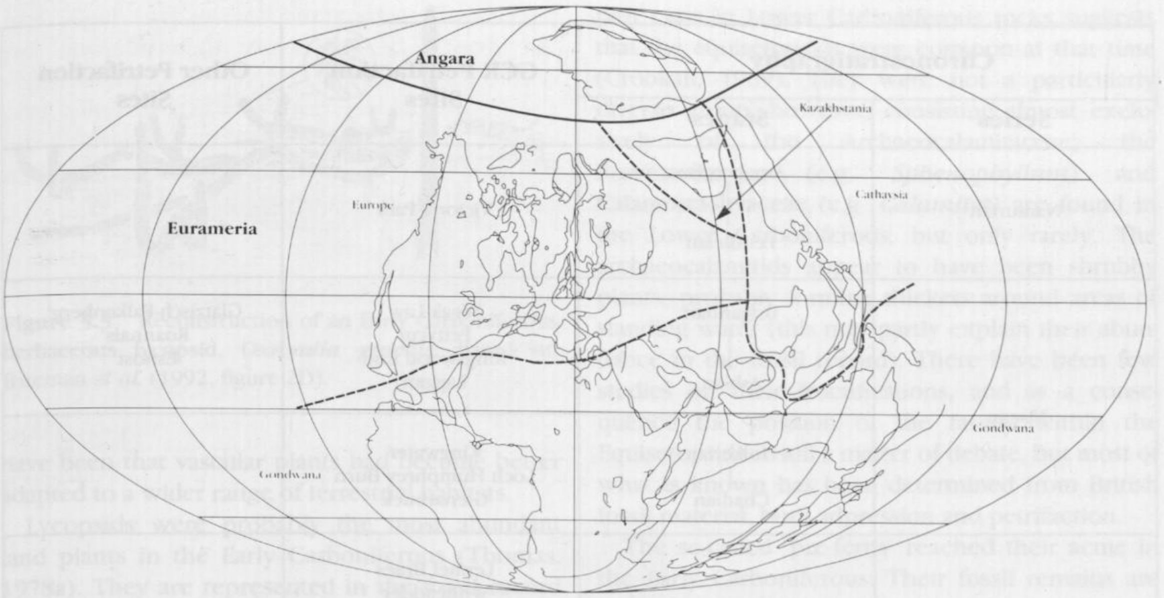

Figure 5.2 The palaeogeography of the Early Carboniferous, showing the distribution of the major floristic zones (phytochoria). Based on Scotese and McKerrow (1990) and Cleal and Thomas *in* Cleal (1991).

Chronostratigraphy		Plant Fossil Biostratigraphy	GCR Adpression sites	Other significant Adpression sites (Palaeoequatorial Belt)
Series	Stages			
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 Arundian	*Lyginopteris bermudensiformis/ Neuropteris antecedens*	Puddlebrook Quarry Moel Hirradug Teilia Quarry Wardie Shore Glencartholm Loch Humphrey Burn	Horton Group[4] Upper Silesia[5]
	Chadian	*Triphyllopteris*		Pocono Formation[1] Geigen near Hof[2] Doberlug-Kirchhain[2] Valdeinfierno[3] Horton Group[4]
Tournaisian	Ivorian			
	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 Pettycur Kingswood End Laggan	Glätzisch-Falkenberg[2] Roannais[1] Esnost[1]
	Holkerian Chadian	Kingwater Loch Humphrey Burn Glenarbuck	
Tournaisian	Ivorian	Lennel Braes Whiteadder Oxroad Bay Loch Humphrey Burn	
	Hastarian		New Albany Shale[3] Saalfeld[2] 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).

The series and stages referred to in this work (see Figures 5.3 and 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 (Figures 4.1 and 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

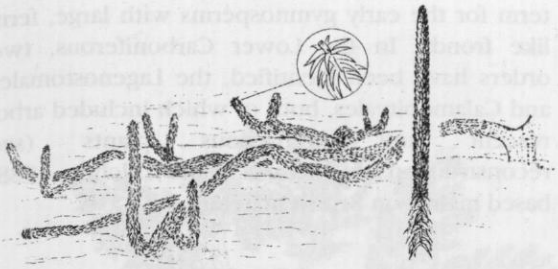

Figure 5.5 Reconstruction of an Early Carboniferous herbaceous lycopsid, *Oxroadia gracilis*. Based on Bateman *et al.* (1992, figure 2D).

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 arborescent (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 pteridospermous 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 (Figures 5.6, 5.7 and 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, fern-like fronds. In the Lower Carboniferous, two orders have been identified, the Lagenostomales and Calamopityales, both of which included arborescent 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

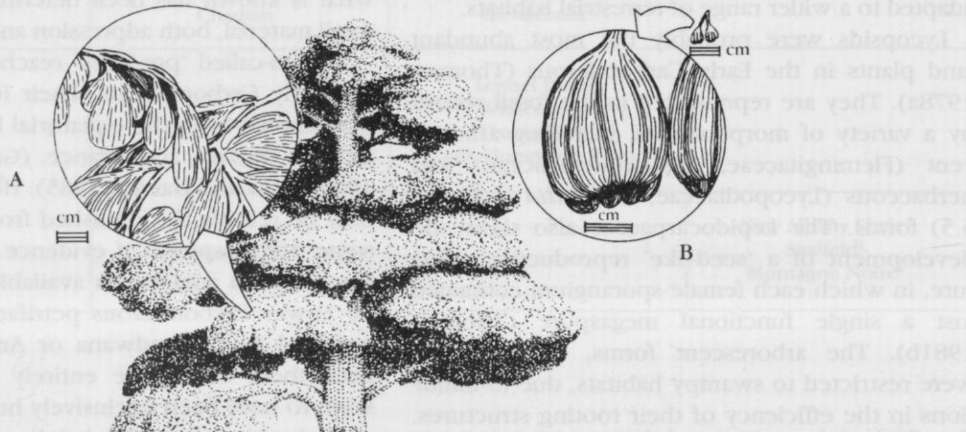

Figure 5.6 Reconstruction of the Early Carboniferous lagenostomalean pteridosperm tree *Stamnostoma*, with insets showing details of foliage (A), pollen organs (B) and seeds (C). Based on Retallack and Dilcher (1988).

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

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.

LENNEL BRAES

Highlights

Lennel Braes is of considerable historical interest as being the origin of some of the earliest described thin sections of fossil wood. The techniques developed here were of fundamental significance to the development of palaeobotany and petrology.

Introduction

This locality, in the bed of the River Tweed, near Coldstream, Borders Region, Scotland (NT 855410), is one of many Cementstone Group sites in the Scottish borders to yield plant petrifactions.

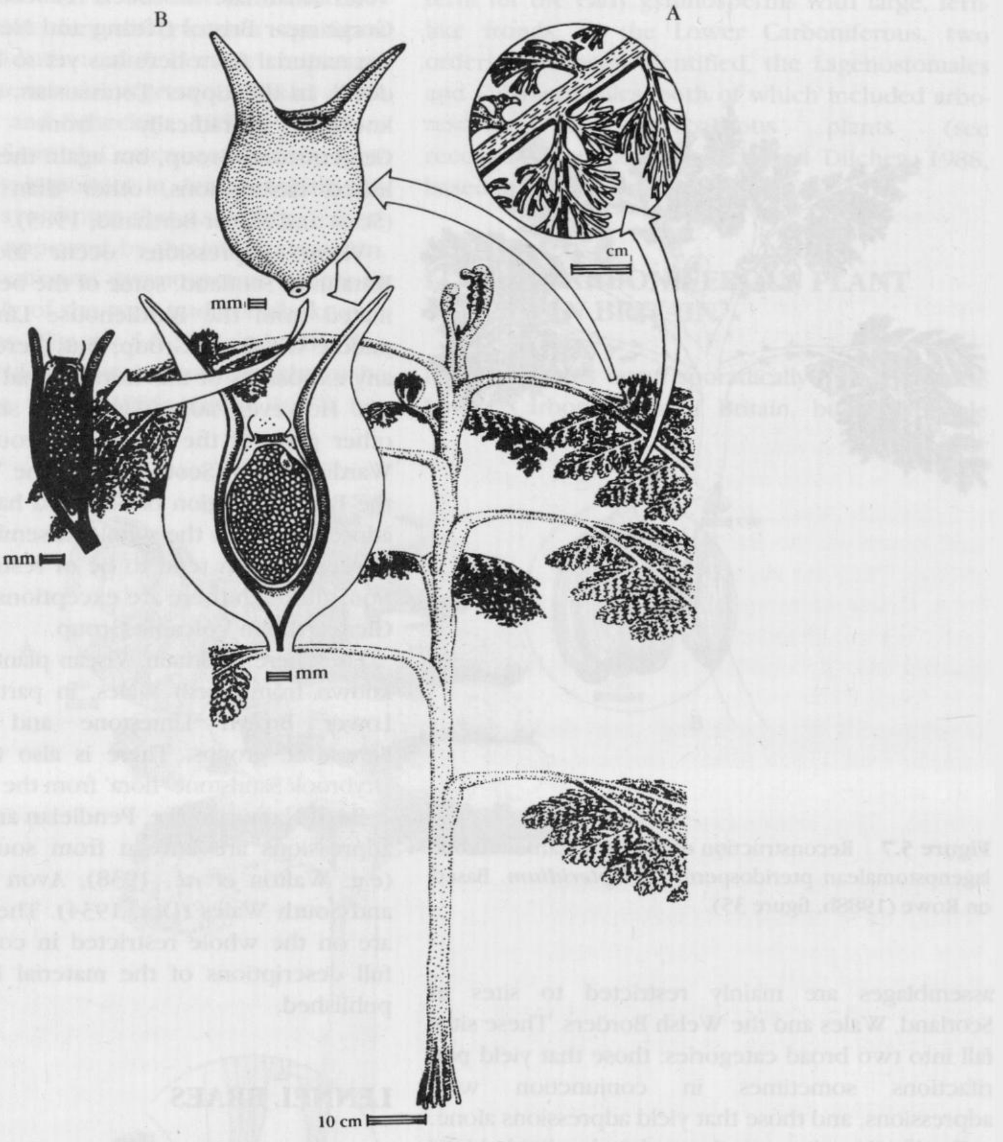

Figure 5.8 Reconstruction of the Early Carboniferous calamopityalean pteridosperm *Lyrasperma*, with insets showing details of foliage (A) and seeds (B). Based on Retallack and Dilcher (1988).

It is of particular historical interest, however, as the origin of some of the specimens used in Witham's pioneering work on fossil wood thin sections (Witham, 1831, 1833; see also Scott, 1899). Subsequently, adpressions were recorded from here by Kidston (1901a, 1923c, 1924), and further petrifactions by Long (1963, 1964a, 1975).

Description

Stratigraphy

The only account of the stratigraphy is that given by Witham (1831). It is unclear where precisely in the Cementstone Group the concretion-bearing shales lie. Not all the 14 metres of rock described by Witham can still be seen, but the shales at the base of the section are still exposed and are

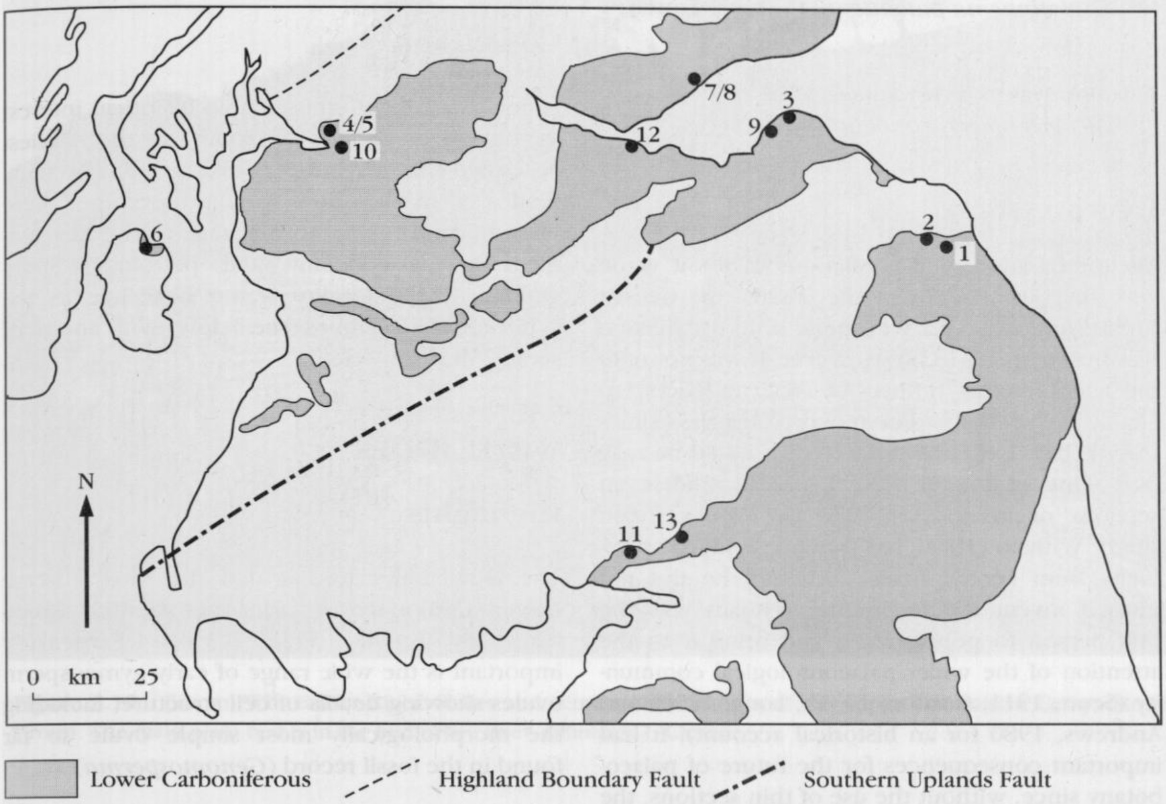

Figure 5.9 Distribution of Lower Carboniferous rocks in Scotland, showing location of GCR palaeobotany sites. 1 – Lennel Braes; 2 – Whiteadder; 3 – Weak Law; 4 – Loch Humphrey Burn; 5 – Glenarbuck; 6 – Laggan; 7 – Pettycur; 8 – Kingswood End; 9 – Oxroad Bay; 10 – Victoria Park; 11 – Glencartholm; 12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

where Long (1963) reported plant fossils. Stratigraphically diagnostic faunas have not been reported from here and so its exact age is uncertain. However, evidence from other localities suggest that the Cementstone Group is mainly late Tournaisian (Scott *et al.*, 1984). The environment represented was probably lacustrine.

Palaeobotany

Only a limited assemblage has been reported from here to date, including the following petrifactions, all of which are pteridosperm (probably Lagenostomopsida and Calamopityales) remains.

Pitus antiqua Witham
Lyginopteris papilio Kidston
Stenomyelon tuediana Kidston and
    Gwynne-Vaughan
Dolichosperma pentagonum Long
Eurystoma burnense Long

In addition, the following adpressions have been found:

Lycopsida:
  Lepidodendron sp.
  Stigmaria ficoides (Sternberg) Brongniart

Lagenostomopsida:
  Diplothmema patentissima (Ettingshausen) Stur

Calamopityales (*incertae sedis*):
  Alcicornopteris convoluta Kidston

Interpretation

The preparation of thin sections of fossil wood was first developed in the 1820s by George Sanderson and an early example of its application was by Sprengel (1828). However, it was not until the method was refined by William Nicol, to enable the sections to be mounted on glass slides (Nicol, 1834), that its full potential could be realized. One of the most widely read studies on sections of fossil wood was by Nicol's friend Henry Witham (1831, 1833), who included specimens from Lennel Braes. Although he did not himself invent the technique, Witham was the first person to popularize it and bring it to the attention of the wider palaeontological community (Scott, 1911; Gordon, 1935b; Long, 1959a and Andrews, 1980 for an historical account). It had important consequences for the future of palaeobotany since, without the use of thin sections, the discoveries in the Rhynie Chert (see Chapter 4) and the Pennsylvanian coal-balls would have been impossible. It was also of major importance in petrology, since the experience obtained from sectioning such fossils was later applied to making rock sections (Sorby, 1858). As pointed out by Gordon (1935b), however, a more regrettable side-effect was that it tended to cause palaeobotany to be divided into biological and geological camps, a problem which still hinders the development of the subject today.

Witham described sections from a number of other Carboniferous and Jurassic localities, as well as Lennel Braes. The latter is the only one for which he gives a detailed account of the geology, however, and the only one from which material can still be collected.

Witham concluded that the fossil wood from Lennel Braes was coniferous, which appears to explain his use of the generic name *Pitus* (Witham, 1833). However, this has since been recognized to be incorrect, and at various times it has been assigned to the cordaites (Scott, 1902) and progymnosperms (Beck, 1960); but the currently available evidence now points to it being from lagenostomalean pteridosperm trunks (Long, 1963, 1979a).

Conclusion

Lennel Braes is of considerable historical interest as being the origin of some of the earliest described thin sections of fossil wood. The techniques of making thin sections developed here were of fundamental significance to the development of palaeobotany and petrology. Stratigraphically the locality is the same age as the Whiteadder limestones (see below) with an age of some 350 Ma.

WHITEADDER

Highlights

The Whiteadder has yielded the most diverse Lower Carboniferous plant petrifaction assemblage in Britain (Figure 5.10). Particularly important is the wide range of early gymnosperm ovules showing details of cell structure, including the morphologically most simple ovule so far found in the fossil record (*Genomosperma*).

Introduction

The Whiteadder River is a tributary of the Tweed, which it joins about 3 km south-west of Berwick-upon-Tweed, Borders Region (Figure 5.11). Finely preserved plant petrifactions have been reported from the limestones of the Tournaisian Cementstone Group exposed between Hutton Bridge (NT 921546) and Cumledge (NT 792564), and particularly from Edrom (NT 821560). Fossils were occasionally recorded from here during the nineteenth century (e.g. Witham, 1830), but it was not until the site was investigated during the early years of the twentieth century by A. Macconochie for the Geological Survey that its real palaeobotanical potential started to be realized. Initially, only adpressions were found, although petrifactions were known from homotaxial strata in the Tweed valley and at Langton Burn (Kidston, 1901a), but petrifactions were soon also found at the Whiteadder (Kidston, 1902a). Kidston clearly recognized the importance of the Berwickshire

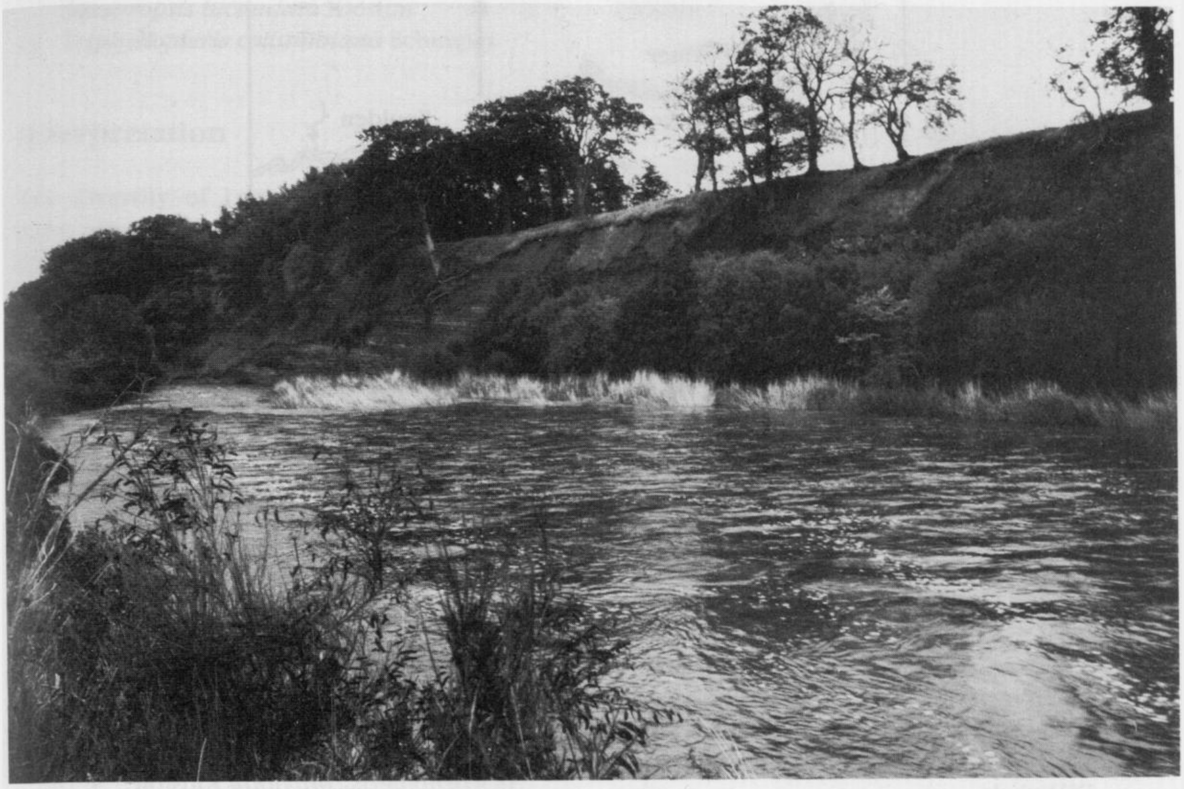

Figure 5.10 Edrom, Whiteadder River. Shales and cemented mudstones of the upper Tournaisian Cementstone Group. The main plant bed is in the bed of the river. (Photo: C.J. Cleal.)

petrifactions and had numerous thin sections prepared. One paper, intended to be the first of a series, was written in 1912 with Gwynne-Vaughan. However, the project was prematurely terminated, partly because of the death of the latter in 1915, and partly because of the discovery of plant fossils at Rhynie (see Chapter 4), which diverted Kidston's attention. Some of Kidston's Whiteadder slides were described by Solms-Laubach (1910), Gordon (1912) and Calder (1934, 1938), and there was also some interest in the adpressions (Chaloner, 1953). It was not until Long started to re-investigate the fossils from here in 1957, that the significance of the assemblage became evident. In a series of papers published since 1959, Long has described 40 form-species, many of which were new to science. Long's work, which for the first ten years he effectively did as an amateur (Long, 1976c; Andrews, 1980), ranks as one of the most significant contributions to British palaeobotany this century.

Description

Stratigraphy

The strata exposed along this stretch of the Whiteadder belong to the Cementstone Group, and comprise mainly alternating shales and harder bands of calcareous rocks, known as cementstones. The majority of the cementstones are calcareous mudstones, probably of diagenetic origin. However, they also include lacustrine, shelly limestones, and it is these that contain the plant petrifactions (Scott *et al.*, 1984; Scott and Rex, 1987). A measured stratigraphical log for the section has never been published, although general descriptions are given by Scott *et al.* (1984). Miospores obtained from both the shales and the lacustrine limestones at Edrom belong to the CM Biozone, thus indicating a late Tournaisian age. The plant adpressions (see next section) appear to belong to the upper *Triphyllopteris* Biozone, which according to Wagner (1984) indicates an

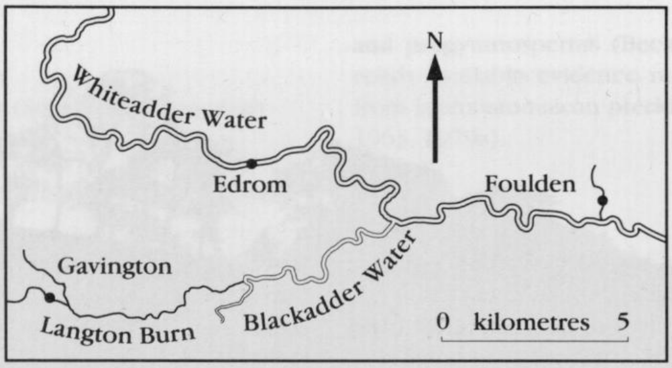

Figure 5.11 Location map for the Whiteadder GCR palaeobotany site. Based on Scott *et al.* (1984, figure 14).

early Visean age. However, few of the adpressions have been studied in recent years and a revision is necessary to verify their biostratigraphical positions.

Palaeobotany

The following taxa have been described from here as petrifactions:

Lycopsida:
- *Lepidodendron calamopsoides* Long
- *Paralycopodites brevifolius* (Williamson) DiMichele
- *Stigmaria* sp.
- *Oxroadia gracilis* Alvin
- *Mazocarpon pettycurense* Benson

Filicopsida:
- *Cladoxylon kidstonii* Solms-Laubach
- *C. waltonii* Long
- *Hierogramma mysticum* Unger
- *Clepsydropsis antiqua* Unger
- *Protoclepsydropsis kidstonii* (Bertrand) Hirmer
- *Psalixochlaena berwickense* Long
- *Stauropteris berwickensis* Long

Lagenostomopsida:
- *Genomosperma kidstonii* (Calder) Long
- *G. latens* Long
- *Hydrasperma tenuis* Long
- *Stamnostoma huttonense* Long
- *S. bifrons* Long
- *Salpingostoma dasu* Gordon
- *Calathospermum fimbriatum* Barnard
- *Deltasperma fouldenense* Long
- *Eosperma edromense* Long
- *Eccroustosperma langtonense* Long
- *Camptosperma berniciense* Long
- *Telangium* sp.
- *Tristichia ovensii* Long
- *Rhetinangium arberi* Gordon
- *Lyginorachis kidstonii* Long
- *L. arberi* Long
- *L. papilio* Long
- *Pitus primaeva* Witham

Calamopityales (*incertae sedis*):
- *Eurystoma angulare* Long
- *E. burnense* Long
- *Lyrasperma scotica* (Calder) Long
- *Dolichosperma sexangulatum* Long
- *D. pentagonum* Long
- *Alcicornopteris convoluta* Kidston
- *Stenomyelon tuedianum* Kidston
- *S. heterangioides* Long
- *S. primaevum* Long
- *Kalymma tuediana* Calder

Uncertain affinities:
- *Mitrospermum bulbosum* Long
- *Cystosporites devonicus* Chaloner and Pettit
- *Triradioxylon primaevum* Barnard and Long
- *Lyginorachis whitadderensis* Barnard and Long

In addition, a number of taxa have been described from adpressions found in the shales:

Lycopsida:
- *Lepidodendron veltheimii* Sternberg
- *L. rhodeanum* Sternberg
- *L. spetsbergense* Nathorst
- *L. nathorstii* Kidston
- *L. berwickense* Crookall
- *Flemingites allantonensis* (Chaloner) Brack-Hanes and Thomas
- *Stigmaria ficoides* (Sternberg) Brongniart

Lagenostomposida:
- ?*Sphenopteridium pachyrrachis* (Göppert) Schimper

Calamopityales (*incertae sedis*):
Samaropsis bicaudata Kidston
Triphyllopteris collumbiana Schimper

Interpretation

The diversity of Lower Carboniferous petrified plant remains found along the Whiteadder is unrivalled anywhere in the world. However, the significance of the site lies not just in the number of taxa that it yields, but also in the importance of many of the individual species for understanding the evolution of Early Carboniferous plants. In order to assess this, the following discussion will deal separately with each of the classes of plant represented.

Lycopsida

Arborescent lycopsids are amongst the commonest plant remains found along the Whiteadder, but have been relatively ignored. Long (1964c, 1971) briefly described petrified aerial stems of *Lepidodendron calamopsoides* (believed to be equivalent to the adpression species *L. spetsbergense*, *L. nathorstii* and *L. berwickense* – Long 1971) and *Paralycopodites brevifolius*, and stigmarian rooting structures. Long (1971) also described some petrifactions of the herbaceous lycopsid *Oxroadia gracilis* from here, providing the first evidence of its rooting structures.

Few lycopsid fructifications have been reported here. Chaloner (1953) described a compression now known as *Flemingites allantonensis* (see also Crookall, 1966), which is very similar in general structure and dimensions to the petrified *Flemingites scottii* (Jongmans) Brack-Hanes and Thomas, the presumed strobilus of *Paralycopodites brevifolius* from Pettycur (see below). Long (1968a) also described two incomplete petrified sporophylls as *Mazocarpon pettycurense*. Little can be determined from these latter specimens, but they are of interest as the oldest known examples of the Sigillariaceae, one of the lycopsid families that came to dominate the equatorial swamp forests later in the Carboniferous.

Cystosporites devonicus was described from here by Long (1968a), who argued that they were megaspores of either lycopsids (e.g. *Lepidocarpon* or *Achlamydocarpon*) or of progymnosperms. Pettitt and Beck (1968) have also linked them with the early gymnosperm *Archaeosperma* (see also comments by Hemsley, 1990b).

Filicopsida

This group of plants is represented here by several taxa. Particularly common are distal parts of vegetative organs, assignable to the artificial form-genera *Hierogramma* and *Clepsydropsis* (Long, 1967, 1968b).

More diagnostic are the main stems of these plants. The Whiteadder has yielded two species of cladoxylids, both of which are unique. The best known is *Cladoxylon waltonii*, 35 specimens of which were described by Long (1968b), demonstrating a range of forms. They fall into two groups: radially symmetrical stems, 8–12 mm in diameter, with a slightly dorsiventral actinostele; and dorsiventral stems, 2–7 mm in diameter, with a 'U'-shaped stele. It is far from certain that they all in fact belonged to the same species, but Long united them in the absence of evidence to the contrary. If they are, then they provide a valuable insight into the anatomical variability of this unusual group of plants, particularly with reference to the anastomosis and dissection of the stele.

Cladoxylon kidstonii is only known from a single imperfect specimen, and is inadequately understood (Solms-Laubach, 1910; Seward, 1917; Scott, 1920–1923).

A single species of zygopterid (Coenopteridopsida) stem has been described – *Protoclepsydropsis kidstonii*. The fragmentary holotype originated from Langton Burn near Gavinton (Bertrand, 1911a, b; Hirmer, 1927), but all other specimens have come from the Whiteadder (Long, 1967). It has been interpreted as a creeping, herbaceous plant with a deeply dissected stele that produced *Clepsydropsis* petioles in a 2/5 phyllotaxy. The anatomy of the stele and the petioles is somewhat similar to *Cladoxylon*, which Long (1967) used as evidence for the close affinity between the Cladoxylopsida and the Coenopteridopsida.

A second type of coenopterid found at the Whiteadder is *Stauropteris berwickense* Long (1966). It has similar vegetative structures to *Stauropteris burntislandica* Bertrand from Pettycur (p.147), except for having a more symmetrical vascular cross-section, but it does not have the significant swelling of parenchymatous tissue at the base of the sporangium. Long (1966) argued that these two features point to *S. ber-*

wickense being less specialized and more primitive than both the Pettycur species and *Stauropteris oldhamia* Binney from the Westphalian.

The only possible true fern described to date from the Whiteadder is *Psalixochlaena berwickense* Long (1976b). It is based on 21 slender stem fragments (although Long suggested that some might be parts of the same stem) and some isolated petioles. In the absence of fructifications or of evidence as to the orientation of the petioles in relation to the stems, its generic position is provisional (contrast the situation with the Westphalian species *P. cylindrica* (Williamson) Holden – Holmes, 1981). However, a point of interest is the possible presence of trifurcate branching of the petioles, produced by a foreshortened double dichotomy, which Taylor (1981) has compared with similar branching in the trimerophytes.

Lagenostomopsida

About two thirds of the form-species described from the Whiteadder belong to the group of gymnosperms with large, divided leaves, known informally as the pteridosperms. The 28 form-species probably originated from 15 whole-plant species, belonging to two classes: the Lagenostomopsida, and a so-far unnamed class that includes the Calamopityles. They are, scientifically, probably the most significant components of the Whiteadder flora. This is not so much because they were dominant in the life assemblage (lycopsids were probably dominant – Long, 1964c), but instead probably reflects a combination of greater species diversity in a group occupying less stable habitats and the greater attention that they have received from palaeobotanists. Although the earliest known ovules originated from the Upper Devonian of the USA (Gillespie *et al.*, 1981; Rothwell and Scheckler, 1988; Rothwell *et al.*, 1989), the Whiteadder has yielded the greatest variety of different primitive types showing details of their anatomy. The site has also yielded key information in relating them to whole-plant reconstructions (e.g. Retallack and Dilcher, 1988). It has thus been central to the development of ideas about early gymnosperm taxonomy and evolution.

The Lagenostomopsida includes pteridosperms with protostelic or siphonostelic stems (e.g. *Heterangium*, *Rhetinangium*, *Lyginopteris*). Long (1975) characterized the ovules by a number of features, but this has to be modified as he included within the Lagenostomales ovules now thought to belong to the Calamopityales and the enigmatic Eospermaceae. The ovules of this order appear now to be characterized as follows: integument free from nucellus at least above the plinth; a single set of vascular bundles in the integument; no vascular tissue in the nucellus; and radial symmetry. The male reproductive organs are of the *Telangium*/*Telangiopsis* type.

Until recently, the Lower Carboniferous lagenostomalean species were only known from isolated organs, which made it difficult to classify the group. However, studies by Long, based mainly on Whiteadder material, have gone a long way towards relating the various organs to one another and it is now possible to think more in terms of whole plants. It must be emphasized that the proposed reconstructions are based mainly on histological similarities of the various organs, and have not been confirmed by organic connection between them (cf. comments under Oxroad Bay – see p. 134). They nevertheless provide a starting point from which to consider these early lagenostomaleans as whole plants.

The most completely known is that which bore the *Stamnostoma* ovules (Long, 1979a; Retallack and Dilcher, 1988). Retallack and Dilcher state that the Foulden site is the main locality for developing this reconstruction, but nearly half the specimens on which Long (1960a, 1962, 1963, 1979a) based his primary studies in fact originated from the Whiteadder. The plant is interpreted as arborescent, over 25 metres tall, with a trunk about one metre in diameter, and of a habit similar to that of the extant Scots pine (*Pinus sylvestris* L.) (see Figure 5.6). The trunk is believed to be of the type commonly described as *Pitus primaeva* Witham (Long, 1963, 1979a). The fronds were bipartite, with at least two pairs of sub-opposite pinnae attached below the dichotomy, and *Lyginorachis papilio* Kidston petioles. There has been disagreement as to the form of these leaves and what they would be called if preserved as adpressions. Long (1963) argued that they would be called *Sphenopteris affinis* Lindley and Hutton, but such fronds are in fact quadripinnate. Based on evidence of association at Foulden (Scott and Meyer-Berthaud, 1985), Retallack and Dilcher (1988) argue that they were *Aneimites acadica* Dawson; but fronds with such flabellate pinnules were probably from calamopityalean plants. Since the details of the *Aneimites* frond architecture are unknown, it is unwise to link it with the *Stamnostoma*-bearing plant. A more convincing link is with the bipartite adpression fronds known as *Sphenopteridium pachyrrachis* (Göppert) Schimper, which are of a similar size and have pinnae attached below the dichotomy (Kidston, 1923b).

The fertile organs of this plant are borne on an axillary branch attached to the dichotomy of some fronds. Such fertile branches differ from the vegetative part of the frond in having a radial symmetry, and were identified with axes described by Long (1962, 1963) as *Tristichia ovensii*. Scott and Meyer-Berthaud (1985) have argued that *Tristichia* was part of a quite different plant with non-cupulate ovules (see also Galtier, 1977), but Long's description of the fertile axillary branch of the *Stamnostoma*-bearing plant nevertheless remains valid. In the female fronds, the fertile branches are terminated by clusters of *Calathiops*-like campanulate cupules (microcupules *sensu* Long, 1977a), which are formed from a sheaf of dichotomously branched, terete telomes. Each cupule contains four *Stamnostoma* ovules. No direct evidence of the male fronds has been reported, but Long (1979a) noted the frequent association of *Telangium* synangia bearing pre-pollen.

The lagenostomalean plant that bore *Genomosperma* ovules was probably rather different. Although the sort of detailed reconstruction outlined above has not been achieved for this plant, there is enough circumstantial evidence to suggest that it was significantly smaller, perhaps only one metre or so high (Long, 1959b, 1964b). The main stem is probably of a type known as *Rhetinangium*, which is only about 20 mm wide, and the longest known example is 260 mm long (Gordon, 1912). Based on association, Long (1964b) argued that the stem bore *Lyginorachis arberi* (syn. *L.* cf. *trinervis* Calder of Long, 1959b) petioles and *Genomosperma latens* ovules. The overall form of the fronds is unknown, but they were probably bipartite, as in many other lagenostomaleans. Again based partly on association, Long (1964b) suggested that a second species of ovule (*Genomosperma kidstonii*) was borne on fronds with *Lyginorachis kidstonii* (syn. *Lyginorachis* sp. Crookall, 1931a) petioles. In all likelihood, these were also probably borne on *Rhetinangium* stems, although supporting evidence has yet to be forthcoming.

Another well-known Lower Carboniferous lagenostomalean plant was that which bore *Salpingostoma dasu* ovules in *Calathospermum fimbriatum* cupules (Retallack and Dilcher, 1988). However, the reconstruction described by Retallack and Dilcher is based mainly on material from Oxroad Bay (p. 134), and the Whiteadder has provided little additional information.

Isolated ovules from the Whiteadder have been described by Long (1961b) as *Hydrasperma tenuis*. However, such ovules have been described from other localities in two quite distinct types of cupules, which have been named *Kerryia* and *Pullaritheca* (Rothwell and Wight, 1989) and it is impossible to be certain which (if either) contained the Whiteadder ovules. Long (1975) included *Hydrasperma* in his new family the Eurystomaceae, most of whose member species probably belong to the Calamopityales (see below). However, *Hydrasperma* does not have the characteristic broad, barrel-shaped lagenostome (or salpinx) of most of the other Eurystomaceae ovules, and is more comparable to the lagenostomalean *Stamnostoma*. Furthermore, *Pullaritheca longii* from Oxroad Bay (see below) was borne on *Sphenopteris bifida* fronds, which is probably lagenostomalean (Long, 1979b).

One of the most significant aspects of the lagenostomaleans from the Whiteadder is the primitive form of the ovules, particularly in the form of the integument (Figure 5.12). The following levels of development of the integumentary sheaf can be recognized.

1. *Genomosperma kidstonii*. The integument comprises a tubiform sheaf of eight more or less terete lobes, which are only attached to the nucellus at the chalaza (Long, 1959b). Niklas (1981) has argued that this in fact is better termed a 'pre-integumentary truss', although most palaeontologists continue to refer to it as a true integument.
2. *Genomosperma latens*. The integumentary telomes are fused to one another in the proximal part of the ovule, and converge at the distal end of the ovule to form a canopy over the lagenostome.
3. *Hydrasperma* and *Salpingostoma*. The integumentary telomes are even more fused, forming a sheath around the entire ovule below the plinth.
4. *Stamnostoma*. The integument is a completely fused sheath forming an open collar around the lagenostome. Long (1975) interpreted the latter as a micropyle but, as it does not cover the lagenostome fully, it cannot have had the same pollen-capturing function as the micro-

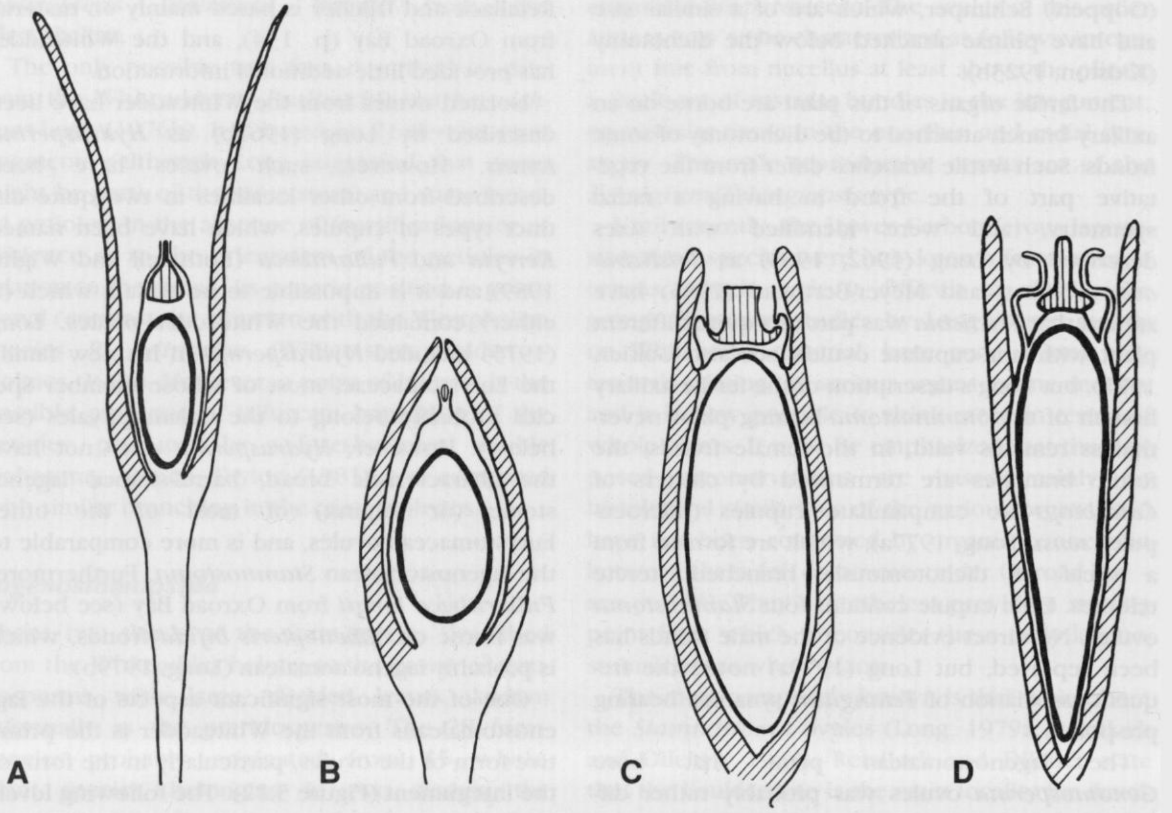

Figure 5.12 Sections through Early Carboniferous seeds from the Whiteadder. (A) *Genomosperma kidstonii* × 5. (B) *G. latens* × 5. (C) *Stamnostoma huttonense* × 20. (D) *Hydrasperma tenuis* x 20. Based on Long (1959b, 1960a, 1961b).

pyles of later lagenostomalean ovules. It may nevertheless represent an early stage in the evolution of the micropyle.

Most of the lagenostomalean ovules from the Whiteadder belong either to the families Genomospermaceae or Elkinsiacaea (Cleal, 1993). However, there is a third group consisting of *Eosperma*, *Deltasperma*, *Eccroustosperma* and *Camptosperma* (Long, 1961a, b, 1966, 1975). There is no evidence as to which plant-type bore them, or even if they were contained in cupules. However, they are all platyspermic and show the same type of short, distally-tapered lagenostome, containing a conical central plug (Figure 5.13) The most distinctive aspect of the group is the variation in curvature of the ovules: *Eosperma* is flat, *Deltasperma* slightly curved, *Eccroustosperma* 'S'-shaped and *Camptosperma* fully campylotropous (i.e. the chalaza and lagenostome are on the same side of the ovule). The latter is particularly unexpected, as it is a condition most usually associated with angiosperms. Long (1961a) argued that it might indicate that the *Camptosperma* ovules were attached directly to a dorsiventral frond, and was to assist in the better exposure of the lagenostome (and presumed pollen drop) for pollination. Long (1975) assigned these ovules to a separate family within the Lagenostomales, the Eospermaceae (see also comments by Barnard, 1959). This is still widely accepted (e.g. Cleal, 1993), although no other lagenostomalean ovule is known to be platyspermic, and there are also differences in the structure of the lagenostome.

The Whiteadder lagenostomalean ovules thus provide strong support to the telomic hypothesis for early ovule evolution, whereby a sporangium containing a single viable megaspore becomes surrounded by a sheath of fused lobes, that eventually fuse to become the integument (Walton, 1940, 1954, 1964b; Smith, 1959; Long,

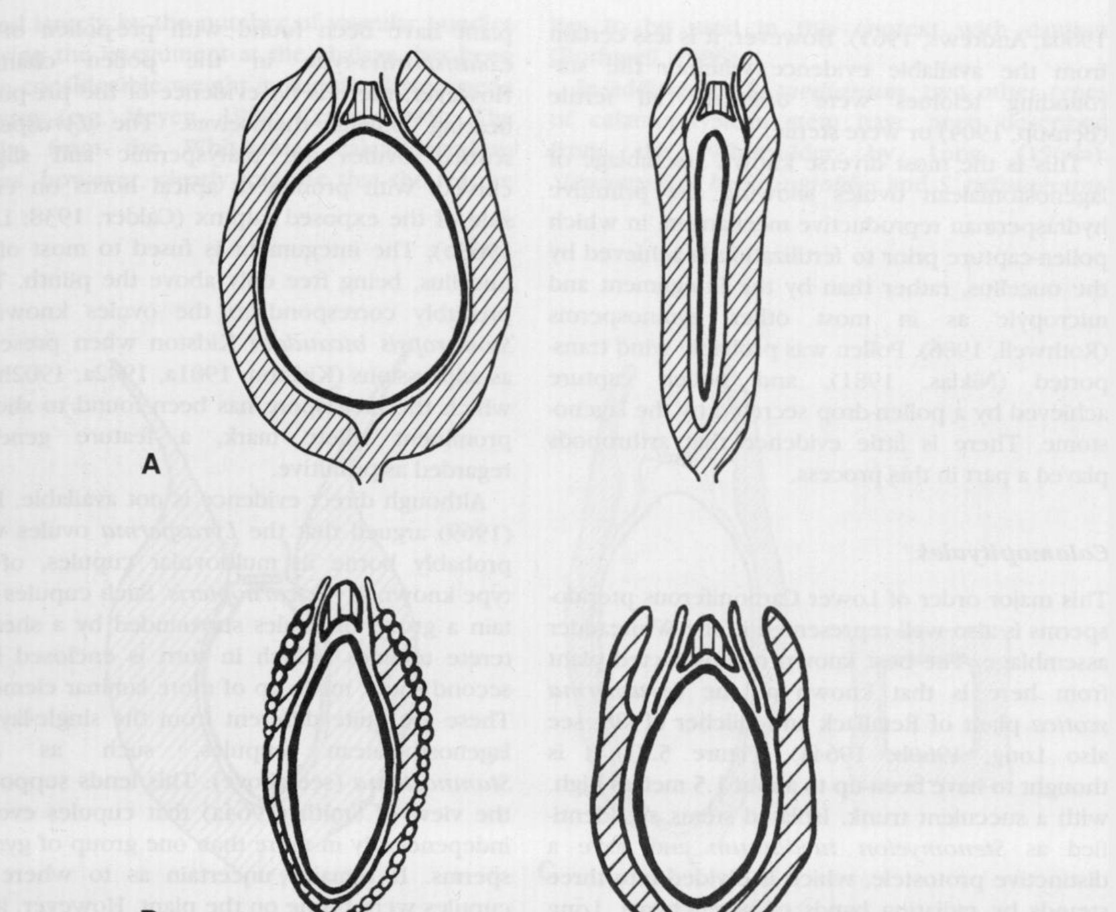

Figure 5.13 Sections through Early Carboniferous seeds from the Whiteadder (Eospermaceae). (A) *Eosperma edromense*. (B) *Deltasperma fouldenense*. (C) *Eccroustosperma langtonense*. (D) *Camptosperma berniciense*. All × 18. Based on Long (1961a, b, 1966).

1960a; Andrews, 1961). However, it is less certain from the available evidence whether the surrounding telomes were originally all fertile (Benson, 1904) or were sterile.

This is the most diverse known assemblage of lagenostomalean ovules showing the primitive hydrasperman reproductive mechanism, in which pollen-capture prior to fertilization is achieved by the nucellus, rather than by the integument and micropyle as in most other gymnosperms (Rothwell, 1986). Pollen was probably wind transported (Niklas, 1981), and pollen capture achieved by a pollen-drop secreted by the lagenostome. There is little evidence that arthropods played a part in this process.

Calamopityales

This major order of Lower Carboniferous pteridosperms is also well represented in the Whiteadder assemblage. The best known reconstructed plant from here is that known as the *Lyrasperma scotica* plant of Retallack and Dilcher (1988; see also Long, 1960b, 1964a) (Figure 5.8). It is thought to have been up to about 1.5 metres high, with a succulent trunk. Isolated stems are identified as *Stenomyelon tuedianum* and have a distinctive protostele, which is divided into three strands by radiating bands of parenchyma. Long (1964a) described petioles known as *Kalymma tuediana* attached to such stems. The overall form of the fronds borne by this plant has caused some difficulties. Retallack and Dilcher state that they probably correspond to foliage known as *Sphenopteridium pachyrrachis* (Göppert) Schimper when preserved as adpressions, but, as correctly pointed out by Long (1964a), there are serious discrepancies in the frond architecture, especially in the absence of pinnae attached to the primary rachis below the main dichotomy. The report by Long (1964a) of *S. pachyrrachis* pinnules associated with *Stenomyelon*/*Kalymma* at nearby Foulden was probably coincidental, the former being more likely to have lagenostomalean affinities (see above). Other types of calamopityalean have been shown to have fronds with rounded, non-digitate pinnules (Sebby and Matten, 1969; Skog and Gensel, 1980). In the Scottish Cementstone Group, foliage with similar pinnules belong to *Aneimites acadica* Dawson and it is thus more likely that this is the adpression form of the foliage in the *Lyrasperma scotica*-bearing plant.

Retallack and Dilcher state that ovules of this plant have been found with pre-pollen of the *Colatisporites*-type in the pollen chamber. However, there is no evidence of the pre-pollen-bearing organs themselves. The *Lyrasperma scotica* ovules are platyspermic and slightly curved, with prominent apical horns on either side of the exposed salpinx (Calder, 1938; Long, 1960b). The integument is fused to most of the nucellus, being free only above the plinth. They probably correspond to the ovules known as *Samaropsis bicaudata* Kidston when preserved as adpressions (Kidston, 1901a, 1902a, 1902b), in which the megaspore has been found to show a prominent trilete mark, a feature generally regarded as primitive.

Although direct evidence is not available, Long (1969) argued that the *Lyrasperma* ovules were probably borne in multiovular cupules, of the type known as *Alcicornopteris*. Such cupules contain a group of ovules surrounded by a sheaf of terete telomes, which in turn is enclosed by a second sheaf, made up of more laminar elements. These are quite different from the single-layered lagenostomalean cupules, such as bore *Stamnostoma* (see above). This lends support to the view of Smith (1964a) that cupules evolved independently in more than one group of gymnosperms. It remains uncertain as to where the cupules were borne on the plant. However, if the outer sheaf of the cupule is the laminate part of a fertile frond (i.e. the structure is a megacupule *sensu* Long, 1977a), then it would probably have been attached directly to the main stem, perhaps near the top of the plant. There is no direct evidence that they were attached to the fronds near the dichotomy of the main rachis, as suggested by Retallack and Dilcher (1988).

A distinctive aspect of *Lyrasperma* ovules is the squat, barrel-shaped lagenostome, with a thin, biconcave central plug at the base, quite different from the more elongate lagenostome, and thicker central plug of the lagenostomalean ovules. Almost identical lagenostomes have also been described in *Eurystoma angulare*, *E. burnense* (syn. *Anasperma burnense* Long), *Dolichosperma pentagonum* and *D. sexangulatum* (Long, 1960b, 1961b, 1965, 1966, 1969, 1975) (Figure 5.14). These are also presumably calamopityalean ovules, although there is no evidence of their attachment to identifiable stems/petioles. They are of particular interest in the great variation that they show in symmetry, varying from bilateral (in *Lyrasperma*) to six-fold (in *D. sexangulatum*). Ovule symmetry, which is controlled largely by the number of vascular bundles entering the integument at the chalaza, has been given considerable weight in certain phylogenetic analyses (e.g. Meyen, 1984; Crane, 1985). The results from the Whiteadder calamopityalean ovules, however, clearly indicate that the feature has to be used in this context with caution (Rothwell, 1986).

In addition to *S. tuedianum*, two other types of calamopityalean stem have been described from the Whiteadder by Long (1964a): *Stenomyelon heterangioides* and *S. primaevum*.

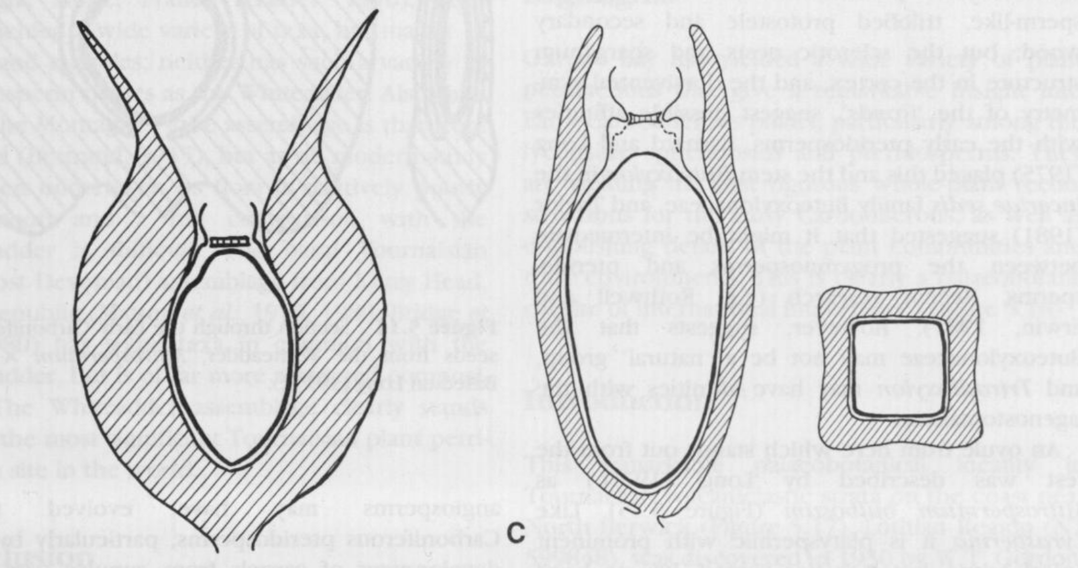

Figure 5.14 Sections through Early Carboniferous seeds from the Whiteadder (Calamopityales). (A) *Lyrasperma scotica* × 4.5. (B) *Eurystoma trigona* × 13.5. (C) *E. angulare* × 9. (D) *Dolichosperma sexangualtum* × 4.5. Based on Long (1960b, 1961b, 1969).

They are distinguished mainly by the distribution of parenchyma in the stele, although it is possible that it merely represents variation in structure at different positions in the plant. A fourth type of stem reported from here, *Stenomyelon tripartum*, Kidston is now regarded simply as a form of *S. tuedianum* (Calder, 1938).

Problematic gymnosperms

Triradioxylon primaevum has a progymnosperm-like, trilobed protostele and secondary wood; but the sclerotic nests and sparganum structure in the cortex, and the dorsiventral symmetry of the 'fronds', suggest possible affinities with the early pteridosperms. Barnard and Long (1975) placed this and the stem *Buteoxylon* in the *incertae sedis* family Buteoxylonaceae, and Taylor (1981) suggested that it might be intermediate between the progymnosperms and pteridosperms. Recent research (e.g. Rothwell and Erwin, 1987), however, suggests that the Buteoxylonaceae may not be a 'natural' group, and *Triradioxylon* may have affinities with the lagenostomaleans.

An ovule from here which stands out from the rest was described by Long (1977c) as *Mitrospermum bulbosum* (Figure 5.15). Like *Lyrasperma* it is platyspermic with prominent apical horns, but it is not curved, has no basal plug in the lagenostome, and has a free nucellus. Long (1977c) argued that it has many features normally associated with the Cordaitales. Other evidence of cordaites in the Lower Carboniferous is equivocal. Crookall (1970, pl. 155 figs 6–7) figures some possible leaves from the Lower Carboniferous of Scotland, but their identity is far from certain. Lacey (1953) and Barnard (1962) have described some petrified stems and roots from elsewhere in Scotland (Oxroad Bay, Glenarbuck, Loch Humphrey Burn – see p. 135) as having possible cordaite affinities, but they have since been interpreted as probably pteridospermous (Long, 1987; Bateman and Rothwell, 1990). The Whiteadder ovules appear to be the best available evidence of Early Carboniferous cordaites, but on their own cannot be used to dismiss Rothwell's (1986) argument that the group probably did not appear before the Westphalian.

Angiosperm origins

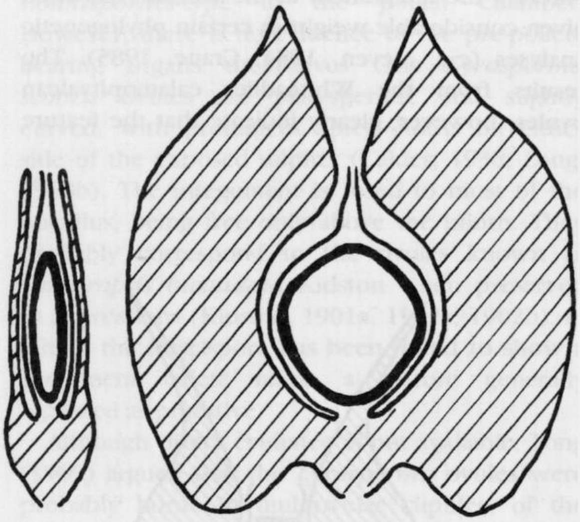

Figure 5.15 Section through the Early Carboniferous seeds from the Whiteadder, *Mitrospermum* × 4.5. Based on Long (1977c).

Long (1966, 1975, 1977b, 1985) has used the evidence from the Whiteadder to argue that angiosperms may have evolved from Carboniferous pteridosperms, particularly by the development of carpels from cupules (see also Delevoryas, 1962; Andrews, 1963). This view has not met with widespread acceptance (e.g. Stewart, 1983; Crane, 1985), although one of the often mentioned objections to it (the long stratigraphical gap between the Lower Carboniferous and where angiosperms appear in the fossil record) may have to be re-assessed in the light of recent work on DNA sequencing in extant angiosperms (Martin *et al.*, 1989; Cleal, 1989).

General remarks

This is by far the best locality for plant fossils in the Lower Carboniferous Cementstone Group. It has yielded 44 petrifaction form-species, including lycopsids, ferns, progymnosperms and pteridosperms, which is far more than any other site. Of the other Cementstone Group localities, the most comparable are Langton Burn and Cove, which have yielded 20 and 11 form-species respectively (Scott *et al.*, 1984), but neither has yielded taxa not found in the Whiteadder. The Oxroad Bay (see below) assemblage has some taxa in common with the Whiteadder, but there are also significant differences. The other major Lower Carboniferous petrifaction sites in Britain, such as Pettycur (p. 144), Loch Humphrey Burn (p. 155) and Glenarbuck (p. 164), yield quite distinct assemblages from Whiteadder, a function of differences of both environment and age.

From outside Britain, the best known Tournaisian petrifaction assemblages are from the New Albany Shales of the USA (Cross and Hoskins, 1951) and the Lydienne Formation in the Montagne Noire, France (Galtier, 1970). Both have yielded a wide variety of taxa, but mainly of stems and rachides; neither has such a variety of pteridosperm ovules as the Whiteadder. Also similar to the Montagne Noire assemblage is that from Saalfeld (Bertrand, 1935), but as no modern study has been undertaken its flora is relatively poorly understood and a full comparison with the Whiteadder is difficult. The basal Tournaisian (topmost Devonian) assemblage from Kerry Head, Irish Republic (Matten *et al.*, 1975, 1980; Bridge *et al.*, 1980) has some taxa in common with the Whiteadder, but is of far more restricted composition. The Whiteadder assemblage clearly stands out as the most significant Tournaisian plant petrifaction site in the world.

Conclusion

The Whiteadder section is one of a series of sites in basal Carboniferous rocks in southern Scotland yielding anatomically-preserved plant fossils, about 350 million years old. Nowhere else in the world has so many sites of this age yielding such well preserved fossils. Of the Scottish sites, the Whiteadder has yielded the most diverse assemblage, with 44 species having been described in the literature. Particularly important is the wide range of 'seeds' of early higher (seed-bearing) plants, whose anatomy has been studied in great detail, revealing features such as their unusual and distinctive pollination structures (later replaced by the micropyle in modern 'seeds'). They include the most morphologically primitive 'seed' so far found in the fossil record (*Genomosperma*). They are marginally pre-dated by the earliest known 'seeds' from West Virginia, USA, but the latter are not preserved in such fine detail. Also, the American site yields just one type of 'seed', whereas the Whiteadder contains 16 distinct types belonging to at least two major plant groups (lagenostomaleans and calamopityaleans). This site is thus of outstanding significance for understanding the early evolution of the seed plants, and thus the origin of most modern groups of plants (including flowering plants).

OXROAD BAY

R.M. Bateman, G.W. Rothwell and C.J. Cleal

Highlights

Oxroad Bay has yielded a wide variety of plant petrifactions that give a remarkable insight into Early Carboniferous plants, particularly among the lycopsids, sphenopsids and pteridosperms. They are yielding the first rigorous whole-plant reconstructions for the Early Carboniferous, as well as establishing details of the plant communities and their environments. This is clearly a palaeobotanical site of international importance (Figure 5.16).

Introduction

This remarkable palaeobotanical locality in Tournaisian volcaniclastic strata on the coast near North Berwick (Figure 5.17), Lothian Region (NT 599848), was discovered in 1930 by W.T. Gordon, who provided the earliest accounts of its plant fossils (Gordon, 1938, 1941). P.D.W. Barnard then applied the rapid acetate peel technique to the petrifactions collected by Gordon. His doctoral thesis (Barnard, 1960a) resulted in several publications (Barnard, 1959, 1960b, 1962). Barnard's work prompted A.G. Long to collect a considerable amount of new material from the site (276 new blocks by 1976 – Long, 1977b), described in a series of important studies (Barnard and Long, 1973, 1975; Long, 1962, 1975, 1976a, 1977a, b, 1979b, 1984, 1986, 1987). Alvin (1965) described a new lycopsid from here, and Alvin (1966) and Pettitt (1969) undertook maceration studies on lycopsids and pteridosperms respectively. Most recently, the site has been investigated by R.M. Bateman, G.W. Rothwell and A.C. Scott, who have integrated palaeobotanical (including maceration and SEM analyses) and sedimentological work. Their main aims have been to reassess the diversity of dispersed organs, reconstruct them into biologically meaningful plants, and establish details of plant communities and their environments of growth and deposition. The project has resulted in the collection of a further 590 blocks

Figure 5.16 Oxroad Bay. View south across the foreshore, with Dinantian lacustrine sediments in the foreground overlain by reworked volcanigenics exposed in the cliffs. Two of the four horizons yielding anatomically-preserved plants are shown: (A) was discovered by W.T. Gordon in 1930, (C) by R.M. Bateman in 1984. Hammer is 0.3 metres long. (Photo: R.M. Bateman.)

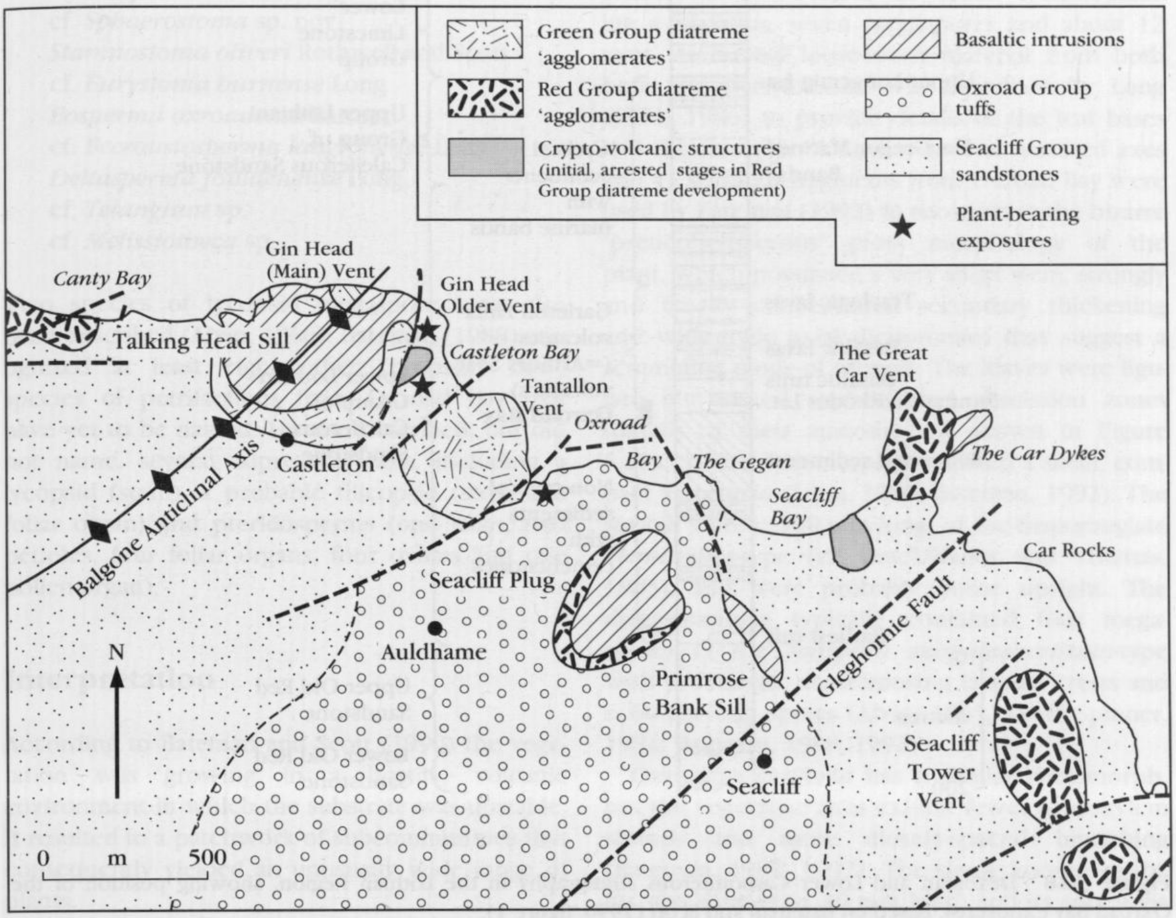

Figure 5.17 Geological map of the Tantallon area of East Lothian, showing location of palaeobotany sites including Oxroad Bay. Based on Bateman and Scott (1990, figure 2).

containing petrifactions, together with numerous adpressions. Some of the results are summarized by Bateman (1988, 1991, 1992), Bateman *in* Cleal (1991), Bateman and Rothwell (1990) and Bateman and Scott (1990).

Description

Stratigraphy

The Oxroad Bay sequence is about 38 metres thick and belongs to the North Berwick Member of the Garleton Hills Volcanic Formation (Figure 5.18; McAdam and Tulloch, 1985; Davies *et al.*, 1986). Its complex sedimentology is discussed by Scott and Rex (1987), Bateman (1988; *in* Cleal, 1991) and Bateman and Scott (1990). The sediments are reworked volcaniclastics deposited along the margins of an active volcano. The plant fossils occur mainly on several discrete bedding-planes, each representing a distinct terrain. Three of these were dominantly lacustrine, the fourth volcanically-induced mass-flow. Palynological evidence suggests that the strata are upper Tournaisian (Tn3, Upper Courceyan – Scott *et al.*, 1984), although some of the plant megafossils are more characteristic of the lower Visean (Bateman, 1988, Appendix 4).

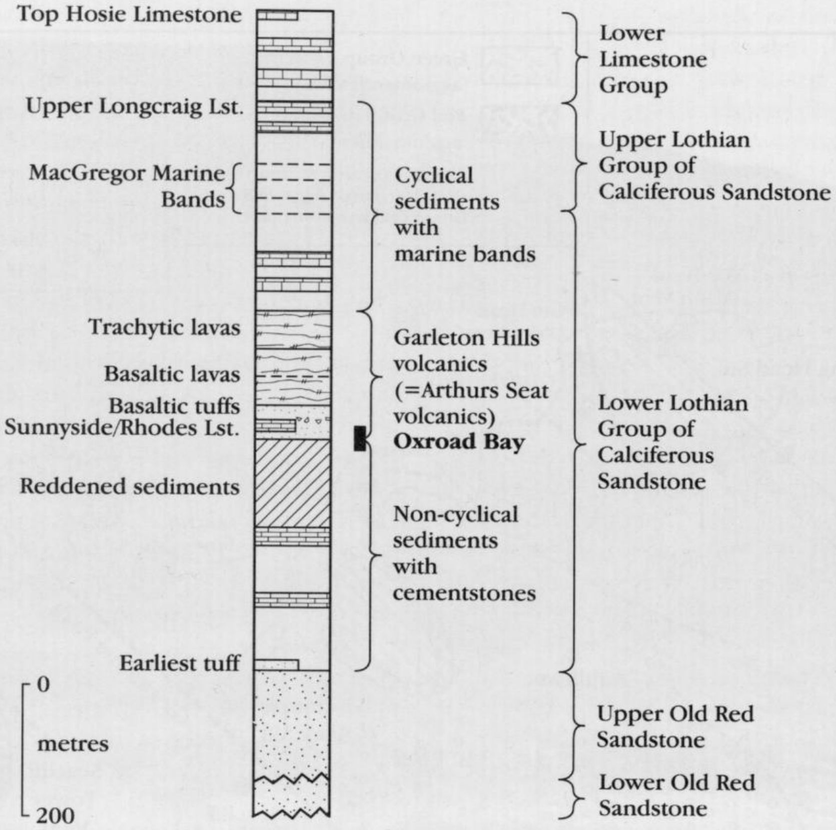

Figure 5.18 Devonian and Lower Carboniferous stratigraphy in the Lothian Region, showing position of the Oxroad Bay exposures. Based on Bateman and Scott (1990, figure 1).

Palaeobotany

All but the most recent species list published for this locality (Barnard and Long, 1973; Long, 1984; Scott *et al.*, 1984) included taxa identified from loose blocks, which were transported into Oxroad Bay from the nearby Castleton Bay and Gin Head plant beds (described by Scott and Galtier, 1988; see also Figure 5.17). The following list of petrifactions is based on material recognized as *in situ* by Bateman (1988) and Bateman and Rothwell (1990), although it uses a different supra-generic nomenclature.

Lycopsida:
- *Oxroadia gracilis* Alvin
- *O. conferta* Bateman

Equisetopsida:
- *Protocalamites longii* Bateman
- *Protocalamostachys farringtonii* Bateman

Filicopsida:
- *Cladoxylon* cf. *waltonii* Long
- *Stauropteris* cf. *berwickensis* Long

Gymnosperms:
- *Amyelon bovius* Barnard
- *Tetrastichia bupatides* Gordon
- *Bilignea* cf. *solida* D.H. Scott
- *Eristophyton beinertianum* Zalessky
- *Buteoxylon gordonianum* Barnard and Long
- *Triradioxylon primaevum* Barnard and Long
- *Oxroadopteris parvus* Long
- *Calathopteris heterophylla* Long
- aff. *Tristichia ovensii* Long
- *Lyginorachis waltonii* Calder
- *Lyginorachis* sp. nov.
- *Calathospermum fimbriatum* Barnard
- *Pullaritheca longii* Rothwell and Wight
- *Salpingostoma dasu* Gordon
- *Dolichosperma* cf. *sexangulatum* Long

Tantallosperma setigera Barnard and Long
Hydrasperma tenuis Long
cf. *Sphaerostoma* sp. nov.
Stamnostoma oliveri Rothwell and Scott
cf. *Eurystoma burnense* Long
Eosperma oxroadense Barnard
cf. *Eccroustosperma langtonense* Long
Deltasperma fouldenense Long
cf. *Telangium* sp.
cf. *Melissiotheca* sp.

Two species of lycopsid megaspore have also been described (Alvin, 1966). Bateman (1988) recognized at least eight other (probably new) species of petrifactions from Oxroad Bay that have yet to be named. He also described, but did not name, several adpression taxa, including a lycopsid (stem), a probable filicopsid (stem and foliar organ) and pteridosperms (one stem, two petioles, four foliar organs, four ovules and one pollen-organ).

Interpretation

According to Bateman and Scott (1990) the vegetation was growing in a hostile, volcanic environment in which the substrate was unstable. It resulted in a patchwork of subcommunities that consequently yielded an unusually wide range of plants.

Lycopsida

Oxroadia axes are distinguished from most penecontemporaneous lycopsids by their consistently small size and prominent protoxylem strands (Figures 5.5 and 5.19b). *Paurodendron* is similar but has unbranched vasculature in its rootstock and much smaller tracheids in the central metaxylem of the axes. Bateman (1992) and Bateman *et al.* (1992) argued that *Oxroadia* and *Paurodendron* are small-bodied lepidodendrids derived by paedomorphosis from relatively primitive arboreous species. Bateman recognized two form-species each of stems, strobili and megaspores (*Setispora*), and reconstructed them to form two whole-plant species of *Oxroadia*. These two lycopsids are mutually exclusive at Oxroad Bay, both stratigraphically and (probably) ecologically. Together with *Protocalamites longii* (Bateman, 1991), they are of particular interest as the first fully reconstructed Lower Carboniferous plants.

Alvin's (1965) original description of *Oxroadia gracilis* Alvin was based on a loose block containing a strobilus, seven megaspores and about 12 axes. Additional loose-block material from both here and Berwickshire was described by Long (1971, 1986) to provide details of the leaf bases and rhizomorphs. A further several hundred axes and 43 strobilus fragments from Oxroad Bay were used by Bateman (1992) to reconstruct the bizarre 'pseudoherbaceous' gross morphology of the plant, which possessed a very short stem, strongly and basally concentrated secondary thickening and wide-angle axial dichotomies that suggest a scrambling mode of growth. The leaves were ligulate but lacked sophisticated abscission zones (details of their anatomy are shown in Figure 5.20a,c). The rhizomorph resembled a small, compact *Stigmaria* (Long, 1986; Bateman, 1992). The strobili were *c.* 120 mm long, of the bisporangiate *Flemingites*-type (cf. Brack-Hanes and Thomas, 1983), and were probably borne upright. The megasporangia typically contained four megaspores of the *Setispora subpalaeocristata*-type with prominent, anastomosing laesural crests and *c.* 60 μm-long spines (Alvin, 1965, 1966; Spinner, 1984; Bateman, 1988, 1992).

Oxroadia conferta has a similar rhizomorph, but the vegetative axes exhibit fewer protoxylem strands and more closely-spaced branching (Bateman, 1988, 1992). The single known strobilus was shorter (*c.* 30 mm long) and its sporangia contained more megaspores (?16) of smaller diameter (Figure 5.20d). Dispersed megaspores of this type were described as '*Triletes*' *pannosus* by Alvin (1966), and later reclassified as *Setispora pannosa* by Spinner (1984). They have coarser, more profoundly fused laesural fimbriae, and longer (*c.* 200 μm) spines than the megaspores of *O. gracilis*. All of the aerial organs of these two *Oxroadia* species can be distinguished, and they are mutually exclusive at individual stratigraphical levels within the Oxroad Bay sequence (Bateman, 1992). This almost certainly reflects an early example of ecological control on the spatial distribution of two closely-related species.

Stems of a third lycopsid were described by Barnard (1960a) as cf. *Paurodendron*; small fragments occur sparsely throughout the sequence here (Bateman and Rothwell, 1990). The xylem lacks wood and the stele is deeply incised into 7–10 rounded lobes. It thus resembles *Asteroxylon* (from the Lower Devonian Rhynie Chert – see Chapter 4) and *Leclercqia* (Banks,

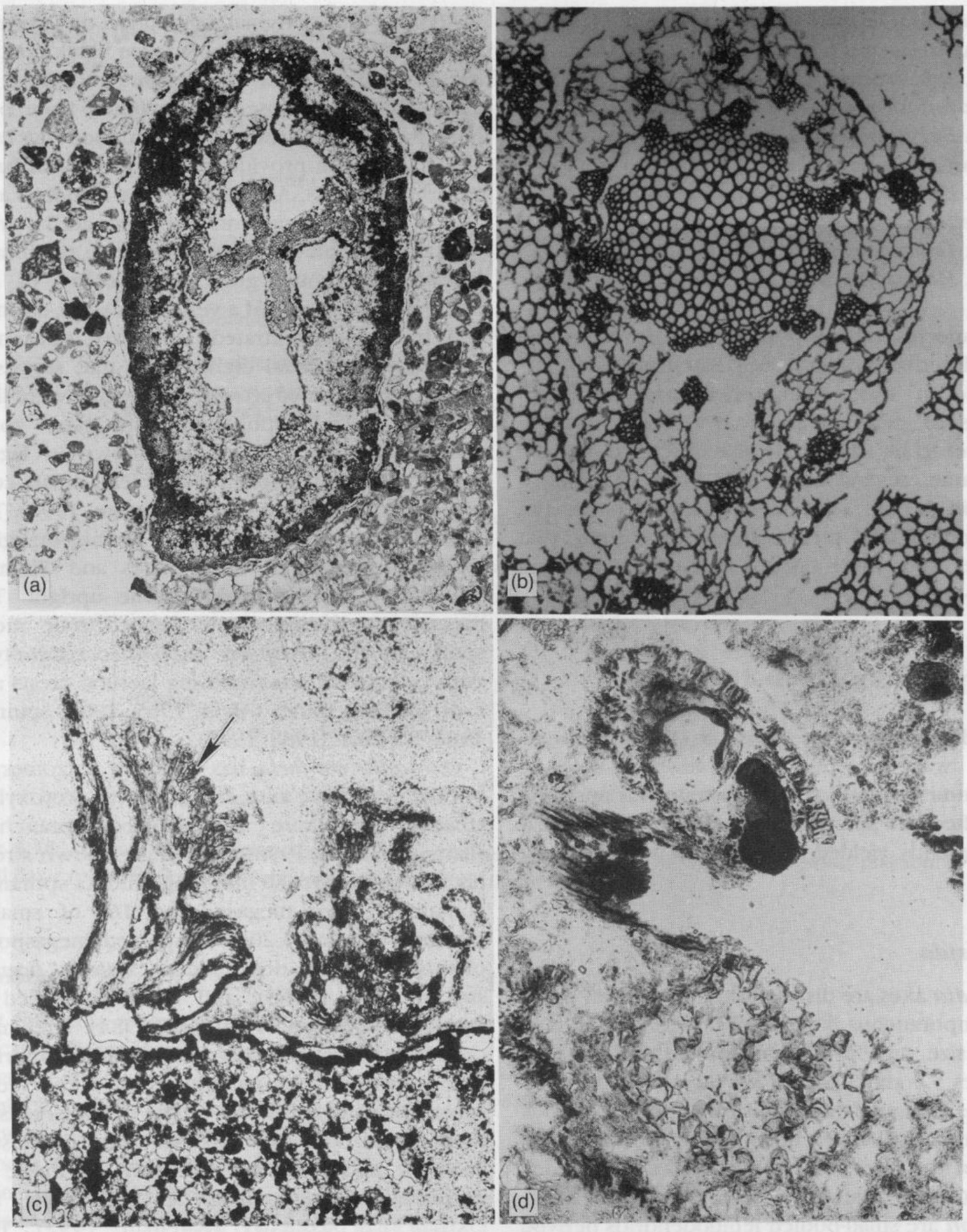

Figure 5.19 Petrified plants from North Berwick Member of the Garleton Hills Volcanic Formation (Courceyan), Oxroad Bay. (A) *Tetrastichia bupatides* Gordon. Transverse section of stem of shrubby pteridosperm, showing the characteristic four-lobed stele emitting paired leaf traces; Natural History Museum, London, Gordon Collection (holotype). × 8.4. (B) *Oxroadia gracilis* Alvin. Transverse section of a branch of the pseudoherbaceous rhizomorphic lycopsid, showing the coronate stele emitting leaf traces through the inner cortex; Bateman Collection, specimen OBD(?2.15)038bT/2. × 118. (C) *Pullaritheca longii* Rothwell and Wight cupule with *Hydrasperma tenuis* Long ovules attached to the placental margin. Rare example of a developmental anomaly in a fossil plant, where the abortive ovule to the right is normal, whereas the ovule to the left has a deformed, proliferated and non-functional pollen chamber (arrowed); Long Collection, Hancock Museum, Newcastle upon Tyne, specimen HM 11718. × 38. (D) *Protocalamostachys farringtonii* Bateman. Sporangiophore axis (left centre) emitting two of four sporangia, the upper being a megasporangium, the lower a microsporangium; Bateman Collection, specimen OBC084gB/5. × 71. (Photo A: G.W. Rothwell; photos B–D: R.M. Bateman.)

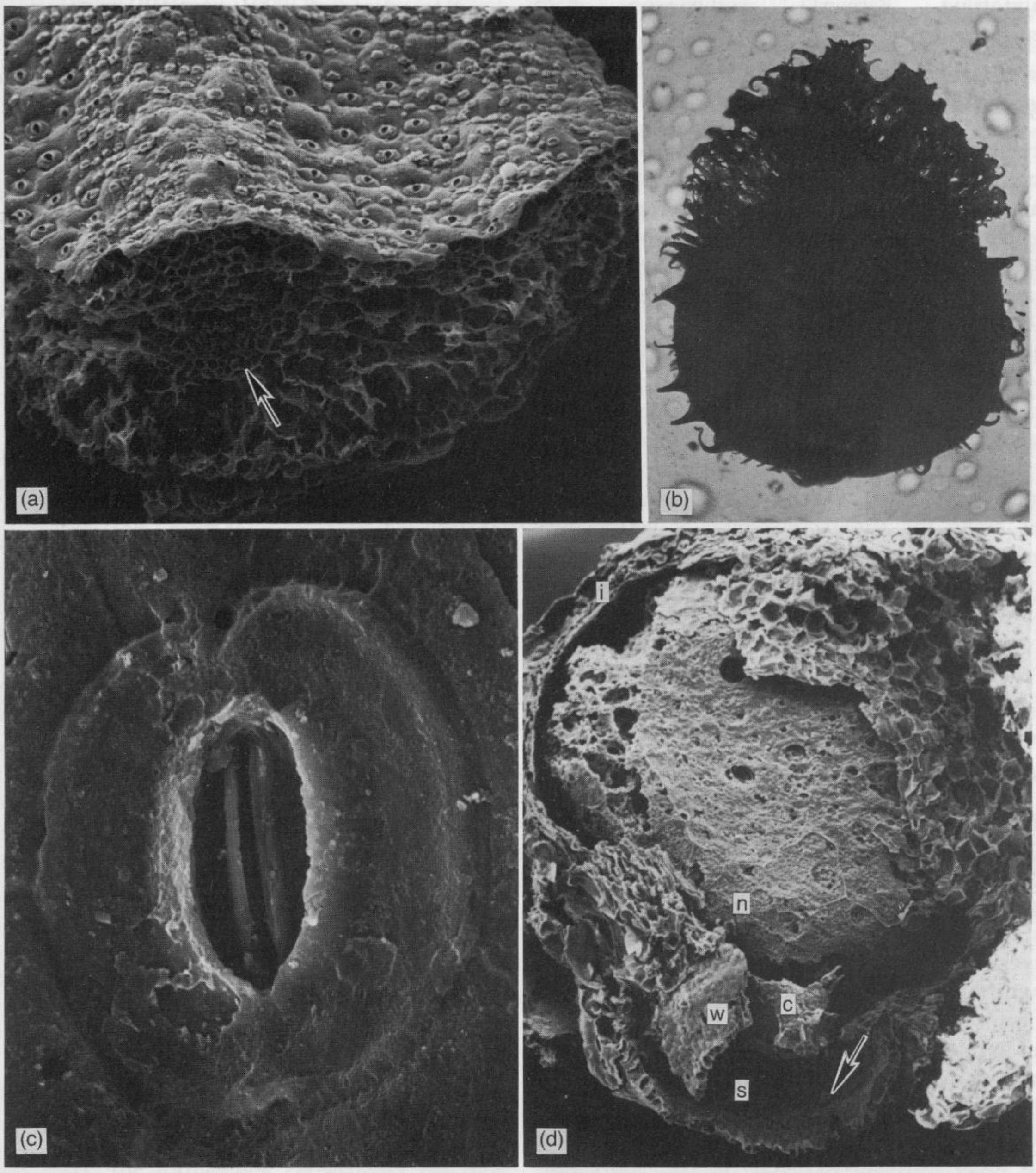

Figure 5.20 Fusainized plants from North Berwick Member of the Garleton Hills Volcanic Formation (Courceyan), Oxroad Bay. (A) *Oxroadia gracilis* Alvin. Transverse section through microphyll leaf of this rhizomorphic lycopsid, showing terete vascular strand (arrowed) surrounded by mesophyll; highlighted abaxial surface shows stomata restricted to two shallow furrows (left, centre right); Bateman Collection, specimen OBD(2.17)176:CP21. × 108. (B) *Setispora pannosa* (Alvin) Spinner. Elaborately ornamented megaspore of the pseudoherbaceous lycopsid *Oxroadia conferta* Bateman; Natural History Museum, London, specimen V.52016e. × 37. (C) *Oxroadia gracilis* Alvin. Detail of stomata of leaf, showing paired sunken guard cells surrounded by putative subsidiary cells; Bateman Collection, specimen OBD(2.17)176:CP21. × 1634. (D) *Deltasperma fouldenense* Long. Platyspermic pteridosperm ovule with one half of the integument (i) removed to reveal the nucellus (n); at the bottom of the photograph is a typical apical pollen chamber; a cylindrical wall (w) surrounds the central column (c) and salpinx (s), containing a single prepollen grain (arrowed); Bateman Collection, specimen OBD(2.26)190:CP17. × 52. (Photos A, C and D: R.M. Bateman. Photo B: C.H. Shute, Natural History Museum, London.)

1960; Grierson and Bonamo, 1979), rather than supporting Barnard's comparison with *Paurodendron*.

Equisetopsida

Petrified equisetopsid remains were first reported here by Bateman (1988). Vegetative axes were named *Protocalamites longii* and reproductive structures *Protocalamostachys farringtonii* (Bateman, 1991). They represent a single whole-plant species with short, slender stems. The tuberoid stem bases generated dense root-balls and were interconnected by rhizomes. The woody stems subtended at least one order of branching and bore repeatedly dichotomizing leaves. Strobili were probably small, with three vertical rows of paired sporangiophores. The sporangia were small and the plant heterosporous, this being the earliest evidence of heterospory amongst the sphenophytes (Figure 5.19d). The thick-walled megaspores vary greatly in diameter from 100-320 µm. They resemble *Protocalamostachys pettycurensis* Chaphekar (1963) more closely than *P. arranensis* Walton (1949b).

Filicopsida

Two filicopsid species have been reported from here (Bateman, 1988; Bateman and Rothwell, 1990). *Cladoxylon* cf. *waltonii* Long (1968b) is represented by a few polystelic stem bases that are greatly expanded and exhibit weakly-developed secondary xylem. Other stem fragments are smaller than the largest petiole-like primary branches, which are adaxially concave and appear to undergo initial equal dichotomies. The more distal branches exhibit typical *Hierogramma*-type anatomy and bear pinnae with clepsydropsid vascular traces. Possible stem and foliar correlatives occur in the adpression assemblages, and resemble those of *Cladoxylon scoparium* (Leclercq, 1970) and *Pseudosporochnus nodosus* (Leclercq and Banks, 1962). These cladoxylalean fragments re-assemble to form a short, stocky, infrequently branched, upright plant.

Several rachises with a characteristic four-lobed stele have been identified as *Stauropteris berwickensis* Long (1966). Also tentatively placed in this species was a single fragment of a larger axis with a five-lobed stele. No filicopsid reproductive organs have been found at Oxroad Bay.

Pteridosperms

There has been much speculation concerning possible whole-plant restorations of pteridosperms from the assemblages of isolated, petrified organs at Oxroad Bay. A hypothetical *Calathopteris-Calathospermum-Salpingostoma* plant postulated by Long (1976a) is in danger of becoming enshrined in the literature as a genuine reconstruction (cf. Retallack and Dilcher, 1988). Other postulated vegetative-reproductive (stem-ovule) correlations were *Buteoxylon* with *Tantallosperma* (Barnard and Long, 1973), and *Tetrastichia* with *Eosperma* (Barnard, 1959, 1960a). Unfortunately, these hypotheses are based only on histological similarity and comparisons with preconceived bauplans. The abundance of pteridosperm organs of all types at Oxroad Bay permits an enormous number of theoretical combinations.

More recent studies (Bateman, 1988; Bateman and Rothwell, 1990) have yielded much information on how to interpret associations of organs from different exposures and different horizons within exposures, thus reducing the number of likely combinations of organs. Individual plants are being reconstructed by organic connection, though the most difficult correlation (megasporangiate and microsporangiate reproductive organs to stem via petiole) has yet to be achieved unequivocally for any Lower Carboniferous pteridosperm. However, sufficient evidence has accumulated to suggest that five or six species of whole plant were present. This is more consistent with the numbers of petioles (4), pollen-organs (4) and ovulate cupules (4) currently recognized at Oxroad Bay. The reported number of taxa of stem (9) has probably been inflated by the use of different names for different ontogenetic stages of the same species (Long, 1984; Wight, 1987; Bateman and Rothwell, 1990). Despite many previous assertions to the contrary, all of these reconstructed plants will probably prove to be lagenostomalean. The large number of recorded isolated ovules (10) probably reflects greater dispersal potential of disseminules (Bateman and Rothwell, 1990; Bateman and Scott, 1990; Bateman *in* Cleal, 1991). In the absence of an unequivocal correlation between them, the following discussion will treat each of the pteridosperm organ-types separately.

Such evidence has stimulated ideas concerning early cupule organization and structure (Matten and Lacey, 1981), the reproductive biology of early pteridosperm ovules (Andrews, 1940;

Walton, 1954; Smith, 1964), and the ontogeny of these ovules (Bateman, 1988; Rothwell and Wight, 1989). An important result of this work has been the development of the 'hydrasperman reproduction' concept, in which pollination was facilitated by an elongate extension of the pollen chamber wall (the lagenostome or salpinx) rather than by a micropyle formed by the integument, and the presence of a specialized structure (the central column) that sealed the pollen chamber after fertilization had occurred (Rothwell, 1986). This work also prompted the controversial ideas on angiosperm origins, put forward by Long (1966, 1975, 1977b, 1985; see discussion on the Whiteadder, above).

Rooting structures

Barnard (1962) attributed certain gymnosperm roots to the form-species *Amyelon bovius* Barnard. The diversity of pteridosperms at the locality obscures their affinities.

Stems

Bateman and Rothwell (1990) list nine pteridosperm stem species, which probably represent five or six whole-plant species. The first four are clearly distinct:

Tetrastichia bupatides Gordon (1938) has a distinctive, cruciform protostele (Figure 5.19a). They are mostly small stems, probably from shrubby plants, and only the largest exhibit secondary xylem (Gordon, 1938; Barnard, 1960a). Dichotomously branching, *Lyginorachis*-like petioles with few abaxial corrugations were borne in four vertical columns of sub-opposite pairs (Gordon, 1938; Wight, 1987). The fronds have been compared with *Sphenopteris affinis* Lindley and Hutton (Gordon, 1938; Andrews, 1948) and *Adiantites*, but the evidence is equivocal. Elsewhere, the form-genus *Tetrastichia* has only been reported from the lower Tournaisian at Ballyheigue, Irish Republic (Matten *et al.*, 1984b).

Bilignea cf. *solida* Scott, consisting of stems up to 70 mm in diameter with a distinctive pith of short tracheids, was first reported by Long (*in* Scott *et al.*, 1984). Attached lyginopterid petioles reported by Bateman (1988), confirm the lagenostomalean affinities of this pteridosperm tree.

The assignment of *Eristophyton beinertianum* Zalessky to the lagenostomalean pteridosperms similarly resulted from studies of Oxroad Bay material. Originally described as calamopityalean by Gordon (1941), it was first recognized as *Eristophyton* by Barnard (1960a). Long (1987) demonstrated that the stems reach 100 mm in diameter and possess a parenchymatous pith that extends into the lateral branches. Associated *Lyginorachis waltonii* petioles are large, with several stelar corrugations that separate near the base; Long (1987) suggested correlation with the adpression frond genus *Diplothmema*.

Stem I of Bateman and Rothwell (1990) resembles a similarly unnamed pteridosperm axis with three sympodia recovered from Visean strata at Kingswood End by Scott *et al.* (1986). A single short length of narrow fusainized axis exhibits parenchymatous pith in intimate association with five mesarch sympodia. They are surrounded by a secondary xylem cylinder of narrow tracheids interspersed with abundant small, uniseriate rays. In the absence of attached petioles, its familial affinities are unclear.

It is uncertain whether *Buteoxylon gordonianum* Barnard and Long represents an additional whole-plant species or should be synonymized with the taxa listed below. The single specimen described from here by Barnard and Long (1973, 1975) was the apical portion of a small stem with a mixed pith and numerous attached petioles. The petioles possessed single protoxylem strands in the centre of both arms of the characteristic Y-shaped stele, and apparently did not dichotomize. A much larger axis of this species with well developed wood was reported by Bateman and Rothwell (1990). Barnard and Long (1975) used *Buteoxylon* and *Triradioxylon* to erect a new family, the Buteoxylonaceae, which they suggested might belong to the progymnosperms. The discovery of protostelic, triradiate stems associated with pteridosperm ovules (Rothwell and Erwin, 1987) renders this less probable.

Although originally described as separate genera, the four remaining pteridosperm stem taxa probably belong to only one whole-plant species (Bateman and Rothwell, 1990; Rothwell and Scott, 1992b). Although not yet fully reconstructed, it has been tentatively interpreted as scrambling or lianascent.

1. *Oxroadopteris parvus* Long (1984) is a small axis with a pith of elongate tracheids. It bears *Lyginorachis*-type petioles that bifurcate close to the stem and possess few stelar corrugations.
2. *Calathopteris heterophylla* Long (1976a) is also small, has a mixed pith and bears two

types of petiole. The more numerous, *Lyginorachis*-type petioles have few stelar corrugations and were probably vegetative. The remainder have three-ribbed xylem strands that trichotomize within the cortex of the stem, and were probably fertile (Long, 1976a).

3. Stem H of Bateman and Rothwell (1990) was ascribed to *Tristichia ovensii* by Long (1962). However, *T. ovensii* as defined by Long includes several different species of protostelic axes, and is clearly in need of revision. The Oxroad Bay stems of this type emit in 1/3 phyllotaxis *Lyginorachis*-type petioles that dichotomize close to the stem.
4. *Triradioxylon primaevum* Barnard and Long (1975) (cf. '*Aneurophyton*' of Barnard, 1960a) resembles Stem H in stelar anatomy. Attached petioles are widely spaced along the stem; each has a Y-shaped stele and a single, central protoxylem strand. Barnard and Long (1975) asserted that these petioles did not dichotomize, and were thus similar to *Rhacopteris* fronds with possible progymnosperm affinities. However, Bateman and Rothwell (1990) have shown that a dichotomy is present and that *Triradioxylon* is thus a pteridosperm.

Other foliar organs

Only four isolated, pteridospermous foliar organs have been named from Oxroad Bay (Bateman and Rothwell, 1990):

1. Barnard's (1960a) *Lyginorachis* sp. A probably represents secondary racheis and therefore is not strictly comparable with the petioles that were used to characterize most other *Lyginorachis* species.
2. Barnard's (1960a) *Lyginorachis* sp. B has since been identified with *L. waltonii* Calder and shown to be attached to *Eristophyton* stems (Long, 1987). It possesses dorsiventrally shallow vascular traces with several abaxial corrugations that divide into discrete bundles near the base.
3. *Lyginorachis* sp. nov. of Bateman (1988) occurs in organic connection with *Bilignea* cf. *solida* Scott. It lacks sclerotic nests, and possesses vascular traces with four corrugations that remain connected at the base.
4. Foliar organ A of Bateman and Rothwell (1990) encompasses a wide range of triradiate axes formerly attributed to *Tristichia ovensii* Long. They have yet to be partitioned into biologically meaningful species.

Compressed petioles and frond segments have not been successfully correlated with the more informative petrified material.

Ovulate cupules

Two types of ovulate cupule found at Oxroad Bay have generated more discussion than any other species present. *Calathospermum fimbriatum* Barnard (1960b) is a large, apparently solitary and bilaterally symmetrical cupule that is dissected into many lobes and probably contained numerous ovules. It was interpreted by Barnard (1960b) and Smith (1964a) as a modified frond borne on an apparently unbranched but otherwise *Lyginorachis*-like petiole. Long (1975) interpreted *Calathospermum* as a 'megacupule', resulting from the fusion of a pair of radially symmetrical cupules. He also argued that it is a possible precursor of the angiosperm carpel (Long, 1966, 1975, 1977b, 1985). Matten and Lacey (1981) interpreted branching of the cupule lobes distal to the basal-most dichotomy as pseudomonopodial. *In situ* ovules reported by Barnard (1960a, b) and Long (1975) resemble *Salpingostoma dasu* Gordon in pattern of organization but are much smaller; they may have been abortive. However, Bateman and Rothwell (1990) report *in situ* ovules more closely resembling *Tantallosperma setigera* Barnard and Long.

A.G. Long (pers. comm. 1988) argued that specimens with unusually long axes that appear to lack pinnae may constitute a second species of *Calathospermum* here. Study of similar compressed cupules from Oxroad Bay may help resolve this question.

Pullaritheca longii Rothwell and Wight (1989) represents cupule aggregates containing *Hydrasperma tenuis* Long ovules (Figure 5.19c). They compare with adpression cupules usually identified as *Sphenopteris bifida* Lindley and Hutton (Long, 1977b; Bateman and Rothwell, 1990). Identical ovules have also been reported in *Kerryia* cupules from the Irish Republic (Matten *et al.*, 1980), which differ from *Pullaritheca* in symmetry, branching pattern and number of ovules enclosed (Rothwell and Scheckler, 1988; Rothwell and Wight, 1989). Nomenclatural instability in the past (cf. Long, 1977a; Matten *et al.*, 1975; Matten *et al.*, 1980; Matten *et al.*, 1984a) reflects reluctance to take full account of ontogenetic variation in the ovules and to treat separately the taxonomy of the ovules and of the cupules. Many of the *Pullaritheca* cupules collected by Bateman and Rothwell (1990) contained several abortive ovules, and a few contained more mature individuals (Bateman, 1988; Rothwell and Wight, 1989).

Long (1977a, b, 1979b) recognized two modes of arrangement of the cupules (paired 'hemicupules' and unpaired 'megacupules') that were both considered to represent an entire megasporophyll, and necessitated revision of his 'cupule–carpel' theory. However, Rothwell and Wight (1989) and Bateman and Rothwell (1990) reported a gradation between these two extremes. Comparison of *Pullaritheca* with adpressions assigned to *Sphenopteris bifida* Lindley and Hutton led Long (1979b) to suggest that both bore cupules in similar fashion, as aggregates attached to the median axes of trichotomous petioles. Indeed, clusters of up to eight *Pullaritheca*-like cupules occur in adpression assemblages at Oxroad Bay (Bateman, 1988). One petrified *Pullaritheca* cupule found by Long (1977a) contained both ovules and deformed sporangia. This suggests a developmental anomaly reflecting the homologous architecture of pollen-organ aggregates that were probably borne on other trifurcating petioles of the same plant (Bateman, 1988; Bateman and Rothwell, 1990; Bateman and DiMichele, in press).

An open, frequently and irregularly dichotomous, hirsute cupule contains *Dolichosperma* cf. *sexangulatum* Long ovules (Bateman, 1988). Its branching pattern resembles that of the cupules bearing the ovule *Eurystoma burnense* (Long, 1960b, 1965).

A similarly open, but pseudomonopodially branched, cupule bears *Stamnostoma oliveri* ovules in aggregates of up to four (Bateman and Rothwell, 1990; Rothwell and Scott, 1992a).

Isolated ovules

Bateman (1988) and Bateman and Rothwell (1990) list ten species of isolated petrified ovule. All appear to be distinct, though an ontogenetic relationship between *Tantallosperma* and *Dolichosperma* is credible. Some potential correlatives occur in the adpression assemblages, notably the ovule megaspore studied by Pettitt (1969), which probably represents *Eosperma oxroadense* Barnard (Bateman, 1988).

Salpingostoma dasu Gordon (1941) is the largest known Lower Carboniferous ovule, up to 50 mm long and 6 mm wide (Bateman and Rothwell, 1990). It usually had six integumentary vascular bundles extending into lobes that project well beyond the tall, narrow lagenostome. The integument also bore large, antapically concentrated trichomes. Gordon (1941) erroneously endowed *Salpingostoma* with an atypical pollen-receiving apparatus (Rothwell, 1986).

Dolichosperma cf. *sexangulatum* was first reported from Oxroad Bay by Bateman (1988). It typically had six integumentary bundles and lobes that extend well beyond the lagenostome and was covered with evenly distributed, coarse trichomes. Very similar but rather smaller is *Tantallosperma setigera*, which possessed four (rarely five or six) vascular bundles, integumentary lobes that extend well beyond the lagenostome, and an even covering of coarse trichomes. Since the two are essentially distinguished only on size and number of integumentary lobes, they may conceivably be ontogenetic stages of the same species.

Hydrasperma tenuis Long was reported by Long (1977a, b, 1979b). It had 8–12 integumentary lobes that extended only slightly beyond the lagenostome, which is the widest part of the ovule. Dispersed *H. tenuis* ovules exhibit a wide range of ontogenetic variation at Oxroad Bay, and were erroneously segregated as *H. longii* by Matten *et al.* (1980).

Cf. *Sphaerostoma* sp. nov. (Bateman, 1988; Bateman and Rothwell, 1990) is characterized by an integument with eight vascular bundles, but no lobes. It differs from *S. ovale* Benson (1914; see also Long, 1961b) in its thicker, denser integument and sparser, but coarser, trichomes.

The 'cf. *Sphaerostoma* sp.' of Barnard (1960a) differs from bona fide *Sphaerostoma* in having a morphologically distinct pollen chamber, and an integument that forms an open collar surrounding the lagenostome. It was therefore assigned to *Stamnostoma huttonense* Long by Barnard and Long (1973; see also Rothwell, 1986). However, it differs from *S. huttonense* Long in having a smaller length:breadth ratio and papillae on the integument. Consequently, it has been referred to a new species, *Stamnostoma oliveri* Rothwell and Scott (1992a).

Cf. *Eurystoma burnense* Long has been reported by Bateman (1988). Elsewhere, Long (1966, 1969) has recognized both pre-prothallial and prothallial ontogenetic phases. Its distinctive, triangular transverse section reflects its three vascular bundles and associated wide lateral keels, which terminate as short lobes projecting slightly beyond the lagenostome.

Eosperma oxroadense Barnard (1959) has only two integumentary vascular bundles and lacks integumentary lobes; short spiny trichomes occur on some specimens. Pettitt (1969) demonstrated attachment of three abortive megaspores to a compressed functional megaspore that probably belonged to *Eosperma*.

Bateman (1988) has demonstrated the presence of cf. *Eccroustosperma langtonense* Long from *in situ* strata, the report by Long (1987) having been based on a loose block that was probably transported from nearby Castleton Bay. It has two vascular traces terminating in fairly short integumental lobes that do not extend beyond the lagenostome. Bateman (1988) observed that Oxroad Bay specimens are more strongly curved than those from elsewhere (cf. Long, 1961b, 1975), and may represent the pre-prothallial ontogenetic stage of *Camptosperma berniciense* Long (1961a).

Deltasperma fouldenense Long (1961a) was first recognized as fusainized material macerated by Bateman (1988) (Figure 5.20d). Two vascular strands terminate in fairly short integumental lobes that do not exceed the lagenostome. Characteristically large superficial cells cover the whole of the more convex face, and the apical region of the less convex face.

Pollen-organs

Three of the four pollen-organs listed by Bateman (1988) and Bateman and Rothwell (1990) appear to be synangiate: cf. *Telangium* sp., cf. *Melissiotheca* sp. and 'pollen-organ C'. The *Telangium*-like synangia terminate repeatedly dichotomous axes. They typically comprise eight, basally-fused, bilaterally-arranged synangia containing finely tuberculate pre-pollen. They therefore share characters with several *Telangium*-like form-genera (e.g. Eggert and Taylor, 1971; Long, 1979a; Millay and Taylor, 1979; Meyer-Berthaud and Galtier, 1986a).

The pedicellate synangia of cf. *Melissiotheca* sp. are shallowly divided into at least two lobes, each consisting of 30–100 basally-fused sporangia that are embedded in a parenchymatous cushion, and contain rugulate pre-pollen (Bateman, 1988; Bateman and Rothwell, 1990). The sporangia are smaller and exhibit less profound lateral fusion than those of *Melissiotheca longiana* Meyer-Berthaud (1986). Numerous compressed synangia from Oxroad Bay are difficult to apportion between cf. *Telangium* sp. and cf. *Melissiotheca* sp. (Bateman, 1988).

Pollen-organ C of Bateman and Rothwell (1990) is a large, hirsute, oviform organ that superficially resembles the ovulate cupule *Calathospermum fimbriatum* Barnard in size and branching pattern. Large sporangia form asymmetrical synangia and enclose dimorphic pre-pollen; the larger pre-pollen morph is considered fertile and the smaller abortive (Bateman, 1988). Similar pre-pollen has frequently been found in the lagenostome of *Salpingostoma dasu* Gordon (Long, 1975; Bateman, 1988). Pollen-organ C was incorrectly referred to cf. *Telangium* by Barnard (1960a) and subsequent workers, and should not be confused with the cf. *Telangium* described above.

Pollen-organ D of Bateman and Rothwell (1990) is a single terete branching axis terminated by a small, thick-walled sporangium. It is associated with abundant foliar organs showing similar histology. Spores found in the sporangium have sparse, blunt-tipped spines, and compare with forms found in the lagenostome of *Deltasperma* (Bateman, 1988).

General remarks

At least 11 whole-plant species of tracheophyte grew at Oxroad Bay, and these have produced one of the most diverse assemblages of Early Carboniferous petrifactions. In Britain, it is second in estimated partial-plant diversity only to the Whiteadder (see above, and Scott *et al.*, 1984; Bateman *in* Cleal, 1991). Other taxonomically similar petrifaction assemblages occur at nearby Castleton Bay (Scott and Galtier, 1988); the upper assemblage at Loch Humphrey Burn (see below); Kingswood (see below); and Ballyheighue, Irish Republic (Matten *et al.*, 1980; Matten *et al.*, 1984b). These occurrences vary considerably in age (Strunian to possible early Asbian), sedimentological regime and geographical location, but evidently reflect similar ecological and taphonomic constraints. However, none of the above localities matches Oxroad Bay in whole-plant diversity, or in the potential for correlating petrifaction, adpression and fusain fossils of the same plant organ.

Conclusion

Oxroad Bay is one of a series of basal Carboniferous sites in southern Scotland that yield anatomically-preserved plant fossils (about 350 million years old). Taken together, they are the most important global source of information on vegetation of this age. This site is especially important for allowing the first rigorous reconstructions for Early Carboniferous representatives of these plant groups. Studies of the club-mosses and horsetails have been completed, but work continues on the more diverse (and thus more problematic) early seed plants and on the ferns. Integration of the reconstructions with palaeoenvironmental data from this unstable volcanic setting has led to recognition of several distinct plant communities. Increasing knowledge of their structure and dynamics will allow comparison with extant vegetation.

WEAK LAW

Highlights

Weak Law yields a potentially significant plant petrifaction assemblage of Early Carboniferous age. Stems of the form-genus *Pitus* are particularly well preserved, and show evidence of attachment of young fronds.

Introduction

Following his work on the plant petrifactions from Pettycur (p. 141), W.T. Gordon extended his investigations to cover similar volcaniclastic deposits in SE Scotland. In 1914, Gordon made his first major discovery, Weak Law, on the coast between Gullane and North Berwick (NT 499858). To investigate further the assemblage, the British Association for the Advancement of Science set up a committee to organize an excavation of the site, employing explosives, but the intervention of the 1914–1918 war prevented Gordon from going ahead (Kidston *et al.*, 1917). The only detailed descriptions of plant fossils from here have been Gordon's (1935a) account of the *Pitus* species, and a description of a *Lyginorachis* by Galtier and Scott (1986a). However, a more detailed investigation is currently in progress by A.C. Scott and his colleagues.

Description

Stratigraphy

In the virtual absence of any biostratigraphical data, it is impossible to estimate the chronostratigraphical position of the site, beyond it being Lower Carboniferous. Kidston *et al.* (1917) argued that it was probably homotaxial with the Pettycur deposits (see below), now known to be Asbian, but the evidence on which this was based was limited. According to Gordon (1935a), the plants probably grew on the side of an active volcano, were killed by a violent eruption and buried by the resulting ash flow. The ash may well have had a high moisture content, and the resulting colloidal solution caused the plants to become permineralized.

Palaeobotany

The assemblage here consists exclusively of petrifactions, including the following:

Lycopsida:
Lepidodendron sp.
Stigmaria sp.

Filicopsida:
Botryopteris sp.
Bensonites sp.

Lagenostomopsida:
Pitus primaeva Witham
Pitus dayi Gordon
Pitus rotunda Gordon
Lyginopteris gordonii Galtier and Scott

Interpretation

Gordon (1935a) described three species of *Pitus* from here, although Long (1979a) has questioned the validity of the distinction. They differ in details of wood structure, particularly the width of the medullary rays. *P. dayi* Gordon was found with spirally-attached leaf-bases, which Gordon interpreted as phyllodes, similar to those found in extant araucarias. However, Long (1979a) suggested that they are more likely the petioles of juvenile, unexpanded fronds, of the *Lyginopteris*-type (see also Beck, 1960).

Of passing interest is the discovery of a *P. primaeva* Witham specimen in the hearth of a nearby Neolithic dwelling (Gordon, 1935b). The fossil resembles closely a piece of drift wood, which must have disappointed its original discoverer on attempting to burn it! This must represent one of the earliest examples of a palaeobotanical discovery.

A single specimen was the basis of Galtier and Scott's (1986a) description of the pteridosperm frond *Lyginorachis gordonii*, which shows a trifurcate petiole. The two lateral racheis probably produced the two foliar halves of a bipartite frond, and the median rachis bore fertile structures (either cupules or pollen-organs). It is essentially similar in structure to other *Lyginorachis* species (Calder, 1935; Long, 1963), as well as *Pitus dayi* Gordon and *Calathopteris heterophylla* Long (1976), but differs in the details of the vascular configuration and the relative positions of the racheis.

Most of the assemblage has not been described in detail, and so a full comparison with other localities cannot be given. However, the reported presence of *Bensonites*, which usually occurs in the upper Visean (such as at Pettycur – see p. 148), contrasts with the abundant *Pitus* stems, which are characteristically Tournaisian and lower Visean (as at Lennel Braes, Whiteadder, Kingwater – see elsewhere in this chapter). The site clearly has potential for further significant palaeobotanical discoveries, which will help unravel the history of Early Carboniferous vegetation in this country.

Conclusion

Weak Law is one of a series of sites showing Lower Carboniferous rocks in southern Scotland, which yield anatomically-preserved plant fossils, about 350 million years old. Nowhere else in the world has so many sites of this age yielding such well preserved fossils. This particular site is so far mainly known for well-preserved stems of early seed plants (known as *Pitus*) in which the position of attachment of young fronds can be recognized. However, the potential of this site has yet to be fully realized.

KINGWATER

Highlights

Kingwater has yielded the best example of *in situ* arborescent pteridosperm stumps in the Lower Carboniferous of Britain, and provides important information as to the size, palaeoecology and density of this type of vegetation.

Introduction

This Visean site lies in the bed of Kingwater Beck, 4 km north-west of Gilsland, near Haltwistle, Cumbria (NY 608697). *In situ* fossil tree stumps were discovered here by Day (1970), and described in detail by Long (1979a).

Description

Stratigraphy

The geology of this site was described by Day (1970). The stumps occur just below the Desoglin Limestone, near the top of the Middle Border Group (Figure 5.21). Fossil marine invertebrates and algae from near this horizon indicate the S_1 Zone, which in modern terms places it in the Arundian Stage. The deposits probably represent a fluvial environment, although detailed sedimentological information is not available.

Palaeobotany

Ten *in situ* stumps found here have been identified as *Pitus primaeva* Witham. The largest is just under 2.5 metres in diameter, and evidently belonged to a tree of considerable size, perhaps 10 metres or more in height. The spacing between the stumps varies from 4 to 40 metres. However, this variation may be partially the result of some stumps being no longer preserved, due to their removal either immediately after death or by recent erosion.

Such examples of a forest floor with surviving *in situ* stumps dating from the Early Carboniferous are rare worldwide, and this is the only one presently available showing a stand of gymnosperm trees.

Interpretation

Based on the fossils present, it can be calculated that there must have been at least 2000 trees per km^2 in this area, indicating an open woodland environment. According to Long (1979a), they grew at sufficiently low altitudes for them to have become flooded and buried by marine deposits.

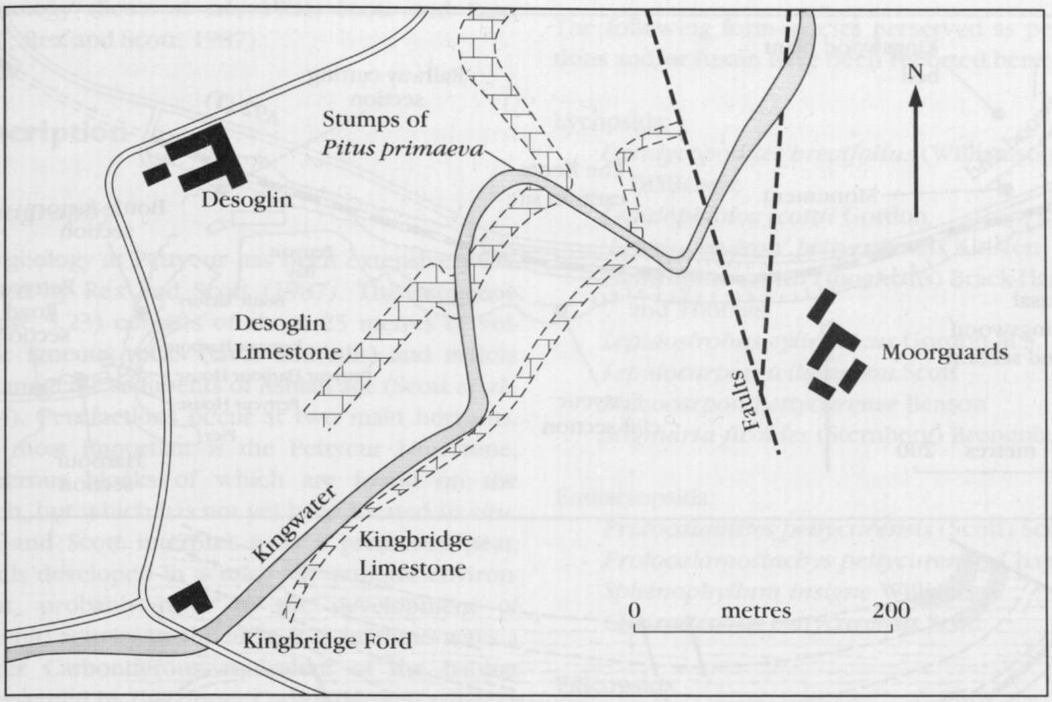

Figure 5.21 Map of that part of Kingwater where *in situ* tree stumps are preserved in the Lower Carboniferous. Based on Day (1970, figure 20).

Conclusion

Kingwater has the only known examples of gymnosperm tree-stumps, still preserved in position, from about 340 million years ago. They provide a valuable insight into the nature of these very early forests, that pre-dated by some 30 million years the tropical coal-swamp forests that covered the palaeoequatorial belt (including Britain) in Late Carboniferous times.

PETTYCUR

Highlights

Pettycur is one of the classic Lower Carboniferous palaeobotanical sites and has yielded the most diverse British Visean petrifaction assemblage. It is the type locality for a number of species and is particularly important for lycopsids and ferns; it is also the only known locality for the equisete family Cheirostrobaceae. It is one of the most important palaeobotanical sites in Britain.

Introduction

Prior to the discoveries at Rhynie (see Chapter 4), Pettycur possessed by far the best known assemblage of pre-Late Carboniferous plant petrifactions in the world. Together with the coal-ball petrifactions from Yorkshire and Lancashire, it played a key role in developing an understanding of Palaeozoic plant life. The site (Figure 5.22), on the coast at Pettycur, near Burntisland, Fife (NT 262863), was discovered in 1871 by the local Fifeshire geologist George Grieve. In May of that year, a fossil was exhibited to the Botanical Society of Edinburgh by J.H. Balfour. However, the 'formal unveiling' of the site may be taken as being at the meeting of the British Association for the Advancement of Science held in Edinburgh in August 1871. Details of the site were described during the meeting and afterwards an excursion was conducted there (Gordon, 1909). Numerous publications followed, dealing with parts of this important Lower Carboniferous flora, usually described in tandem with material from the Upper Carboniferous coal balls (Williamson, 1872, 1873, 1874a, b, 1877, 1893; Williamson and Scott, 1894,

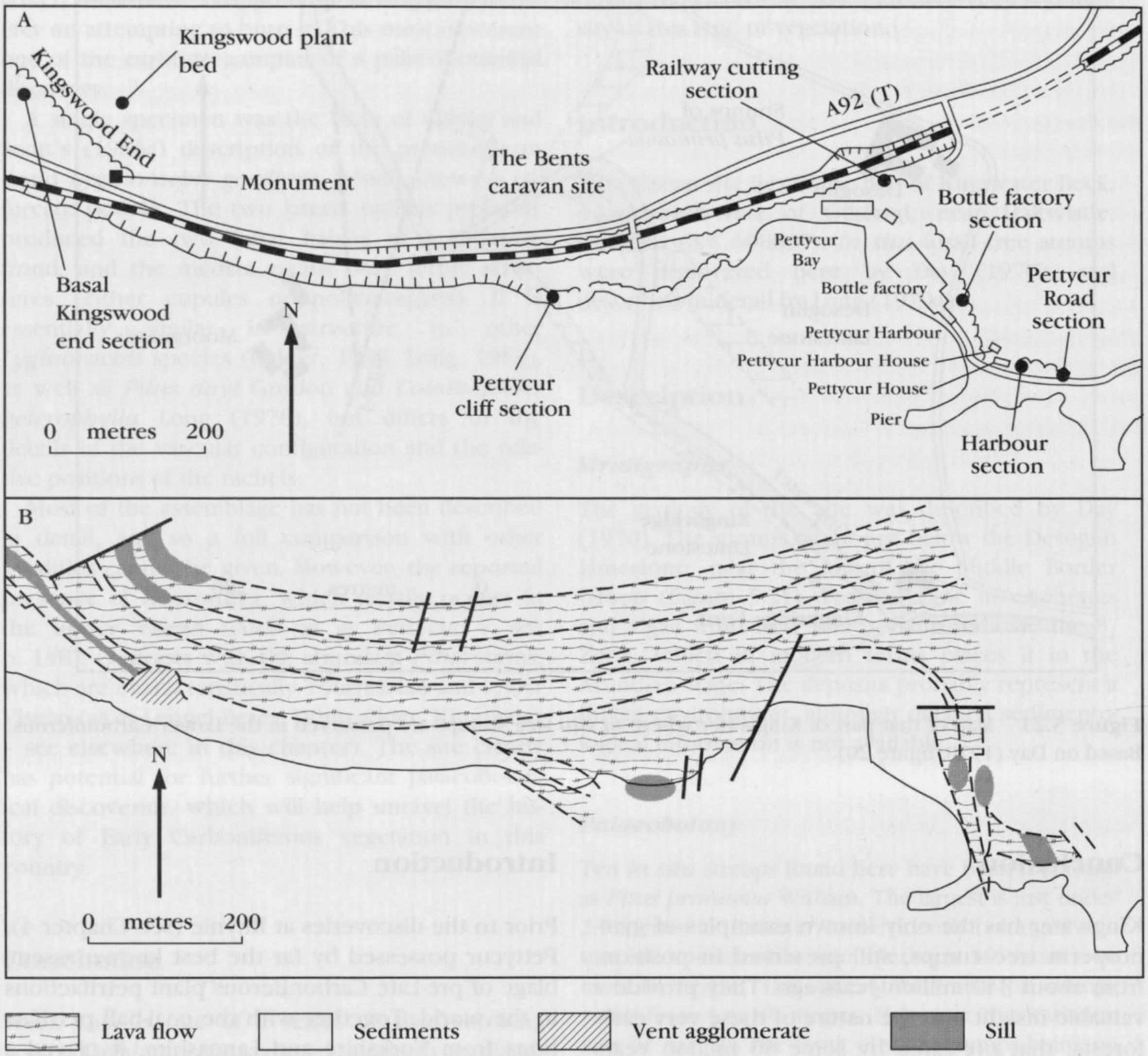

Figure 5.22 Maps of the Pettycur and Kingswood End GCR palaeobotany sites. The upper illustration is a locality map. The lower illustration shows the distribution of the main lithologies. Based on Rex and Scott (1987, figure 2).

1895; Scott, 1897, 1900, 1901, 1908; R. Scott, 1908).

The most detailed investigation of the site was by Gordon (1908b, 1909, 1910a, b, 1911a, b, 1912). Other significant publications were by Benson on the lycopsids, ferns and pteridosperms (Benson, 1908, 1911, 1914, 1922, 1933), as well as some shorter contributions by Kidston (1907, 1908), Bertrand (1907, 1909), Chodat (1912) and Graham (1935).

As at Rhynie, the development of the acetate peel method of investigating petrifactions (Joy *et al.*, 1956) had a significant impact on the study of the Pettycur fossils, allowing more detailed reconstructions to be achieved. It proved particularly significant for the ferns, whose complex branching patterns could only be properly resolved by very fine serial sectioning. The most important contributions using the method have been by Surange (1952a, b), Lacey *et al.* (1957), Chaloner (1958), Holden (1962), Chaphekar (1963) and Chaphekar and Alvin (1972). In subsequent years, there has been little published work on the palaeobotany of Pettycur, although there has been considerable interest in its stratigraphy and sedimentology (Scott *et al.*, 1984; Scott and Rex, 1987; Rex and Scott, 1987).

Description

Stratigraphy

The geology at Pettycur has been extensively discussed by Rex and Scott (1987). The sequence (Figure 5.23) consists of about 25 metres of volcanic igneous rocks (lavas and sills) and mainly volcanogenic sediments of Asbian age (Scott *et al.*, 1984). Petrifactions occur at two main horizons. The most important is the Pettycur Limestone, numerous blocks of which are found on the beach, but which has not yet been located *in situ*. Rex and Scott interpret it as a preserved peat, which developed in a relatively tranquil environment, probably prior to the development of volcanic activity in the area; it is in some ways a Lower Carboniferous equivalent of the habitat represented by the Upper Carboniferous coal-balls (Scott and Rex, 1987). The second plant-bearing bed is the Zygopterid Limestone, which also includes abundant fusain. This does not represent an *in situ* peat, but probably the remains of plants growing in a volcanically disturbed habitat, which were transported into a small lake and buried. Rex and Scott also report less well-preserved petrifactions together with fusain at four other horizons (the Harbour 'Peat' and Ashy Limestones 1–3), and some adpressions in a dolomitic mudstone.

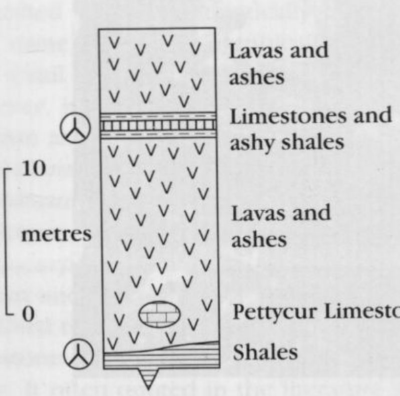

Figure 5.23 Generalized stratigraphical section at Pettycur. Based on Scott *et al.* (1984, figure 9).

Palaeobotany

The following form-species preserved as petrifactions and/or fusain have been reported here:

Lycopsida:
- *Paralycopodites brevifolius* (Williamson) DiMichele
- *Lepidophloios scottii* Gordon
- '*Lepidodendron' pettycurensis* Kidston
- *Flemingites scottii* (Jongmans) Brack-Hanes and Thomas
- *Lepidostrobus cylindricus* Gordon M.S.
- *Lepidocarpon wildianum* Scott
- *Mazocarpon pettycurense* Benson
- *Stigmaria ficoides* (Sternberg) Brongniart

Equisetopsida:
- *Protocalamites pettycurensis* (Scott) Scott
- *Protocalamostachys pettycurensis* Chaphekar
- *Sphenophyllum insigne* Williamson
- *Cheirostrobus pettycurensis* Scott

Filicopsida:
- *Botryopteris antiqua* Kidston
- *Metadineuron ellipticum* (Kidston) Galtier
- *Diplolabis roemeri* (Solms-Laubach) Bertrand
- *Metaclepsydropsis duplex* (Williamson) Bertrand
- *Musatea duplex* Chaphekar and Alvin
- *Stauropteris burntislandica* Bertrand
- *Bensonites fusiformis* Scott

Lagenostomopsida:
- *Heterangium grievii* Williamson
- *Rhetinangium arberi* Gordon
- *Sphaerostoma ovale* (Williamson) Benson
- *Physostoma* sp.
- *Bensoniotheca grievii* (Benson) Mickle and Rothwell
- *Amyelon* sp.

In addition, Rex and Scott (1987) list as adpressions *Lepidodendron* sp., *Lepidocarpon* cf. *waltonii* Chaloner, *Sphenopteris affinis* Lindley and Hutton, *Sphenopteris* sp., *Sphenopteridium* sp., *Adiantites machanekii* Stur and *Cardiopteridium* sp.

Interpretation

Lycopsida

Lycopsid fragments are the most abundant fossils here, particularly in the Pettycur Limestone. The commonest type is *Paralycopodites brevifolius* (Figure 5.24), a lycopsid stem found abundantly in both the Lower and Upper Carboniferous (Williamson, 1872, 1893; DiMichele, 1980). It had a straight, rarely dichotomizing trunk, with a crown of deciduous lateral branches, at the ends of which were small, bisporangiate strobili. The strobili found at Pettycur are known as *Flemingites scottii* (in the Upper Carboniferous, slightly different strobili are associated with *Paralycopodites*, known as *F. diversus* (Felix, 1954) and *F. schopfii* (Brack, 1970)). Megaspores found in *F. scottii* have been reported with endosporal gametophytes (Gordon, 1908a, 1910b; D.H. Scott, 1908–1909), similar to those of the extant *Selaginella* (Gordon, 1908a; Phillips, 1979). The rooting structures are unknown, although Williamson (1872) noted that *Stigmaria ficoides* is often found in close association. Evidence from the Upper Carboniferous suggests that these lycopsids were opportunistic plants, occupying slightly drier parts of the coal-swamps (Phillips and DiMichele, 1992). Its predominance in the Pettycur Limestone (Rex and Scott, 1987), appears to confirm that it favoured peat-accumulating swamps. However, the detailed community structure of the Pettycur swamp has still to be worked out.

Smith (1962c) argued that the stems now called *Paralycopodites* were intermediate between *Lepidodendron* and *Lepidophloios*, but DiMichele (1980) clearly showed they differed from both these lycopsids in having a smooth-surfaced siphonostele, a homogeneous periderm and cortex, and deciduous branches. He further argued that it could be distinguished by the presence of persistent leaves, although some large *Lepidodendron* stems have also now been shown to have been leafy (Leary and Thomas, 1989). A closer analogue might be with the adpressions stems known as *Ulodendron*, as defined by Thomas (1967b). There are differences in the epidermis of the

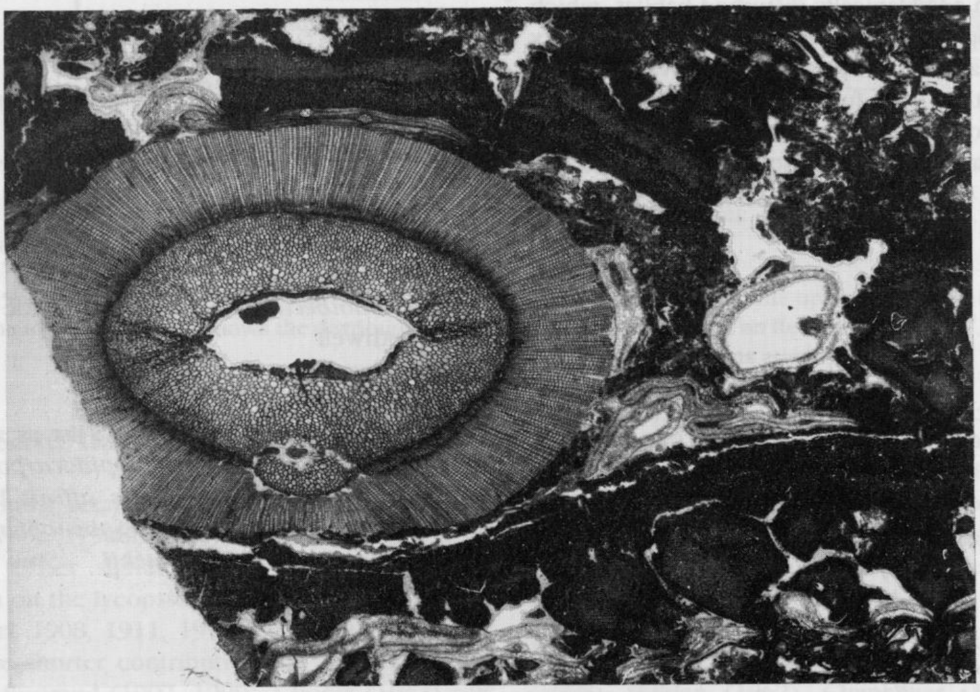

Figure 5.24 *Paralycopodites brevifolius* (Williamson) DiMichele. Transverse section through lycopsid stem; Natural History Museum, London, specimen WC.502. Pettycur Limestone (Asbian), Pettycur. × 4. (Photo: Photographic Studio, Natural History Museum, London.)

leaves, the stomata being restricted to two bands along each leaf in *Paralycopodites* (Graham, 1935), whereas in *Ulodendron* they are more evenly distributed (Thomas, 1967b); but this may just reflect differences at the species level.

Neither DiMichele (1980) nor Thomas and Brack-Hanes (1984) give any opinion as to the taxonomic position of *Paralycopodites*. However, the likelihood that it bore *Flemingites* strobili must surely place it at least as a satellite form-genus of the Flemingitaceae, as defined by Thomas and Brack-Hanes.

A second, but less abundant, lycopsid in the swamps produced the stem known as *Lepidophloios scottii* Gordon (1908b). These stems have a siphonostele surrounding a mixed pith, a feature which is normally regarded as relatively 'primitive'; other *Lepidophloios* species usually have a fully medullated siphonostele, except in the more distal branches (DiMichele, 1979). Gordon noted that it has leaf cushions similar to those seen in the adpression species *Lepidophloios scoticus* Kidston, which occurs commonly in the Lower Carboniferous of Scotland (see also Galtier and Scott, 1986b). Sections through stomata on the leaf cushions have been described by Thomas (1974).

Lepidophloios is thought to have borne megasporangiate strobili known as *Lepidocarpon* (Phillips, 1979; Thomas, 1981b). It is not surprising, therefore, that isolated sporophylls known as *Lepidocarpon wildianum* Scott (1900, 1901) are associated with *Lepidophloios scottii* at Pettycur. Being found as isolated sporophylls supports Phillips' (1979) view that they operated as seed-like disseminules. The Pettycur sporophylls are very similar to *Lepidocarpon lomaxii* Scott from the Upper Carboniferous coal-balls, and Scott distinguished them taxonomically mainly because they came from stratigraphically different horizons. Until complete strobili are found at Pettycur, however, it will be impossible to make any final decision as to the relative taxonomic positions of *L. wildianum* and *L. lomaxii*. The relationship of *L. wildianum* to the adpression from the Pettycur mudstones, described by Rex and Scott (1987) as *Lepidocarpon* cf. *waltonii* Chaloner, is also at present unclear.

A third type of lycopsid stem from the Pettycur Limestone is known as '*Lepidodendron*' *pettycurense*. It often quoted in the literature as a prime example of a primitive *Lepidodendron*, since it has a solid protostele (e.g. Taylor, 1981). However, it is only known from two decorticated axes (Kidston, 1907), and there is little definitive evidence that the fossil really is a *Lepidodendron*. Significantly, the axes are found closely associated with *Mazocarpon pettycurense* Benson (1908) sporophylls, this type of fructification usually being linked with the Sigillariostrobaceae (Schopf, 1941). To determine the taxonomic position of these stems will clearly need better preserved material.

The *Mazocarpon* described by Benson (1908) is only known from incomplete sporophylls, but appears to represent a reproductive strategy similar to that adopted by *Lepidocarpon* (see above). If correctly assigned to the Sigillariostrobaceae, these sporophylls are the oldest evidence of this family in the fossil record.

A fourth type of lycopsid fructification is *Lepidostrobus cylindrica* Gordon M.S. Although mentioned in species lists for the site (Gordon, 1914; Walton and Long, 1964), it has never been effectively published and so for the time being must remain a *nomen nudum*.

Equisetopsida

The remains of two equisetopsid orders have been found at Pettycur: the Equisetales ('archaeocalamitids') and Bowmanitales ('sphenophylls'). Equisetalean stems are relatively abundant, although Rex and Scott (1987) state that they are often preserved 'in the immature form'. They were originally described as *Calamites pettycurensis* Scott (1902) and then *Protocalamites pettycurensis* D.H. Scott (1908–1909). Chaphekar (1963) argued that the differences from '*Archaeocalamites*' *goeppertii* (*Protocalamites goeppertii* (Solms-Laubach) Bateman) merely reflected different positions within the plant. However, Bateman (1991) has found that the Pettycur stems have consistently fewer primary vascular strands than typical *P. goeppertii*, such as found at Laggan and Loch Humphrey Burn (Walton, 1949b; Chaphekar, 1963), and that they probably represent smaller, shrubby plants.

Associated with these stems are strobili, *Protocalamostachys pettycurensis* Chaphekar (1963). Although never found in organic attachment, the structure of the pedicle is very similar to that of the smaller branches of *Protocalamites pettycurensis*. It differs from *Protocalamostachys arranensis* Walton found at Laggan (p. 155) in being smaller, having more sporangiophores in each whorl, fewer vascular strands in the pedicle, and containing smaller spores (Bateman, 1991).

The Bowmanitales are rare in the Pettycur Limestone. Stems described by Williamson (1874a) and Williamson and Scott (1894) have a primary xylem strand with the characteristic triangular cross-section of this order (cf. Meyen, 1987, fig. 21), and are known as *Sphenophyllum insigne* Williamson. Two specimens have been reported with roots attached to one side (Williamson and Scott, 1894), which supports the evidence from the Upper Carboniferous that *Sphenophyllum* was a creeping or scrambling plant (Batenburg, 1981).

The order is generally rare in the Lower Carboniferous, although there is evidence of its range extending down to the Upper Devonian (Remy and Spassov, 1959). Petrifactions have also been reported from Saalfeld (Solms-Laubach, 1896) and the Montagne Noire (Galtier, 1970), but the Pettycur specimens remain the best documented Lower Carboniferous examples to date.

Cheirostrobus pettycurensis (Figure 5.25) is also often included in the Bowmanitales, based partly on its occurrence in a deposit supposedly 'rich with *Sphenophyllum* stems' (e.g. Taylor, 1981); in fact such stems are relatively rare at Pettycur, and Scott (1897) argued that they could not have borne *Cheirostrobus* strobili. Nevertheless, there is an underlying similarity between the peltate sporangiophores of *Cheirostrobus* and those of *Bowmanites* and other bowmanitalean strobili. The most significant difference is that *Cheirostrobus* is a far more complex structure than any other reported bowmanitalean strobilus, and it superficially resembles certain lycopsid strobili such as *Flemingites*. It has whorls of thirty-six sporophylls, each sporophyll bearing four elongate sporangia (Scott, 1897). Its taxonomic position is uncertain, but is usually assigned to a monospecific family (Cheirostrobaceae) within the Bowmanitales. If correct, it suggests that there was a marked reduction in structural complexity of bowmanitalean strobili during the Carboniferous. It remains a considerable palaeobotanical enigma, and is only known from Pettycur.

Filicopsida

The ferns fall broadly into two groups: (1) species of Zygopteridaceae (Coenopteridales), which occur mainly in the Zygopterid Limestone; and (2) species of Stauropteridaceae (Coenopteridales) and Botryopteridaceae (Botryopteridales), which occur mainly in the Pettycur Limestone (for details of their distribution, see Rex and Scott, 1987, fig. 11).

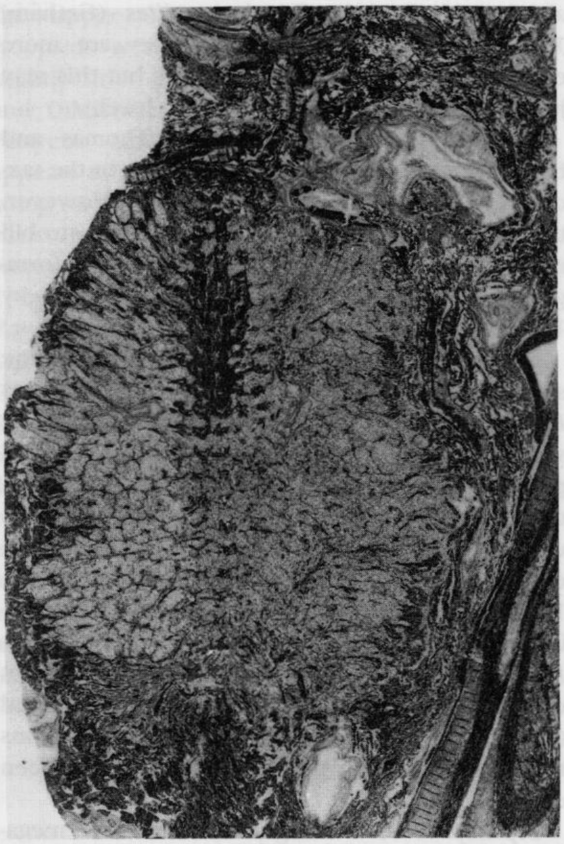

Figure 5.25 *Cheirostrobus pettycurensis* Scott. Longitudinal section through complex equisetopsid cone showing distribution of sporangia; Natural History Museum, London, SC.3661. Pettycur Limestone (Asbian), Pettycur. × 2. (Photo: Photographic Studio, Natural History Museum, London.)

Zygopterid community

Pettycur is probably the best known British locality for zygopteridacean ferns, and it has provided valuable information on the evolution of the vascular systems of the stem (Gordon, 1911a, b, 1912; Dennis, 1974) and the phyllophores (Gordon, 1911b; Galtier, 1964). They appear not to have been growing in the main peat-swamp, but were probably a pioneer community which would have invaded the areas nearer the volcanic centres during periods of eruptive quiescence (Rex and Scott, 1987). The best understood of the

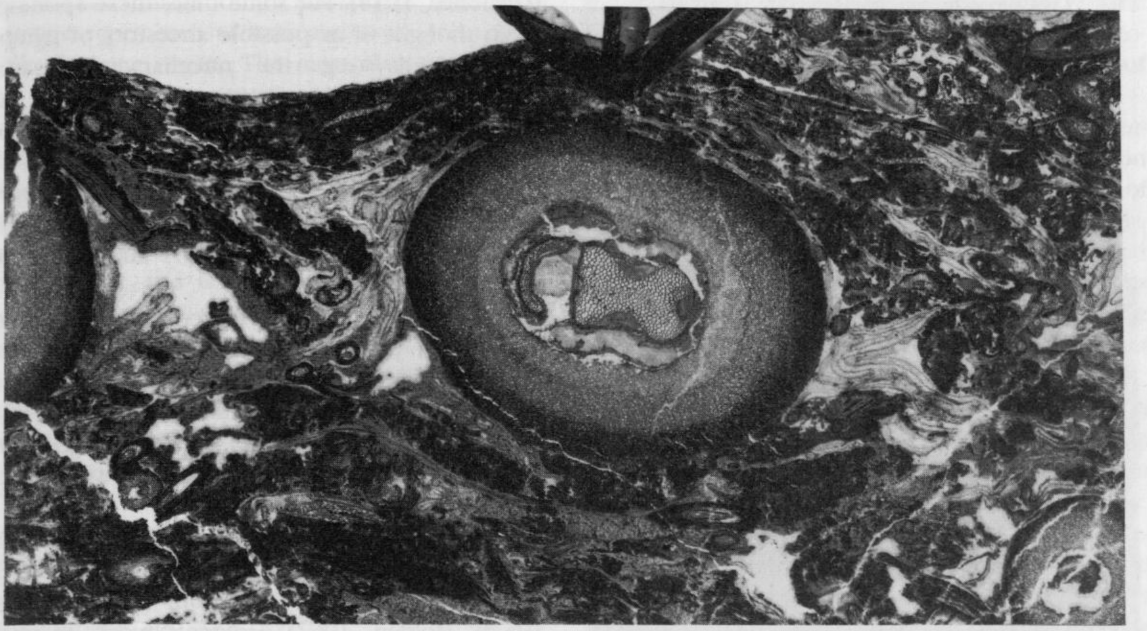

Figure 5.26 *Metaclepsydropsis duplex* (Williamson) Bertrand. Transverse section through fern rachis; Natural History Museum, London, specimen WC.223. Pettycur Limestone (Asbian), Pettycur. × 4. (Photo: Photographic Studio, Natural History Museum, London.)

Pettycur species is *Metaclepsydropsis duplex* (Figure 5.26; Williamson, 1874b; Bertrand, 1909; Gordon, 1911b; Chaphekar and Alvin, 1972). For many years, it was only known from here, although there are now reliable records also from Glenarbuck (see below), Roannais (Galtier, 1970) and Esnost (Galtier, 1980). It is interpreted as a scrambling plant with little or no secondary wood in the stems and bearing upright fronds. The branching pattern of the vascular traces within the fronds (Gordon, 1911b, text-figs 2–3) is a characteristic feature of the early members of the family. Fertile pinnules associated with these fronds have been named *Musatea duplex* Chaphekar and Alvin (1972); these have sporangial clusters apparently borne superficially at the margins of the abaxial surface (Galtier, 1981). They are similar to fructifications associated with other Lower Carboniferous zygopteridaceans (Galtier, 1968), but contrast markedly with the more complex *Biscalitheca* borne by Upper Carboniferous to Permian zygopteridaceans (Mamay, 1957).

Of similar habit and anatomy was *Diplolabis roemeri* (Figure 5.27) (synonyms *Zygopteris pettycurensis* Gordon, *Diplolabis esnostensis* Renault and *D. forensis* Renault) (Renault, 1896; Gordon, 1909, 1911a). As with *Metaclepsydropsis*, there is little evidence of secondary wood development. The fertile pinnules were also similar to those of *Metaclepsydropsis*, and have been named *Musatea globata* Galtier (1968).

The third of the Pettycur zygopteridacean axes, *Metadineuron ellipticum*, is only known from fragments of phyllophore (Kidston, 1908; Galtier, 1964, 1970). It is presumed to have been of similar habit to the other members of the family from Pettycur.

Filicopsids of the swamp community

Within the peat-forming swamp, the Coenopteridales were represented by *Stauropteris burntislandica* (Williamson, 1874b; Bertrand, 1907, 1909). It has also been reported from Roannais in central France (Galtier, 1971), but most work on the species has been based on Pettycur material. Although the overall form of the plant has not been confirmed, it is assumed to have been herbaceous. The fronds were reconstructed by Surange (1952a), and are generally similar to those of the Zygopteridaceae, including the presence of basal aphlebiae (Lacey *et al.*, 1957), but have a less-planated, more primitive aspect.

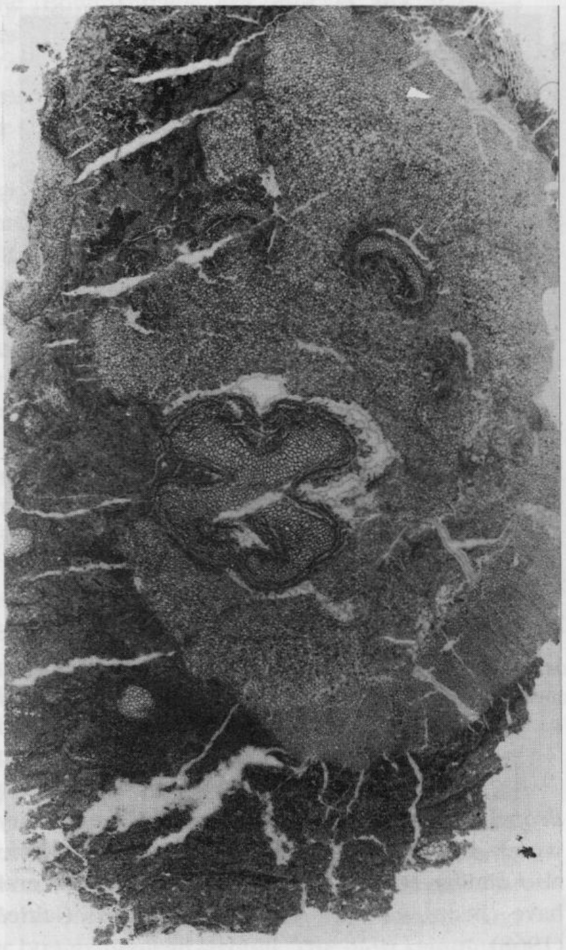

Figure 5.27 *Diplolabis roemeri* (Solms-Laubach) Bertrand. Transverse section through fern rachis; Natural History Museum, London, specimen GC.789. Pettycur Limestone (Asbian), Pettycur. × 4. (Photo: Photographic Studio, Natural History Museum, London.)

Of particular interest is the fact that *S. burntislandica* was heterosporous. The megasporangia had been initially identified as *Bensonites fusiformis* R. Scott (1908) but the connection with *Stauropteris* was confirmed by Chodat (1912; see also Surange, 1952a). They are spindle-shaped structures, consisting mostly of parenchyma with a longitudinal vascular strand, but with a distal cavity that opens out to the sporangium apex via a narrow tube. The cavity contains a tetrad of two operative and two aborted megaspores, corresponding to *Didymosporites scottii* Chaloner (1958) (see also Hemsley, 1990b). Similar dispersed megaspores are known from various Lower Carboniferous localities in Britain (Chaloner, 1958). For some time, these sporangia were thought of as possible ancestors of gymnosperm seeds (e.g. the nucellar modification concept of Andrews, 1961), but this view has now lost favour (see discussion on the Whiteadder earlier in this chapter). Instead, it would appear that it represents a seed-like reproductive strategy, comparable to that achieved by the lycopsids (*Lepidocarpon*) and equisetes (*Calamocarpon*).

Microsporangia have not been found in organic connection with *S. burntislandica*, but R. Scott (1908) reported that structures very similar to *Stauropteris oldhamia* Binney sporangia occur in close association. Unlike most fern sporangia, they lacked an annulus, and spore-release was achieved via a small stomium.

The Botryopteridales are represented by *Botryopteris antiqua*, for which this is the type locality (Kidston, 1908; Benson, 1911; Surange, 1952b; Holden, 1962). Holden's work, in particular, has clarified the overall habit of the plant, which seems to have had a creeping stem, giving off erect fronds with digitate, three-dimensional pinnules, and a similarity to the adpression form-genus *Rhodeopteridium*. A distinctive character of the fronds is the frequent presence of small plantlets, which were presumably a means of vegetative propagation (see also Galtier, 1969), a feature generally rare in the Filicopsida. The sporangia were borne laterally to the ultimate segments of the frond (Galtier, 1967, 1981). They have a transverse annulus and contain spores of the form-genus *Granulatisporites*.

There has been some disagreement as to the taxonomic position of *B. antiqua*. It differs from typical *Botryopteris* (e.g. *B. forensis* Renault, *B. globosa* Darrah), which has fertile organs consisting of large clusters of several hundred sporangia. Good (1981) argued that it should therefore be transferred to *Psalixochlaena*, but this ignores the differences in vascular structure and position of attachment of the sporangia (Holden, 1960; Holmes, 1977, 1981). It is arguable that *B. antiqua* should be transferred to a different form-genus but, in the absence of a detailed taxonomic analysis of the problem, the traditionally accepted combination is used here.

Lagenostomopsida

Unlike most other Lower Carboniferous petrifaction sites in Britain, Pettycur does not have a diverse assemblage of pteridosperms; there are just two types each of stem and seed, and one of pollen-bearing organ. The most abundant fossils are the stems *Heterangium grievii*, for which Pettycur is the type and best locality (Williamson, 1873; Williamson and Scott, 1895; Benson, 1933). This is the best known of the 'primitive' group of *Heterangium* species, which are assigned to the subgenus *Heterangium* (synonym *Eubeterangium* auct.), and is characterized by a mesarch protostelic vascular system and transverse sclerotic plates in the cortex. The latter feature imparts a transverse bar-pattern to the outer surface of the stems, allowing a correlation with *Sphenopteris elegans* Brongniart and *S. affinis* Lindley and Hutton types of foliage preserved as adpressions. These fronds have deeply dissected pinnules, in contrast to the *Eusphenopteris* fronds borne by *Heterangium* subgenus *Polyangium* from the Upper Carboniferous, which have rounded pinnules (Shadle and Stidd, 1975).

The present distribution of *H. grievii* suggests that it came from a plant that was abundant in the Pettycur Limestone peat-swamp (Rex and Scott, 1987), and was probably a ground-cover creeper, growing below the arborescent lycopsids.

Associated with *H. grievii* are small *Sphaerostoma ovale* seeds (Williamson, 1877; Benson, 1914). Although never found in organic connection, Benson argued strongly that they were parts of the same plant. Such seeds have a number of 'primitive' features, such as the integument and nucellus being only partially fused and an abscission layer between the integument and the cupule. However, the salpinx is considerably reduced and there is a well-developed micropyle. It is thus apparently intermediate between the primitive lagenostomalean seeds from the Tournaisian (e.g. *Stamnostoma* from the Whiteadder – see above) and *Lagenostoma* from the Upper Carboniferous.

Also in association with *H. grievii* are some poorly preserved pollen-bearing organs identified by Benson (1922) as *Heterotheca grievii* (later renamed *Bensoniotheca grievii* by Mickle and Rothwell (1979)). Consisting of an ovoid cluster of completely fused sporangia, they contrast markedly with the loose clusters of free sporangia associated with other Lower Carboniferous *Heterangium* stems, and known as *Telangium* or *Telangiopsis* (e.g. Jennings, 1976). It is possible, however, that they are merely immature forms of *Telangium*.

The second type of pteridosperm stem found at Pettycur is *Rhetinangium arberi* Gordon (1912), for which this is again the type locality. Like *Heterangium*, these stems have a single protostele, but it is exarch and there is no evidence of sclerotic plates in the cortex.

No seeds have been found in organic connection with *Rhetinangium* at Pettycur, but Gordon (1910a) reported a poorly preserved example of what seemed to be *Physostoma* in close association. Gordon's description is only brief and was not accompanied by an illustration. It is perhaps worth noting that in the Tournaisian assemblage at the Whiteadder, there is evidence that *Rhetinangium* bore *Genomosperma* seeds.

Walton and Long (1964) reported *Amyelon* from Pettycur, which may represent pteridosperm roots. However, they have not been described in the literature.

Rex and Scott (1987) list and illustrate a number of pteridosperm foliage fragments preserved as adpressions. However, there is no published taxonomic account of these fossils, and they are thus difficult to judge.

General remarks

This site has yielded the most diverse Visean plant petrifactions known from Britain, and is of great historical significance, having been central to the work of such leading palaeobotanists as W.C. Williamson, D.H. Scott and W.T. Gordon. One of the plant-bearing horizons (the Pettycur Limestone) is the best known example of an *in situ* peat-swamp from the Lower Carboniferous. It provides a useful comparison with the Late Carboniferous coal-swamps, which were not formed in a volcanic setting, but in a more tranquil, lower delta-plain setting (see Chapter 6). Elsewhere in Britain, Glenarbuck (p. 164) has yielded the most comparable Lower Carboniferous fossil plant assemblage, being also dominated by lycopsids, but the preservation is not so good and it does not have such diverse fern or equisete components. The ferns (especially those from the Zygopterid Limestone) provide a ready comparison with upper Visean petrifactions from Esnost and Roannais in France (Galtier, 1970, 1971, 1980; Scott *et al.*, 1984), but there, in contrast to Pettycur, pteridosperms are virtually absent. Also similar is the Visean assemblage from Glätzisch-Falkenberg, Germany (Solms-Laubach, 1892), but the absence of recent work on that assemblage makes a detailed comparison difficult (Scott *et al.*, 1984). Visean petrifactions from outside Europe are virtually unknown, and this presumably reflects the unusual conditions necessary for the formation and preservation of petrified plant fossils (in this case lake sediments and peats accumulating in a lowland, volcanic environment).

Conclusion

Pettycur is one of the classic Palaeozoic palaeobotany sites in Britain, yielding anatomically-preserved plant remains about 330 million years old. Together with the peat-floras of the Devonian Rhynie Chert (see Chapter 4) and the Upper Carboniferous coal-balls (see Chapter 6), it was for many years regarded as the best guide to the vegetation of the Palaeozoic. Although many other Lower Carboniferous sites, in this country, France and Germany, are now known to yield anatomically-preserved plant fossils, Pettycur remains of great palaeobotanical significance, particularly for the study of the early fern-like plants and club-mosses. It is also the only known locality for the horsetail family, the Cheirostrobaceae. Despite being one of the oldest known types of equisete, it has by far the most complex reproductive organs ('cones') that have been found in that group of plants, either living or in the fossil record.

KINGSWOOD END

Highlights

Kingswood End has yielded a distinctive Visean assemblage of petrifactions and fusain fragments. It differs markedly from the nearby Pettycur assemblage, which is thought to represent a different environmental setting, and is the only known locality for the enigmatic microsporangiate organs *Phacelotheca* and *Melissiotheca*. It has considerable potential for future work on the vegetation of this time.

Introduction

This site lies on the hillside above Pettycur, near Burntisland, Fife (NS 265864) (Figure 5.22). It was discovered as part of a re-investigation of the Lower Carboniferous plant-bearing rocks near Pettycur, during the mid-1980s. A preliminary report on the assemblage is provided by Scott *et al.* (1986), but to date only two taxa have been subject to detailed systematic analysis (Meyer-Berthaud, 1986; Meyer-Berthaud and Galtier, 1986a).

Description

Stratigraphy

The geology of this site is detailed by Scott *et al.* (1986) and Rex and Scott (1987) (Figure 5.28). The plant fossils occur in the Kingswood Limestone, a brown, fine-grained microsparite that occurs as large (one metre plus), derived blocks incorporated in the upper part of a volcanic agglomerate. Although the limestone bed has not yet been found *in situ* in a sedimentary sequence, it is believed to have been a lacustrine deposit. Palynological evidence given by Scott *et al.* suggests an Asbian age.

Palaeobotany

The plant fossils here fall broadly into two groups: petrified lycopsids, and fusainized pteridosperms, ferns and equisetes. Taxa reported to date are as follows:

Lycopsida:
    Oxroadia cf. *gracilis* Alvin
    Achlamydocarpon sp.

Equisetopsida:
    Protocalamites pettycurensis (Scott) Scott

Filicopsida:
    Unidentified fragments

Lagenostomopsida:
    Lyginorachis spp.
    cf. *Calathospermum* sp.
    Dadoxylon sp.

Uncertain affinities:
    Phacelotheca pilosa Meyer-Berthaud and Galtier
    Melissiotheca longiana Meyer-Berthaud
    Amyelon sp.

In addition, adpressions from a mudstone exposed here have been identified by Rex and Scott (1987) as *Lepidostrobus* sp. and *Lepidostrobophyllum* sp.

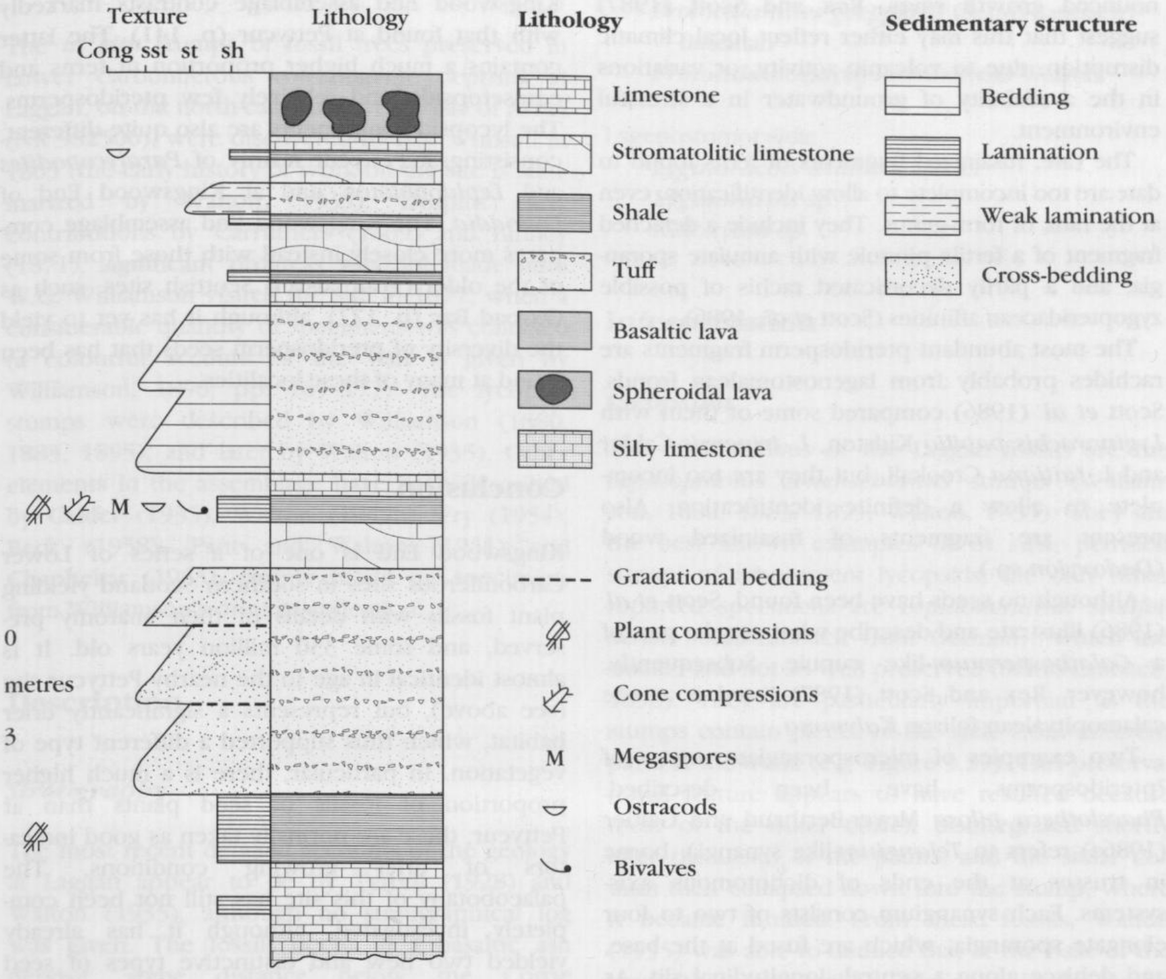

Figure 5.28 Stratigraphical section at Kingswood End, showing distribution of plant fossils. Based on Rex and Scott (1987, figure 4).

Interpretation

Oxroadia stems are amongst the most abundant and well preserved fossils from here. They have been interpreted as having lived near the margins of the lake in which the limestone was deposited, and had been subjected to little transportation. Their anatomy compares closely with the well-documented *Oxroadia gracilis* Alvin from Oxroad Bay (p. 131), except that the larger stems developed a siphonostele, as opposed to a protostele. As pointed out by Scott *et al.* (1986), however, the Oxroad Bay stems do not reach such a large diameter as the Kingswood End specimens, which may explain the apparently anomalous vascular structure.

Also abundant here are isolated lycopsid megasporophylls. They compare with *Achlamydocarpon varius* (Baxter) Taylor and Brack-Hanes, but have a rather simpler sporangial wall structure (Scott *et al.*, 1986). Phillips (1979) suggests that *Achlamydocarpon* may have been borne by giant lycopsids with *Lepidodendron*-like trunks, but no evidence of the latter has so far been reported from Kingswood End.

The rest of the assemblage consists mainly of fusain fragments. Scott *et al.* (1986) regard them as the transported remains of plants growing some distance away from the lake, and which had been subject to burning induced by volcanic eruption. They report just two decorticated stems of *Protocalamites*, which are principally of interest in that they have secondary wood with pronounced growth rings. Rex and Scott (1987) suggest that this may either reflect local climatic disruption, due to volcanic activity, or variations in the availability of groundwater in a stressful environment.

The rare, fusainized fragments of ferns found to date are too incomplete to allow identification, even at the rank of form-genus. They include a detached fragment of a fertile pinnule with annulate sporangia, and a partly decorticated rachis of possible zygopteridacean affinities (Scott *et al.*, 1986).

The most abundant pteridosperm fragments are rachides probably from lagenostomalean fronds. Scott *et al.* (1986) compared some of them with *Lyginorachis papilio* Kidston, *L. trinervis* Calder and *L. taitiana* Crookall, but they are too incomplete to allow a definite identification. Also present are fragments of fusainized wood (*Dadoxylon* sp.).

Although no seeds have been found, Scott *et al.* (1986) illustrate and describe what may be part of a *Calathospermum*-like cupule. Subsequently, however, Rex and Scott (1987) listed it as the calamopityalean foliage *Kalymma*.

Two examples of microsporangiate organs of ?pteridosperms have been described. *Phacelotheca pilosa* Meyer-Berthaud and Galtier (1986a) refers to *Telangium*-like synangia, borne in trusses at the ends of dichotomous axis-systems. Each synangium consists of two to four elongate sporangia, which are fused at the base, and dehisce along a ventral, longitudinal slit. As pointed out by Meyer-Berthaud and Galtier, *Telangium*, as currently interpreted, includes a diverse range of microsporangiate organs. They therefore opted to place the Kingswood End specimens in their own, tightly circumscribed form-genus. Virtually all characters point to it belonging to the Lagenostomales, except that the sporangial trusses are rather more complex than in other described species, and the pre-pollen has an ornamented sexine.

A rather more complex structure was described by Meyer-Berthaud (1986) as *Melissiotheca longiana*. It consists of synangia comprised of 50–150 elongate sporangia, embedded in a lobed, parenchymatous, basal cushion, which in turn was borne distally on a stalk. The pre-pollen are similar to those contained in *Phacelotheca*. Meyer-Berthaud pointed out a number of features which again suggest lagenostomalean affinities, but was unwilling to assign it there because of its complexity and the differences in pre-pollen structure.

Despite its geographical proximity, the Kingswood End assemblage contrasts markedly with that found at Pettycur (p. 141). The latter contains a much higher proportion of ferns and equisetopsids, and relatively few pteridosperms. The lycopsid components are also quite different, consisting at Pettycur mainly of *Paralycopodites* and *Lepidophloios*, and at Kingswood End of *Oxroadia*. The Kingswood End assemblage compares more closely instead with those from some of the older (Tournaisian) Scottish sites, such as Oxroad Bay (p. 127), although it has yet to yield the diversity of pteridosperm seeds that has been found at many of these localities.

Conclusion

Kingswood End is one of a series of Lower Carboniferous sites in southern Scotland yielding plant fossils with details of their anatomy preserved, and some 330 million years old. It is almost identical in age to the nearby Pettycur site (see above), but represents a significantly drier habitat, which thus supported a different type of vegetation. In particular, there is a much higher proportion of fossils of seed plants than at Pettycur; these are normally taken as good indicators of drier growing conditions. The palaeobotany of this site has still not been completely investigated, although it has already yielded two new and distinctive types of seed plant pollen-bearing organs (*Melissiotheca* and *Phacelotheca*). There is much potential here for new discoveries, which may help in determining aspects of the early evolution of the seed plants.

LAGGAN

Highlights

This is a significant site for Lower Carboniferous plant petrifactions, particularly for lycopsids. They include the best known examples of *in situ* petrified stumps of arborescent lycopsids, and some early examples of herbaceous lycopodiaceans. It has also yielded some of the best known examples of anatomically-preserved strobili of the Archaeocalamitaceae (Sphenopsida).

Laggan

Introduction

The *in situ* stumps of fossil trees preserved in Lower Carboniferous volcanogenic deposits at Laggan, on the north-east coast of the Isle of Arran (NR 982506), were discovered by E.A. Wunsch in 1865 (the early history of work on the site is summarized by Walton, 1935). Despite early contributions by Carruthers (1869) and Binney (1871), significant progress was not made until W.C. Williamson visited the site in 1877, when a considerable quantity of specimens was collected (a colourful account of the visit is given by Williamson, 1896, pp. 169–177). The lycopsid stumps were described by Williamson (1880, 1883, 1895), and later by Walton (1935). Other elements in the assemblage have been described by Calder (1935), Walton (1949b), Fry (1954), Beck (1958), Pant and Walton (1961) and Chaphekar (1963), mainly based on specimens from Williamson's original collection.

Description

Stratigraphy

The most recent detailed accounts of the geology at Laggan appear to be by Tyrrell (1928) and Walton (1935), although no stratigraphical log was given. The fossils occur in a basaltic ash deposit, some distance below the Corrie Limestone, probably in the Upper Sedimentary Group. Their exact chronostratigraphical position is uncertain, but the deposits probably fall in the upper Visean.

Palaeobotany

The following taxa, preserved as calcite petrifactions, have been described to date:

Lycopsida:
- *Lepidophloios wuenschianus* (Williamson) Walton
- *Levicaulis arranensis* Beck
- *Paurodendron arranensis* Fry
- *Lycostachys protostelicus* Pant and Walton
- *Lepidostrobus* (?) *ambiguus* Binney
- *L. wuenschianus* Binney
- *L. latus* Binney
- *Lepidocarpon* sp.
- *Stigmaria* sp.

Equisetopsida:
- *Protocalamites goeppertii* (Solms-Laubach) Bateman
- *Protocalamostachys arranensis* Walton

Lagenostomopsida:
- *Lyginorachis waltonii* Calder
- *Lyginorachis* sp.
- *Kaloxylon* sp.

Interpretation

Lycopsida

The most famous of the Laggan fossils are the *Lepidophloios wuenschianus* stumps (Williamson, 1880, 1883, 1895; Walton, 1935). They are the best known examples of *in situ*, petrified stumps of arborescent lycopsids; the only other reported specimens are *Lepidodendron saalfeldense* Solms-Laubach from Germany, which are smaller and not so well preserved (Solms-Laubach, 1896). They are particularly important as the stumps contain pieces of the stele from different parts of the trunk (e.g. Figure 5.29). This preservational feature appears to have resulted because most of the outer cortex disintegrated shortly after the death of the plants, and the stelar column then collapsed down into the stump, where it became lithified. From these fossils, Walton (1935) was able to deduce that at the base of the trunk there was only a relatively slender protostele, surrounded by a thick layer of secondary wood. In more distal positions, however, the primary xylem formed a wider, medullated siphonostele, but the surrounding secondary wood became concomitantly narrower. These results had important consequences for subsequent ideas about the developmental growth of the arborescent lycopsids (Andrews and Murdy, 1958; Eggert, 1961). Where pieces of the cortex are still preserved, they show that this tissue had clearly developed bands of secretory cells.

Also found in the stumps are fragments of the distal branches of the tree, which are similar to the adpression species *Lepidophloios scoticus* Kidston. They can also be compared with the *Lepidophloios* shoot described from Bearsden by Galtier and Scott (1986b). However, similar shoots are also found associated with *Lepidophloios scottii* Gordon at Pettycur (see above), which differs from the Laggan fossils in not having secretory cells in the cortex. Evidently, different species of

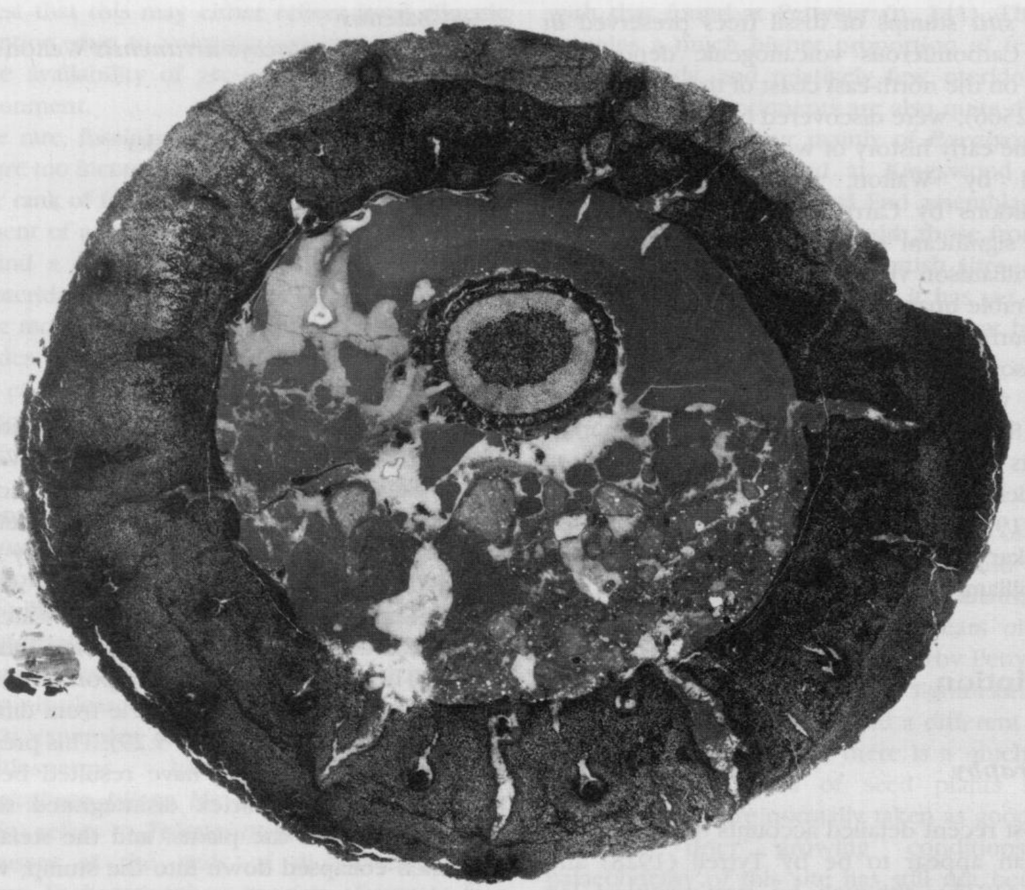

Figure 5.29 *Lepidophloios wuenschianus* (Williamson) Walton. Transverse section through lycopsid stem; Natural History Museum, London, specimen WC.456a. Visean ash deposits, Laggan. × 2. (Photo: Photographic Studio, Natural History Museum, London.)

lycopsid could produce shoots of essentially identical form.

DiMichele (1979) used *L. wuenschianus* as the 'type' of one of the two groups of *Lepidophloios* species that he recognized, characterized by features of periderm structure, leaf cushion anatomy, and lateral branch architecture. Other members of the group include *L. scottii* Gordon from Pettycur (see above) and *L. johnsonii* from the basal Upper Carboniferous of North America, but *L. wuenschianus* is by far the best known. The differences between the two groups of *Lepidophloios* may reflect palaeoenvironmental differences, the *L. wuenschianus* group occupying more open habitats, whereas the *L. harcourtii* group were forest dwellers.

It has been argued that *Lepidophloios* bore *Lepidocarpon* strobili (e.g. Phillips, 1979). It is not surprising, therefore, that Walton (1935) recorded *Lepidocarpon* in the Laggan stumps, although no description was given.

Binney (1871) described three species of *Lepidostrobus* from Laggan, but they are all incomplete and in need of renewed investigation.

Two other types of lycopsid in the Laggan assemblage were herbaceous, and are both unique to this locality. The stems known as *Levicaulis arranensis* Beck (1958) were less than 40 mm in diameter, with a terete protostele, and apparently without ligules. An associated strobilus known as *Lycostachys protostelicus* Pant and Walton (1961) has a central axis with an almost identical structure and is assumed to have belonged to the same plant. The preserved part of the strobilus was exclusively microsporangiate, although some megaspores were found in association. If this association is merely coincidental and the cone was homosporous, as suggested by Pant and Walton, then the affinities of this plant probably lie with the Lycopodiaceae.

A second type of herbaceous lycopsid is represented by the stems *Paurodendron arranensis* Fry (1954). Unlike *Levicaulis*, *Paurodendron* is ligulate and thus more similar to *Oxroadia* from Oxroad Bay (p. 131), except for details of the vascular anatomy. It was placed in synonymy with *Selaginella fraipontii* (Leclercq) Schlanker and Leisman from the Upper Carboniferous of North America by Schlanker and Leisman (1969). However, in view of their stratigraphical separation, and the fact that details of the strobili are known from *S. fraipontii*, but not the Laggan plant, it seems wiser to keep them separate. Bateman (1988) has argued that *Paurodendron* and *Oxroadia* represent a distinctive order of lycopsids, which is probably a sister group of the Lepidocarpales, although he has subsequently recanted this view (Bateman *et al.*, 1992).

Equisetopsida

The Laggan equisetopsid stems, known as *Protocalamites goeppertii* (Walton, 1949b) differ from *Protocalamites pettycurensis* from Pettycur in having more primary vascular strands, and probably representing larger plants (Bateman, 1991). They are also associated with larger strobili, known as *Protocalamostachys arranensis* Walton (1949b). Historically, the latter are of interest because they were the first strobili of these primitive equisetopsids to be discovered petrified, which helped clarify the distinctive characters of the Archaeocalamitaceae (i.e. the sporangia were borne on peltate sporangiophores, and there were few intervening sterile bracts).

Pteridosperms

There has been little work on the pteridosperms at Laggan. Calder (1935) described a distinctive lagenostomalean rachis as *Lyginorachis waltonii* Calder, whilst Walton (1935) recorded *Kaloxylon*, which usually refers to lagenostomalean rooting structures.

General remarks

Laggan is another of the internationally important Lower Carboniferous petrifaction sites in Britain, which includes a particularly significant lycopsid component. Some of the species have been described from elsewhere, such as *Lepidophloios wuenschianus* from Dalmeny (Seward and Hill, 1900), *Protocalamites goeppertii* and *Protocalamostachys arranensis* from Loch Humphrey Burn, and *Lyginorachis waltonii* from Oxroad Bay and Loch Humphrey Burn. Nevertheless, the balance of taxa at Laggan remains unique, as well as being the only known locality for two herbaceous lycopsids.

Conclusion

Laggan is one of a series of important sites that show Lower Carboniferous rocks in southern Scotland, and which yield plant fossils with their anatomy preserved; they are probably about 340 million years old. This particular site is especially important for its club-mosses, which include both trees (*Lepidophloios*) and small, herbaceous forms (*Levicaulis* and *Paurodendron*). It has also yielded important specimens of horsetails, including a number of reproductive cones, that have been important for understanding the evolutionary history of this group of plants.

LOCH HUMPHREY BURN

R.M. Bateman and C.J. Cleal

Highlights

Loch Humphrey Burn has yielded two pivotal assemblages of Lower Carboniferous plant petrifactions, the lower reputedly of Tournaisian and the upper of Visean age (Figure 5.30). The lower is dominated by filicopsids, unlike most Tournaisian petrifaction assemblages; it includes the earliest possible examples of tedeleacean, corynepteridacean and marattialean ferns. The upper assemblage includes the only known fertile specimens of the progymnosperm order Protopityales. It has also provided invaluable information on the anatomy of the early sphenopsid *Protocalamites* and several evolutionarily significant pteridosperms such as *Calathospermum*. Finally, it is one of the few Lower Carboniferous localities that yields both petrifactions and adpressions, thereby offering the potential for correlating features of anatomy and gross morphology. It is a site of outstanding palaeobotanical importance.

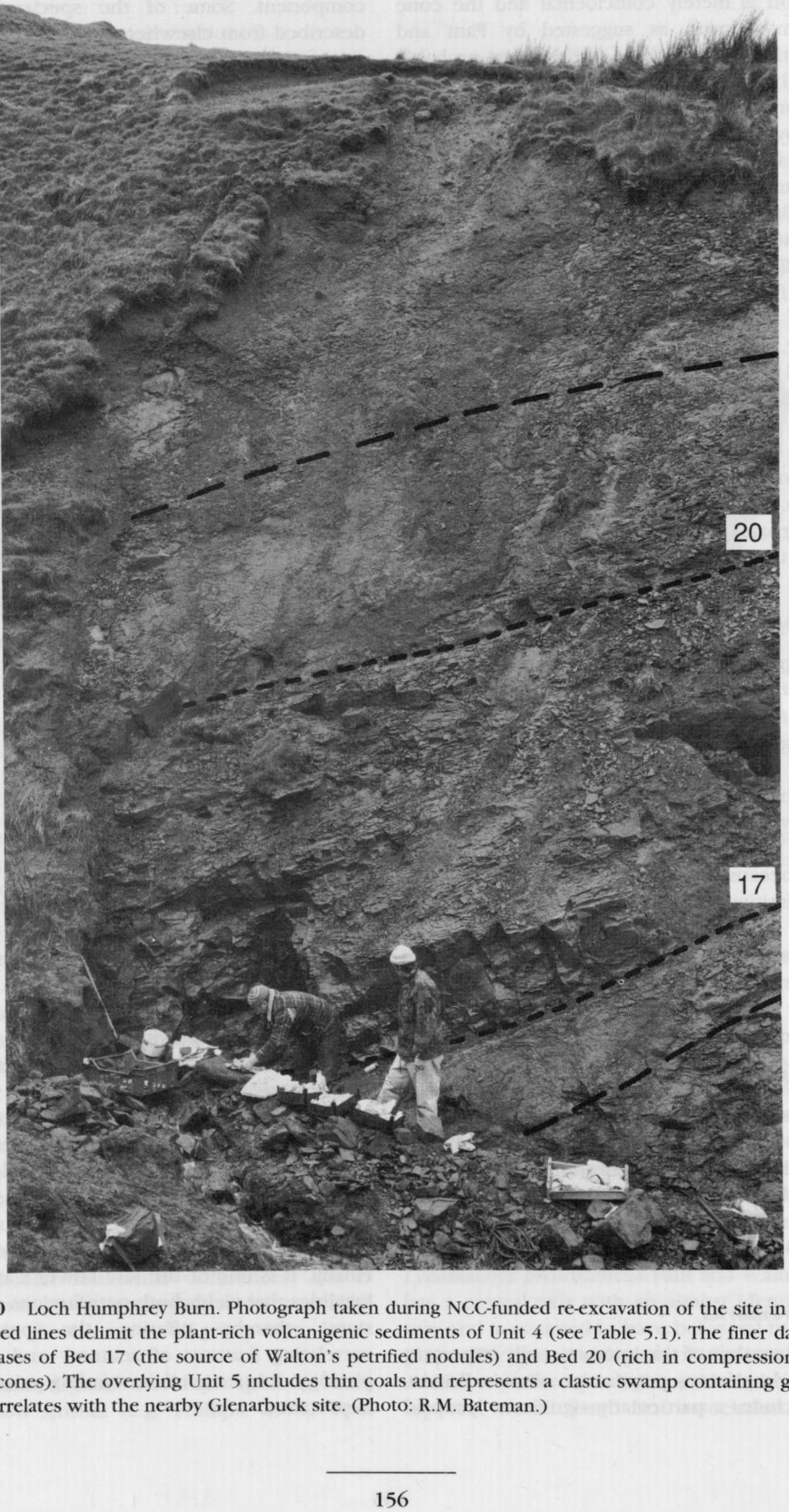

Figure 5.30 Loch Humphrey Burn. Photograph taken during NCC-funded re-excavation of the site in 1985. The coarse dashed lines delimit the plant-rich volcanigenic sediments of Unit 4 (see Table 5.1). The finer dashed lines mark the bases of Bed 17 (the source of Walton's petrified nodules) and Bed 20 (rich in compressions, notably *Pothocites* cones). The overlying Unit 5 includes thin coals and represents a clastic swamp containing giant lycopsids; this correlates with the nearby Glenarbuck site. (Photo: R.M. Bateman.)

Introduction

This locality straddles a small tributary of Loch Humphrey Burn (NS 467753) (Figure 5.31). It is one of two classic palaeobotanical localities in the Kilpatrick Hills, near Glasgow (the other, Glenarbuck, is described in the next section). Lower Carboniferous plant fossils were probably first discovered at Loch Humphrey Burn in about 1870 by the Geological Survey, but the earliest documentary evidence is a letter that accompanied specimens sent by James Bennie to Robert Kidston in 1886 (Smith, 1960; Scott *et al.*, 1984). Kidston published many descriptions of the adpressions from here in his classic 1923–1925 monograph, but passed the petrifactions to D.H. Scott for description (Scott, 1899, 1902, 1918, 1920–23, 1924b). The next phase of collecting was undertaken during the early 1930s by Robert Brown, Jessie Wilson and John Walton, who amassed a considerable quantity of material. This formed the basis for a series of studies by Calder (1935), Walton (1940, 1949a, b, c, 1957), Lacey (1953), Smith (1959, 1960, 1962a, b, 1964b) and Chaphekar (1965) (see also Walton *et al.*, 1938). Most recently Scott and Bateman have clarified the stratigraphy and sedimentology at the site. Although Scott *et al.* (1984, 1985) reviewed some of the fossils discovered during their 1982 excavations, there have been only two detailed descriptions published to date (Meyer-Berthaud and Galtier, 1986b; Bateman, 1991).

Description

Stratigraphy

The geology of this site is briefly described by Scott *et al.* (1984, 1985), whose work was in turn amended by Bateman (unpublished) following re-excavation of the most important exposure. The sequence is in the lower part of the Clyde Plateau Volcanic Formation (Hall, 1978). The plant-bearing strata immediately underlie the lowermost of several lava flows and represent a fluvio-deltaic complex rich in volcanigenic sediments (Figure 5.32). Detailed logging of the section has resulted in a revised classification of the sequence into five lithostratigraphical units, which will be described fully elsewhere (Bateman, in prep., see summary in Table 5.1). Comparison with palynological evidence summarized by Scott *et al.* (1984, 1985) suggests that Units 1 and 2 are in the CM Zone (upper Tournaisian), Unit 3 in the lower Pu Zone (Chadian, lower Visean) and Units 4 and 5 in the uppermost Pu Zone (Holkerian, middle Visean). Scott *et al.* (1984) postulated a depositional break

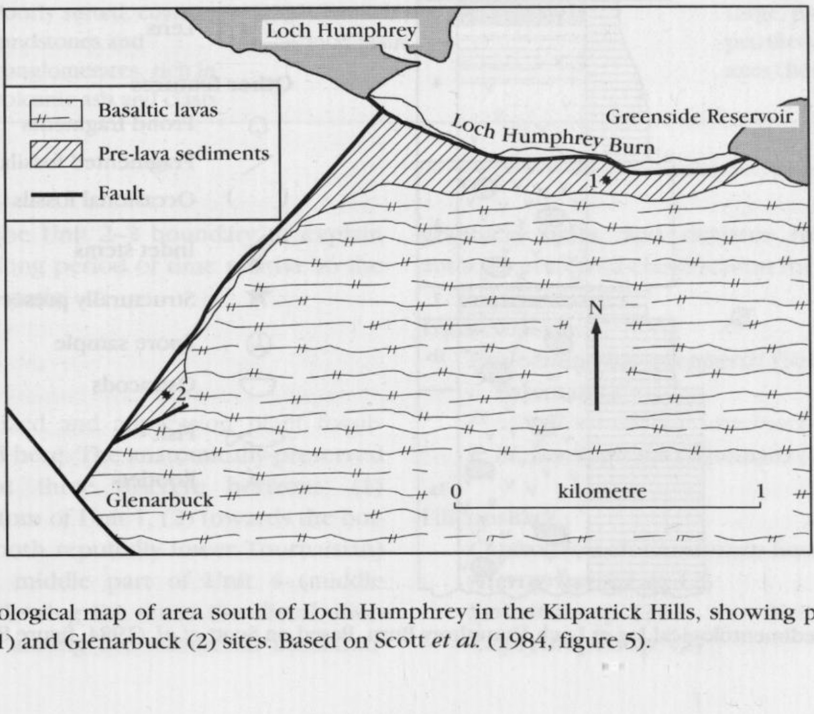

Figure 5.31 Geological map of area south of Loch Humphrey in the Kilpatrick Hills, showing positions of Loch Humphrey Burn (1) and Glenarbuck (2) sites. Based on Scott *et al.* (1984, figure 5).

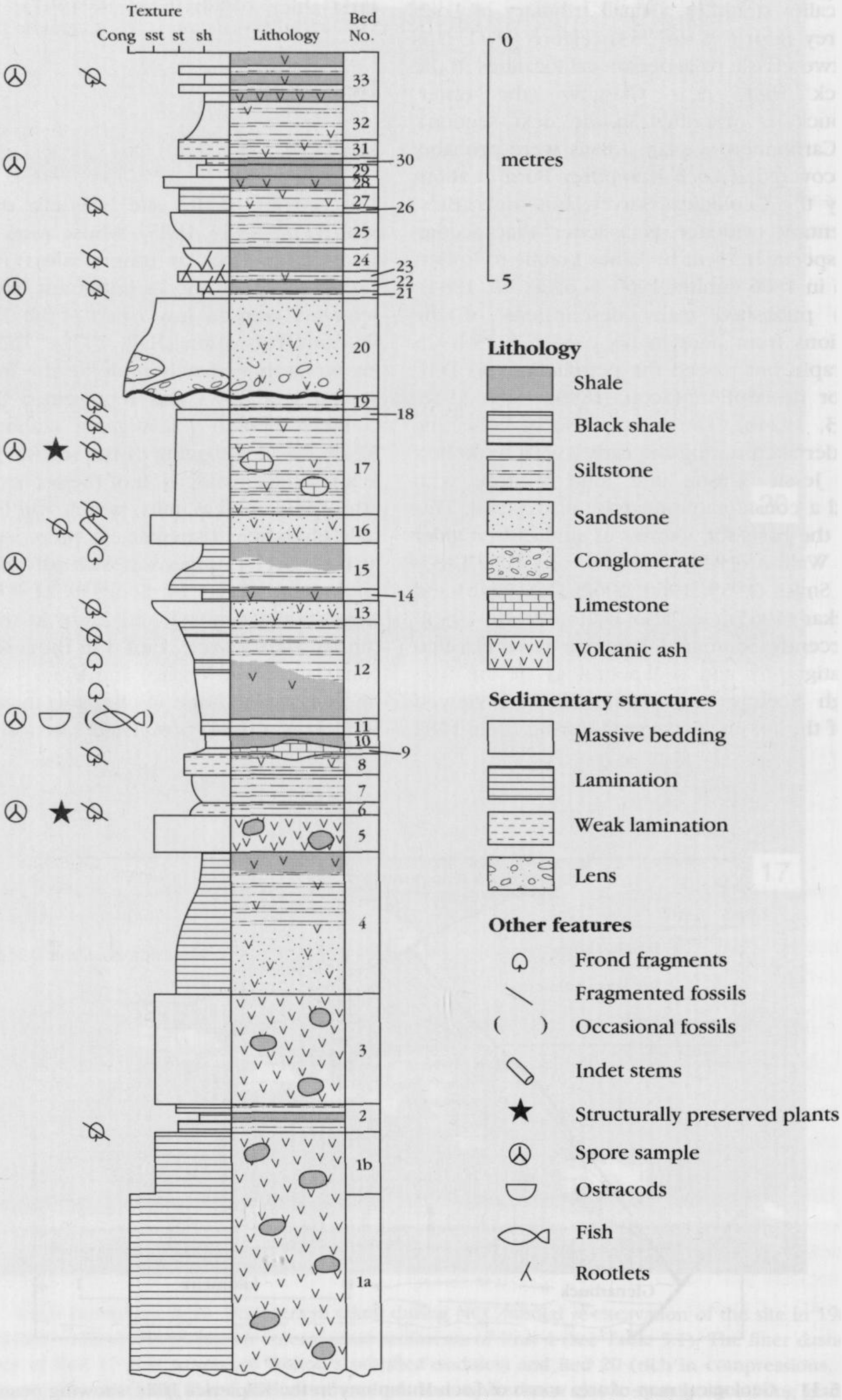

Figure 5.32 Sedimentological log at Loch Humphrey Burn. Based on Scott *et al.* (1984, figure 8).

Table 5.1 Lithostratigraphy of Loch Humphrey Burn (R.M. Bateman, unpublished)

Lithostratigraphical Unit	Main Lithologies	Environmental Interpretation	Bed Numbers of Scott *et al.* (1984, fig. 8)	Fossil Plant Assemblages
Unit 5	Siltstones and fine sandstones with intercalated coarse sandstones, thin shales, coals and rooted palaeosols	Extensive flood plain	21–33	Compressions of rhizomorphic lycopsid rootlets, with rare rhizomorph and aerial axis fragments
Unit 4	Medium to coarse, gritty sandstones, with a few thin shales	Fluvial channel	13–20	Nodular petrifactions of many organs representing a wide range of higher taxa (Bed 17); also compressions, especially of pteridosperm and putative progymnosperm foliage
Unit 3	Thinly laminated shales and an impure limestone	Flood plain/ lacustrine	9–12	Compressions, especially pteridosperm and putative progymnosperm foliage
Unit 2	Siltstones and fine sandstones	Flood plain	6–8	Nodular petrifactions of fragmentary filicopsids, sphenopsids and pteridosperms, especially reproductive organs (Bed 6)
Unit 1	Poorly sorted, coarse sandstones and conglomerates, rich in volcanic ash and clasts	?Channel/ flood plain	1–5	Large, partially petrified pteridosperm axes (Bed 1)

approximating the Unit 2–3 boundary to explain this apparently long period of time relative to the thickness of the strata.

Palaeobotany

Petrified, fusainized and adpression plant fossils have been found here. The anatomically-preserved fossils occur at three discrete horizons: (1) towards the bottom of Unit 1, (2) towards the bottom of Unit 2 (both reputedly lower Tournaisian) and (3) in the middle part of Unit 4 (middle Visean). The following list notes the distribution of each species among the numbered lithostratigraphical units, and deviates from the senior author's preferred classification for higher taxa:

Equisetopsida:
Protocalamites goeppertii (Solms-Laubach) Bateman (2,4)
Protocalamostachys arranensis Walton (2,4)
P. cf. *farringtonii* (Bateman) (2)

Filicopsida:
Cladoxylon cf. *taeniatum* Bertrand (2)
Hierogramma sp. (2)
Syncardia sp. (2)
Clepsydropsis sp. (2)

Metaclepsydropsis sp. (2)
Botryopteris cf. *antiqua* Kidston (2)
cf. *Senftenbergia* sp. (2)
cf. *Musatea* sp. (2)
Burnitheca pusilla Meyer-Berthaud and Galtier (2)
Etapteris tubicaulis Göppert (4)

Progymnospermopsida:
Protopitys scotica Walton (4)

Gymnospermopsida

Lagenostomales:
Eristophyton fasciculare (Scott) Zalessky (?4)
E. waltonii Lacey (4)
Bilignea resinosa Kidston (?4)
Lyginorachis trinervis Calder (4)
Lyginorachis spp. several (2,4)
Calathospermum scoticum Walton (4)
Geminitheca scotica Smith (4)
cf. *Pullaritheca* sp. (4)

Calamopityales:
'*Calamopitys*' *radiata* Scott (?1)
Kalymma cf. *tuediana* Long (2)
Kalymma sp. (4)
Alcicornopteris hallei Walton (4)

Gymnosperms (*incertae sedis*):
Amyelon sp. (2)

The best preserved adpressions occur in the middle Visean part of the sequence (units 3 and 4). The following taxa have been identified:

Lycopsida:
Lepidophloios cf. *kilpatrickensis* Smith
Stigmaria ficoides (Sternberg) Brongniart

Equisetopsida:
Archaeocalamites radiatus (Brongniart) Stur
Pothocites grantoni Paterson

Filicopsida (?):
Rhodeopteridium sp.

Progymnospermopsida (?):
Rhacopteris lindsaeformis Bunbury,
R. inaequilaterata Göppert
R. robusta Kidston
R. petiolata Göppert

Gymnospermopsida

Lagenostomales:
Sphenopteridium pachyrrachis (Göppert) Schimper
S. crassum (Lindley and Hutton) Kidston
Sphenopteris affinis Lindley and Hutton
S. bifida Lindley and Hutton
Calathiops trisperma Smith

Calamopityales:
Spathulopteris ettingshausenii (Feistmantel) Kidston
S. obovata (Lindley and Hutton) Kidston
Staphylotheca kilpatrickensis Smith
Alcicornopteris convoluta Kidston
A. zeilleri Kidston

Interpretation

Lycopsida

Although lycopsids are considered to be very poorly represented at Loch Humphrey Burn (Smith, 1964b), one of us (RMB) has found in Unit 5 frequent, poorly preserved *Stigmaria* and an axial compression that compares with the outer surface of the petrified *Lepidophloios kilpatrickensis* Smith from nearby Glenarbuck (see below).

Equisetopsida

Protocalamites goeppertii occurs in both petrifaction assemblages here, and its adpression/cast analogue (*Archaeocalamites radiatus*) is frequent in the Visean part of the section. The anatomical details of the stem nodes described by Walton (1949b) prompted Chaphekar (1963) to unify *Archaeocalamites* with *Protocalamites* (the two principal form-genera for Lower Carboniferous sphenophytes), but this action was subject to detailed criticism by Bateman (1991).

Chaphekar (1965) identified adpressions from here as *Pothocites grantonii*, and showed that it was probably the fertile organ of *Archaeocalamites*. Bateman (1991) has demonstrated that a new specimen of petrified *Protocalamostachys arranensis* from Unit 4 is the anatomically-preserved analogue of *Pothocites grantonii*. *Protocalamostachys arranensis*, which was previously only known from a single fragment from Laggan (see above), provides a valuable comparison with the smaller *P. farringtonii* Bateman; fragments from both cone species were recorded in Unit 2 by Scott *et al.* (1985; see also Bateman, 1991; Hemsley *et al.*, in press).

Filicopsida

Only one petrified fern, the zygopterid phyllophore *Etapteris tubicaulis*, has been reported from the upper assemblage (Walton *et al.*, 1938; Scott *et al.*, 1984). It has not been described in detail, even though Loch Humphrey Burn is the only known British locality for this species.

The Tournaisian assemblage described below is much richer in anatomically-preserved ferns (Scott *et al.*, 1985). The Cladoxylales is represented by the stem *Cladoxylon* cf. *taeniatum* (its only British record) and its branches *Hierogramma* and *Syncardia*. No demonstrably cladoxylalean fructifications have yet been found.

The zygopterids are represented by the phyllophores *Clepsydropsis* and *Metaclepsydropsis*, this being regarded as the lowest recorded stratigraphical occurrence of the latter (Scott and Galtier, 1985). Scott *et al.* (1985) also recorded sporangia similar to *Musatea*, which is generally regarded as the fertile organ of *Metaclepsydropsis*. Another sporangial type recorded by Scott *et al.* (1985) appears to be a precursor of the more familiar genus *Corynepteris*, a relatively common fern in the Upper Carboniferous.

Scott *et al.* (1985) identified axes with a simple xylem anatomy as *Botryopteris* cf. *antiqua*, again the oldest known examples of this species. Associated isolated annulate sporangia are similar in general form to those known from *B. antiqua* (Galtier, 1967) but differ in the details of the annulus. Another coenopteridalean fructification was compared by Scott *et al.* (1985) with the tedeleacean form-genus *Senftenbergia*, which again would represent an oldest known record.

The only sporangium so far described in detail from Unit 2 is *Burnitheca pusilla* Meyer-Berthaud and Galtier (1986b). It consists of a bilaterally symmetrical cluster of eight sporangia, fused basally around a central column. Although it broadly resembles lagenostomalean microsporangiate organs such as *Telangium*, the form of the tapetum and the spores that it contains suggest affinities with the marattialean ferns. If this interpretation is correct, *Burnitheca* is the oldest known example of this extant order. Two further types of sporangia, possibly belonging to ferns, are mentioned by Scott *et al.* (1985) as 'Fructifications G and H'.

The evidence from Loch Humphrey Burn documents the rapid diversification of the ferns in the Early Carboniferous. The supposedly upper Tournaisian Unit 2 contains a remarkable number of first recorded occurrences of fern species, genera and even families, and its taxonomic composition is more consistent with the mid-Visean age attributed to the overlying units at Loch Humphrey Burn. Many of these early ferns lacked fully planated fronds, but possessed fructifications characteristic of recognized fern taxa. By the early Late Carboniferous, more modern-looking ferns had developed, especially in the palaeoequatorial areas. The fossils found at Loch Humphrey Burn, although fragmentary, are thus of considerable value in recording this group of plants at a key stage in its evolutionary history.

Progymnospermopsida

Loch Humphrey Burn is one of the most important localities for Lower Carboniferous progymnosperms. They are thought to have been widespread in the equatorial and northern-temperate palaeolatitudes. However, progymnosperms are difficult to identify with confidence since this requires demonstrating the absence of ovules, and anatomically-preserved fertile material is rare. Loch Humphrey Burn has yielded the only known fertile specimens of the order Protopityales (Walton, 1957; Smith, 1962b). Stems from Loch Humphrey Burn share many anatomical features with *Protopitys buchiana* Solms-Laubach from Yorkshire and Falkenberg (Solms-Laubach, 1893; Walton, 1957, 1969); both have oval siphonosteles emitting distichous leaf-traces, features that characterize the Protopityales. However, the Loch Humphrey specimens have less extensive primary wood, no high biseriate rays, and secondary wood with multiseriate pitting, and so were placed in a new species, *Protopitys scotica* by Walton (1957).

Sporangia attached to these stems were described by Walton (1957) and Smith (1962b). This was the first recorded example of a plant that had both gymnospermous wood and pteridophytic reproductive organs.

Together with the correlation of *Callixylon* wood and *Archaeopteris* foliage by Beck (1960), this was one of the main arguments for recognizing the class Progymnospermopsida as a precursor to the pteridosperms (and arguably the conifers: Beck, 1970, 1971). The spores of *P. scotica* show little variation within sporangia, but considerable variation among adjacent sporangia, and the overall size distribution determined by Smith (1962b) is weakly bimodal. Thus, it is unclear whether the plant was heterosporous (Bateman and DiMichele, in press).

Archangelsky and Arrondo (1966) and Beck (1976) suggested that the adpression foliage *Rhacopteris* is progymnospermous, based on its similarity to *Archaeopteris*. The co-occurrence at Loch Humphrey Burn of adpressed *Rhacopteris* and petrified *Protopitys* lends some support to this argument, though the former is abundant and the latter rare.

Pteridosperms

Seed plants dominate the assemblages in Units 3 and 4, but Scott *et al.* (1985) reported that they are subordinate in Unit 2. Both the Lagenostomales and Calamopityales are represented.

Lagenostomopsida

Petrified stems of *Eristophyton* and *Bilignea* were probably found in the Visean part of the section, although their precise origin was not stated. They include the type and one of only two known specimens of *Eristophyton fasciculare* Scott (1899, 1902, 1918), and the only known specimen of *E. waltonii* Lacey (1953). The latter differs from *E. fasciculare* in having a larger parenchymatous pith with sclerotic nests, smaller primary xylem strands emitting undivided leaf traces, and in its ability to develop larger wood rays. *Bilignea resinosa* Scott (1924b) is similarly known from only a single specimen. It resembles *Eristophyton* in many characters, but has a large core of pitted tracheids interspersed with large resin sacs, rather than a parenchymatous pith. Although affinities with the cordaites (Scott, 1899, 1924b; Andrews, 1940; Lacey, 1953) and the calamopityales (Read, 1937) have been suggested for these genera, Long (1987, pers. comm. 1988) and Bateman and Rothwell (1990) have shown that they are lagenostomalean.

Abundant and diverse *Lyginorachis* petioles occur at Loch Humphrey Burn, mainly in the upper part of the section. Of these, only *L. trinervis* Calder (1935) has been formally described. Its unusual tripartite stele and rapid decrease in diameter along its 2 mm length suggest that it is the basal portion of a petiole. Similar petioles have recently been identified from approximately coeval deposits at Kingswood (see above). Another well-preserved petiole from Loch Humphrey Burn resembles *Lyginorachis waltonii*, first described from Laggan on the Isle of Arran (see above). Long (1987) has reported similar axes attached to *Eristophyton beinertianum* stems at Oxroad Bay (see above).

Loch Humphrey Burn is the only known locality for the petrified lagenostomalean cupules *Calathospermum scoticum* Walton (1949a) and *Geminitheca scotica* Smith (1959). *C. scoticum* is the type species of *Calathospermum*, a genus of large, multi-ovular 'megacupules' that also includes *C. fimbriatum* Barnard from Oxroad Bay (see above). These 'megacupules' have been interpreted as entire reduced fronds and are assumed to have been borne directly on the stem (Long, 1977b); in contrast, 'microcupules' are thought to have been only a distal part of a fertile frond that otherwise resembled conspecific sterile fronds. Clusters of microcupules were thus attached to foliage (usually in the fork of a vegetatively bipartite frond) rather than directly to the stem.

Many of the several known specimens of *C. scoticum* are barren, the ovules having been released; the few ovulate cupules are either immature or mature but unfertilized. The ovules resemble *Salpingostoma dasu* Gordon, as found in *C. fimbriatum* Barnard, but are smaller and have more integumental lobes (Walton, 1949a; Barnard, 1960b). *C. scoticum* probably bore a greater number of ovules (*c.* 48 according to Matten and Lacey, 1981) than *C. fimbriatum*, but had only six undissected lobes. Furthermore, Matten and Lacey (1981) suggested that the *C. fimbriatum* cupule is characterized by an initial dichotomy followed by monopodial or pseudomonopodial divisions, but that *C. scoticum* has basally-fused cupular lobes. Some enigmatic structures in one *C. scoticum* cupule were interpreted by Walton (1949a) as microsporangia, who thus believed that these cupules were bisexual.

In contrast, *Geminitheca scotica* is a microcupule containing only two ovules. A specimen recently discovered by Scott shows *c.* 15 cupules borne on a repeatedly dichotomizing fertile frond. Like *Calathospermum scoticum*, it has up to six cupular lobes, but according to Matten and Lacey (1981) shows monopodial branching. Its ovules are also unusual in having an integument that is joined to the nucellus only at the base. This primitive characteristic is shared with *Genomosperma* from the Whiteadder (see earlier in this chapter). However, a salpinx with a central column and a vascular strand extending to the base of the nucellus, characters typical of *Genomosperma*, have not been reported for *Geminitheca*, which has also been correlated with different spores.

Smith (1959, 1960) reported *Telangium*-like sporangia associated with *Geminitheca*. Since they contained similar spores to those found within the lagenostome of *G. scotica*, he argued that they probably belonged to the same plant.

A compressed ovulate cupule was described by Smith (1962b) as *Calathiops trisperma*. It resembles *Geminitheca*, but is smaller and supposedly contains three ovules. The apparently ubiquitous development of ovulate cupules by repeated dichotomies (cf. Matten and Lacey, 1981) renders tri-ovulate cupules uncommon, though the condition has been reported in some specimens of *Stamnostoma oliveri* from Oxroad Bay (see above). *Calathiops trisperma* may be an immature form of *G. scotica*.

A third type of lagenostomalean cupules has been found by one of us (RMB) at Loch Humphrey Burn. Like *Geminitheca*, it is a small cupule pair, but unlike that genus it has numerous cupular lobes and ovules with about ten integumental lobes. It may have affinities with *Pullaritheca longii* from Oxroad Bay (see above).

There is thus evidence of at least three lagenostomalean plants preserved as petrifactions in the upper assemblages of Loch Humphrey Burn. Their foliage presumably occurs in the diverse fern-like foliage preserved here as adpressions. Perhaps the best candidate is *Sphenopteridium*, which has pinnules attached below the main dichotomy, and racheis with transverse bars. Two form-species have been recorded here, *S. pachyrrachis* and *S. crassum*, although there is a morphological continuum between them and they may be conspecific. Other probable lagenostomalean fronds recorded by Walton (1957) and Smith (1964b) were *Sphenopteris affinis*, *S. bifida* and *Rhodeopteridium* sp.

Calamopityales

The only known specimen of the stem '*Calamopitys' radiata* Scott (1924b) originated from an unspecified horizon at Loch Humphrey Burn; its poor state of preservation suggests that it was from Unit 1, recently rediscovered at the base of the sequence. It is characterized by wide rays and probable exarch primary wood, but may be more appropriately segregated from *Calamopitys*. Scott *et al.* (1985) also illustrate, from the lower part of the section (Unit 2), a specimen of *Kalymma* cf. *tuediana*, which is probably part of a calamopityalean frond.

The upper part of the Loch Humphrey Burn section has yielded some of the best preserved examples of calamopityalean reproductive organs, *Alcicornopteris hallei*. These appear to be exclusively microsporangiate (Walton, 1949c; Smith, 1962a), in contrast to the apparently ovulate *Alcicornopteris* described from the Cementstone Group of Berwickshire (Long, 1969). Thus, this genus can encompass both male and female reproductive organs.

The affinities of a second sporangial cluster found at Loch Humphrey Burn are far less certain. The compression *Staphylotheca kilpatrickensis* Smith (1962b) consists of infrequently dichotomizing racheis with clusters of linear organs that bear sporangia. Smith tentatively assigned it to the pteridosperms on the basis of its tracheidal pitting, but its spores are enigmatically dimorphic: Type A is large, round and thin-walled and Type B is small, subtriangular and thick-walled. Smith argued that this morphological discontinuity between the two spore types is rather extreme to represent a contrast between viable and abortive spores. If so, this would imply the presence of heterospory and possible assignment of *Staphylotheca* to the progymnosperms.

The most likely calamopityalean foliage at Loch Humphrey Burn is *Spathulopteris*. Characteristics of these fronds include the thick-limbed, spathulate pinnules, longitudinal striae on the racheis but no transverse markings, and the absence of pinnae attached to the petiole below the initial dichotomy of the petiole. The two form-species described from Loch Humphrey Burn (*S. ettingshausenii* and *S. obovata*) probably represent ontogenetic variations of a single biological species.

General remarks

Loch Humphrey Burn is of special interest in that it contains two speciose assemblages of anatomically-preserved plant fossils that are taxonomically, stratigraphically and (supposedly) temporally distinct. Fossils in the older assemblages (summarized by Scott *et al.*, 1985) are fragmentary and thus difficult to interpret, both taxonomically and palaeobiologically. Many of its diverse ferns are potential first occurrences of genera or families (e.g. Marattiaceae, Tedeleaceae), but this interpretation requires acceptance of the upper Tournaisian age attributed to the assemblage on palynological evidence; the megafloras and lithostratigraphy are more consistent with the mid-Visean age of the overlying petrifaction assemblages.

The better known upper assemblages are

dominated by pteridosperms and putative progymnosperms, many of the species being endemic. It is quite different in general aspect to the other well-known Visean petrifaction site in Britain at Pettycur (see above), where the assemblage is dominated by ferns and lycopsids. Lycopsids also dominate the more restricted petrifaction assemblage from nearby Glenarbuck (discussed in the next section). Overall, the plant fragments would reconstruct to yield at least eight whole-plant species in the lower assemblage and seven in the upper assemblage. Loch Humphrey Burn is the most significant Visean site in Europe for understanding the evolutionary history of the early gymnosperms and late progymnosperms.

Conclusion

Loch Humphrey Burn has yielded exceptionally well-preserved plant fossils that reputedly range in age from 340 to 350 Ma. Early ferns predominate in the lower part of the succession and, if correctly dated, include the oldest examples known from anywhere in the world of two families which were common in the Late Carboniferous (Tedeleaceae and Corynepteridaceae), and the earliest known example from anywhere in the world of the extant fern order Marattiales. It has also provided invaluable information on the morphology and anatomy of early sphenophytes ('horsetails') and seed plants, especially reproductive structures such as the 'megacupule' *Calathospermum*. Loch Humphrey Burn is one of the few localities of this age to yield both anatomically-preserved and compressed plant fossils. Although these are not in organic connection, further work may allow correlation by indirect methods, thereby combining features of anatomy and gross morphology. Stratigraphical and palaeoecological investigations have proved fruitful and will continue.

GLENARBUCK

R.M. Bateman and C.J. Cleal

Highlights

Glenarbuck has yielded an important assemblage of Visean plant petrifactions that is richest in arborescent lycopsids and ferns, including several endemic species. The plants probably grew in a clastic swamp environment.

Introduction

This Lower Carboniferous locality (Figure 5.31) lies east of a waterfall in Glenarbuck Burn, in the Kilpatrick Hills, near Glasgow (NS 452748). It was probably discovered by the Geological Survey in about 1870 (Smith, 1960). A petrified *Stigmaria* was collected at the locality in 1872, and the presence of this genus was reported by Young (1873) in a general description of the area. Calcareous nodules (possibly pedogenetic) containing a more diverse petrified flora were collected from the upper part of the sequence between 1930 and 1935 by Robert Brown (Smith, 1960), who also redescribed the locality (Brown, 1935). Plants collected by Brown and presented to John Walton were described by Calder (1935), Lacey (1953) and Smith (1960, 1962c, 1964b). A summary of the assemblage is given by Scott *et al.* (1984), who were unable to relocate the now degraded main petrifaction-bearing horizon.

Description

Stratigraphy

The 12 m-thick Glenarbuck sequence (Figure 5.33) is part of the 'Green tuffs and agglomerates' (the lowest member of the Clyde Plateau Lava Formation), underlain by the 'Spout of Ballagan Sandstone' of the Cementstone Group and overlain by the basaltic Clyde Plateau Lavas (Hall, 1978). Miospores recovered during a recent attempt to date the plant-bearing rocks (Scott *et al.*, 1984) were poor, but appear to belong to the Pu Biozone of the lower Visean (Chadian to Arundian stages). More recently, one of us (RMB) has correlated the entire Glenarbuck section lithostratigraphically with the mid-Visean (Arundian/Holkerian) Unit 5 of the nearby Loch Humphrey Burn sequence.

The sediments consist of siltstones (including reworked volcanigenic material) and shales with thin, often discontinuous coals and abundant, apparently *in situ* rootlets delimiting several palaeosols. They are probably river channel and flood plain deposits, suggesting that the plants represent a local swamp community.

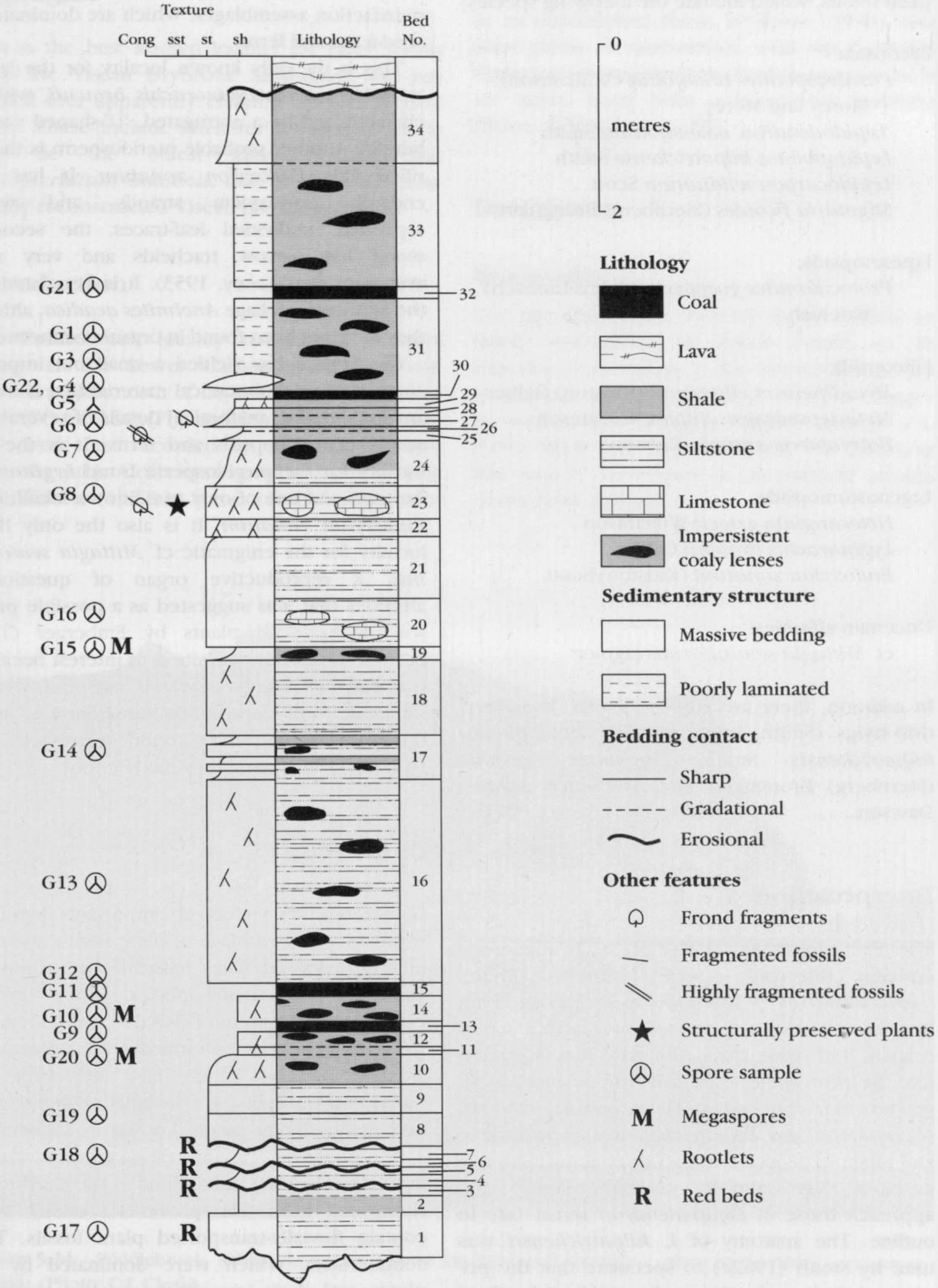

Figure 5.33 Sedimentological log for Glenarbuck. Based on Scott *et al.* (1984, figure 6).

Palaeobotany

This locality is significant mainly for the petrified plant fossils, which include the following species:

Lycopsida:
- *Paralycopodites brevifolius* (Williamson) Morey and Morey
- *'Lepidodendron' solenofolium* Smith
- *Lepidophloios kilpatrickense* Smith
- *Lepidocarpon wildianum* Scott
- *Stigmaria ficoides* (Sternberg) Brongniart

Equisetopsida:
- *Protocalamites goeppertii* (Solms-Laubach) Bateman

Filicopsida:
- *Metadineuron ellipticum* (Kidston) Galtier
- *Metaclepsydropsis duplex* Williamson
- *Botryopteris antiqua* Kidston

Lagenostomopsida:
- *Heterangium grievii* Williamson
- *Lyginorachis brownii* Calder
- *Endoxylon zonatum* (Kidston) Scott

Uncertain affinities:
- cf. *Mittagia seminiformis* Lignier

In addition, there are adpressions of 'lepidodendrid twigs' (Smith, 1960); possibly *Lepidophloios kilpatrickensis* Smith, *Stigmaria ficoides* (Sternberg) Brongniart, and *Aneimites acadica* Dawson.

Interpretation

The main interest of the site lies in its apparently endemic lycopsid species (Smith, 1962c). *'Lepidodendron' solenofolium* is known from only two specimens, a small twig and a larger branch, both with attached leaves. It is characterized by protostelic axes and leaf cushions with prominent lateral 'wings'. The several known axes of *Lepidophloios kilpatrickensis* are protostelic and range in diameter from 5 to 20 mm. Their leaf cushions are almost equidimensional and approach those of *Lepidodendron sensu lato* in outline. The anatomy of *L. kilpatrickensis* was used by Smith (1962c) to speculate that the primary cortex of these lycopsids remained meristematic for much of the plant's life. This is one of the earliest known diverse assemblages of arborescent lycopsids that show details of the axial anatomy; the ferns too are important. It contrasts with the majority of Lower Carboniferous petrifaction assemblages, which are dominated by seed-ferns and ferns.

This is the only known locality for the lagenostomalean rachis *Lyginorachis brownii*, which is characterized by a corrugated, 'U'-shaped vascular bundle. Another probable pteridosperm is the petrified axis *Endoxylon zonatum*. It has eight endarch protoxylem strands, and widely-separated, undivided leaf-traces; the secondary wood has narrow tracheids and very small, uniseriate rays (Lacey, 1953). It is associated with the adpression foliage *Aneimites acadica*, although they have not been found in organic connection.

Glenarbuck has yielded a small but important amount of palaeobotanical material that is important for showing anatomical details of several early arborescent lycopsids and ferns. It is the type locality for the pteridosperm frond *Lyginorachis brownii* and one of only two known localities for *Endoxylon zonatum*. It is also the only British locality for the enigmatic cf. *Mittagia seminiformis*, a reproductive organ of questionable affinities that was suggested as a possible precursor of the seed plants by Emberger (1968). Palaeoecologically, the site is of interest because it probably represents a swamp community of the same age and depositional environment as the uppermost community found nearby at Loch Humphrey Burn (see previous section).

Conclusion

Glenarbuck has yielded an important anatomically-preserved assemblage of plant fossils about 340 million years old. They indicate the presence of about ten whole-plant species, which formed a clastic swamp community that was dominated by lycopsid trees with subordinate seed plants. The lycopsid species, which have only ever been found at this locality, are distantly related to small, herbaceous living plants known as club-mosses. The flora provides an interesting contrast with the main plant-bearing units found at the nearby Loch Humphrey Burn (see previous section), which contain fluvially-transported plant fossils. These communities, which were dominated by seed plants and their immediate progymnospermous ancestors, are thought to immediately pre-date those at Glenarbuck.

PUDDLEBROOK QUARRY

Highlights

This is the best known locality for plant fossils from the Visean Drybrook Sandstone, and has yielded four apparently endemic species (Figure 5.34). These include *Muscites plumatus*, which may be the oldest known moss, and *Diplopteridium holdenii*, one of the most completely reconstructed Visean pteridosperms.

Introduction

The Puddlebrook locality consists of a small quarry in the Lower Carboniferous Drybrook Sandstone, just north of Drybrook in the Forest of Dean (SO 647184) (Figure 5.35). Plant fossils from here were first recorded by Allen (1961), and were the subject of a monographic study by Lele and Walton (1962b). Some of the component species have been reviewed by Thomas (1972) and Thomas and Purdy (1982), but the only comprehensive re-assessment of the assemblage is in an unpublished thesis by Rowe (1986), work done partly in conjunction with the Geological Conservation Review Unit. Certain parts of the latter study have been subsequently published (Rowe, 1988a, b, c, 1992).

Description

Stratigraphy

The geology is described by Rowe (1986), and briefly summarized by Rowe (1988b, c). The exposed strata belong to the Drybrook Sandstone Formation, and palynological evidence suggests an Asbian age. The plant fossils occur in a 1.2 metre thick lens of shale within the sandstone. The lens is interpreted as the infill of an abandoned river channel.

Figure 5.34 Puddlebrook. Asbian fluvial deposits of the Drybrook Sandstone, prior to the 1982 excavations at the site. (Photo: C.J. Cleal.)

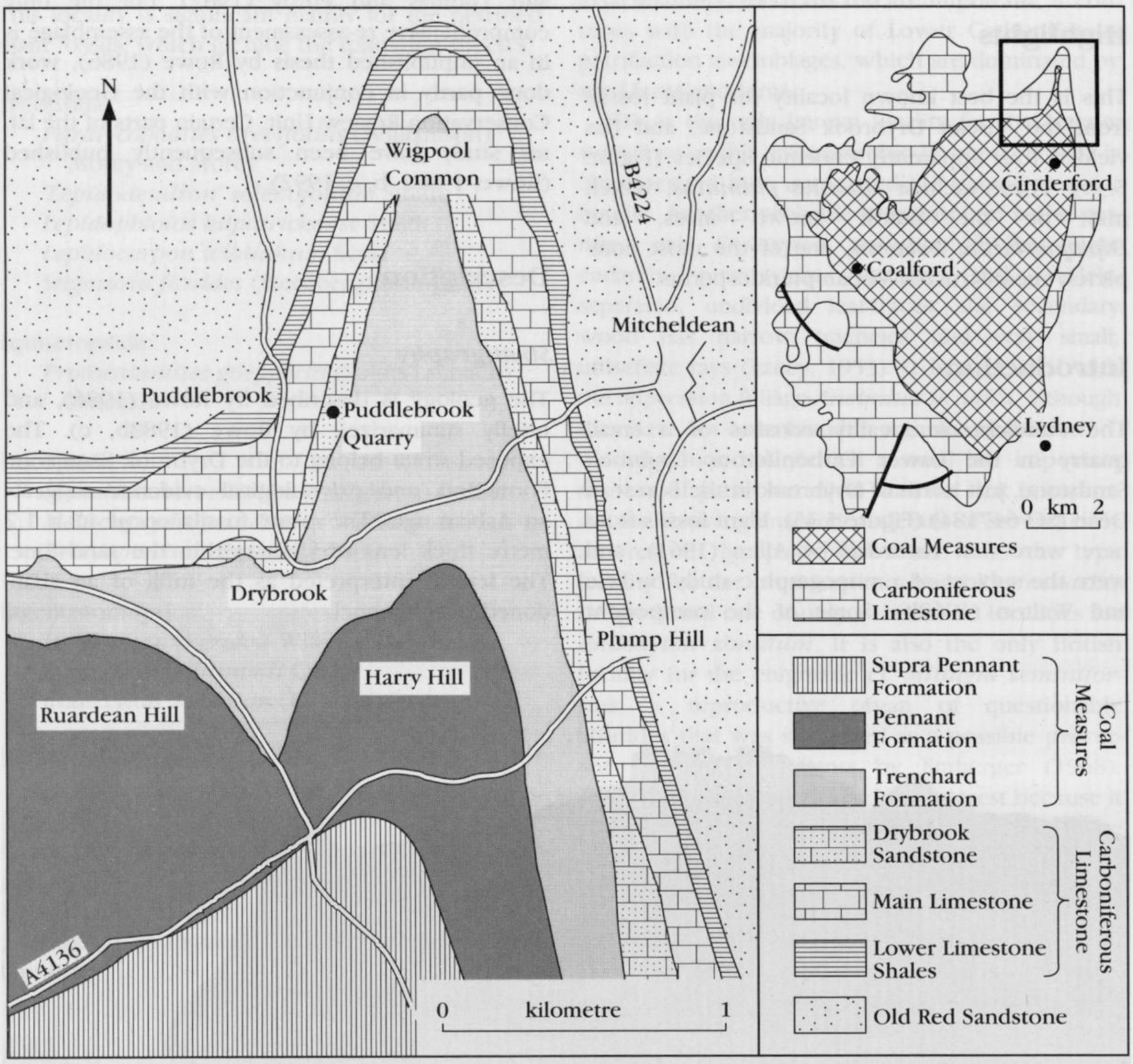

Figure 5.35 Geological map of the northern part of the Forest of Dean, showing the location of Puddlebrook Quarry. Based on Sullivan (1964, text-figure 1).

Palaeobotany

The fossils are preserved as adpressions, sometimes with cuticles preserved, or as fusain. The following species have been described to date:

Bryophyta(?):
  Muscites plumatus Thomas

Lycopsida:
  Eskdalia variabilis (Lele and Walton) Rowe
  E. fimbriophylla Rowe
  Lepidostrobophyllum fimbriatum (Kidston) Allen
  cf. *Stigmaria* sp.
  Selaginellites resimus Rowe

Lagenostomopsida:
  Diplopteridium holdenii Lele and Walton
  Dichotangium quadrothecum Rowe
  Sphenopteris obfalcata Walton
  S. cuneolata Lindley and Hutton
  Archaeopteridium tschermakii (Stur) Kidston

Telangiopsis sp.
Carpolithus puddlebrookense Thomas and Purdy

Interpretation

Thomas (1972) described a small, leafy shoot from here as *Muscites plumatus*. Although there is no evidence of fertile structures, Thomas argued that it could be a bryophyte, possibly a moss. If so, it would be the oldest known moss, the next oldest being from the Stephanian of France (Renault and Zeiller, 1888). No liverworts have so far been described from Puddlebrook, but Sullivan and Hibbert (1964) reported *Tetrapterites visensis* from another outcrop in the Drybrook Sandstone, which Lacey (1969) has argued might be a spore-bearing body of a liverwort.

The most abundant lycopsid remains here belong to the form-genus *Eskdalia*. The stems were initially described by Lele and Walton (1962b) as *Scutelocladus variabilis* Lele and Walton, who interpreted them as having no leaf cushions, ligule pits or parichnos tissue. Thomas and Purdy (1982) subsequently demonstrated that they had expanded leaf cushions with a lateral wing, basal heel and adaxial ligule pit. They also described grooves in the middle of the leaf cushions as being possibly the surface manifestation of infrafoliar bladders (spongy tissue connected to the parichnos, and thought to be part of an aerating system in certain lycopsids). As a result, they transferred the species to *Tomiodendron*, a form-genus previously only reported from Angaran assemblages of Siberia and the north slope of Alaska (Spicer and Thomas, 1987). Most recently, Rowe (1988c) has investigated fusainized fragments, which indicate that an infrafoliar, aerating bladder was not in fact present in the stems, and so he transferred the species to *Eskdalia*, as interpreted by Thomas and Meyen (1984).

Rowe (1988c) also described several specimens of *E. variabilis* stems with small, terminally-borne strobili (Figure 5.36). The strobili have a slender central axis with spirally-arranged sporophylls with entire margins. Although some evidence of sporangia was found, none yielded spores, and so it is still not possible to place *Eskdalia* in any of the families outlined by Thomas and Brack-Hanes (1984). Nevertheless, these Puddlebrook specimens are of considerable interest as the only known evidence of the fructifications of the shrubby lycopsid *Eskdalia*, although Thomas (1992) has argued that not all species of this stem form-genus may have had the same fructifications.

Rooting structures associated with *E. variabilis* were described by Lele and Walton (1962b) as cf. *Stigmaria* sp. Very similar structures are known from Moel Hiraddug (see below), where they are associated with *'Lepidodendron' perforatum* Lacey, a species that may belong to *Eskdalia* (Rowe, 1988c).

A second species of *Eskdalia* from Puddlebrook has been described by Rowe (1988c) as *E. fimbriophylla*. Isolated leaves were originally identified by Lele and Walton (1962b) as *Lepidophyllum* cf. *fimbriatum*, but no evidence was found of attached sporangia, as would be expected if they were sporophylls. Rowe demonstrated that they were leaves attached to *Eskdalia*-like stems, although they are wider and have larger leaf cushions than *E. variabilis* stems. *E. fimbriophylla* has not been identified from any other locality; however, there is a possible comparison with the leaf *Lepidophylloides fisheri* Crookall, described by Crookall (1966) from the more or less coeval Scremerston Coal Group of Northumberland.

Allen (1961) described abundant, isolated lycopsid sporophylls from here as *Lepidostrobophyllum fimbriatum* (Kidston) Allen. They have a clearly fimbriate margin, and thus differ from the entire-margined sporophylls of the *Eskdalia variabilis* strobili. It is tempting instead to speculate a connection with *E. fimbriophylla*, whose leaves are also fimbriate, but direct evidence of attachment is so far lacking.

A third type of lycopsid found at Puddlebrook is a small herbaceous plant known as *Selaginellites resimus* Rowe, 1988a. Although only represented by fragmentary material, Rowe was able to reconstruct it as having mainly recumbent, rambling stems, which produced vertical, dichotomous shoots. Some of these vertical shoots bore what Rowe interpreted as terminal strobili, which included sporangia containing megaspores. It thus appears to be a typical example of the Selaginellaceae, one of the most conservative families of vascular plants, which has remained essentially unaltered since the Late Devonian (Fairon-Demaret, 1977).

The most completely understood pteridosperm from Puddlebrook is *Diplopteridium holdenii* (Figure 5.37). The basic features of the foliage were described by Lele and Walton (1962b), but a more comprehensive study by Rowe (1988b) has enabled him to provide a reconstruction of most of the plant, including some details of the

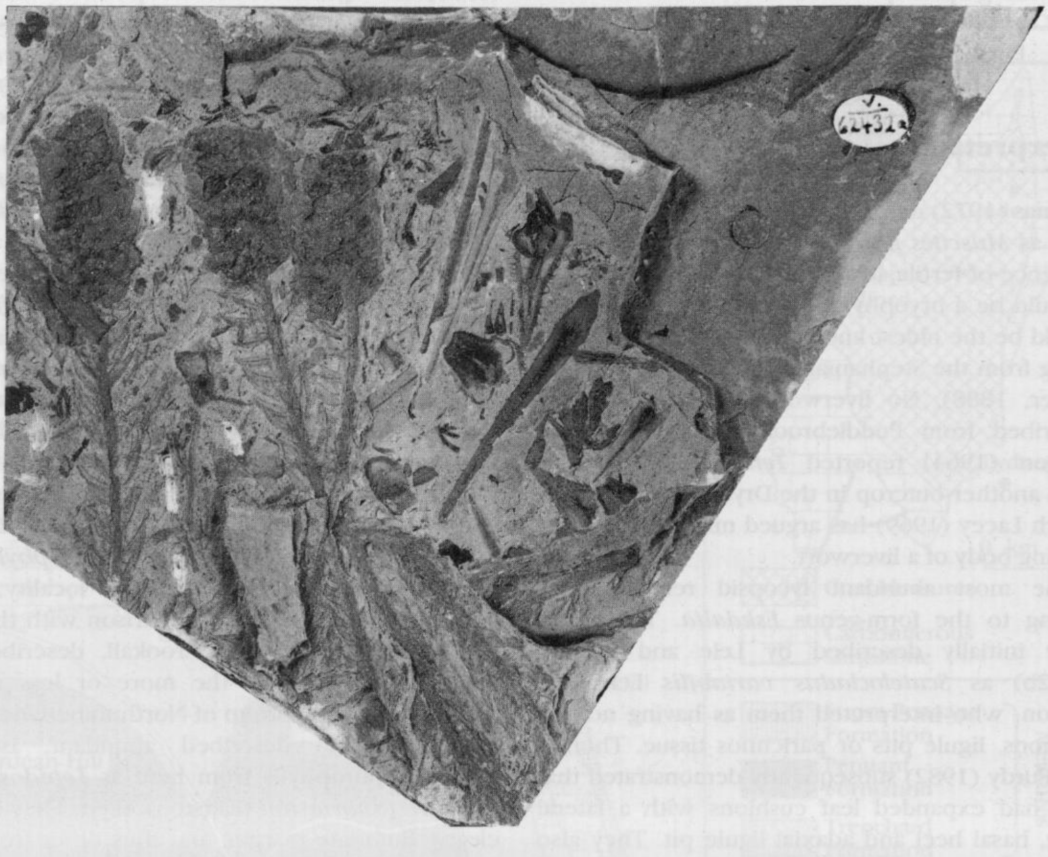

Figure 5.36 *Eskdalia variabilis* (Lele and Walton) Rowe. Leafy lycopsid shoots bearing terminal fructifications; Natural History Museum, London, specimen V.62432a. Drybrook Sandstone (Asbian), Puddlebrook Quarry. x 1. (Photo: Photographic Studio, Natural History Museum, London.)

fructifications (Figure 5.7). It appears to have been herbaceous, with an upright stem bearing a crown of fronds. As in most pteridosperms, the fronds have an essentially bipartite architecture, the main rachis dichotomizing near the base to produce bipinnate branches. In fertile fronds, however, there is a trichotomy, the third branch bearing the fructifications. Rowe was able to demonstrate organic connection between the fertile branches of the *D. holdenii* frond and cupulate seed/ovule-bearing structures, that Lele and Walton (1962b) had earlier named as *Calathiops* sp. This is only the second known species of *Diplopteridium*; the other being *D. teilianum* Walton from Teilia (p. 178), from which it differs in having narrower pinnule segments.

Rowe (1988b) also described a synangiate organ associated with *D. holdenii*, which Lele and Walton (1962b) had initially identified as *Telangium* sp. Although Rowe presented considerable circumstantial evidence that it was the pollen organ of *D. holdenii*, in the absence of direct evidence of attachment he assigned it a separate name, *Dichotangium quadrothecum*. Rowe (1986) described other sporangial structures from Puddlebrook, including one that he compared with *Telangiopsis*. However, the results of this work have yet to be published.

Other pteridosperm fronds from Puddlebrook, were identified by Lele and Walton (1962b) as *Sphenopteris obfalcata* and *S. cuneolata*. The former is only otherwise known from Teilia (p. 179), and there is as yet inadequate knowledge of its frond architecture or fructifications for its taxonomic position to be firmly established.

The holotype of *S. cuneolata*, from the Oil Shale Group of Scotland, was poorly illustrated and Kidston (1923b, p. 156) reported that it was lost. Kidston (1923b, pl. 214) illustrated a second

Figure 5.37 *Diplopteridium holdenii* Lele and Walton. Pteridosperm frond with fructifications; Natural History Museum, London, specimen V.62331a. Drybrook Sandstone (Asbian), Puddlebrook Quarry. x 0.5. (Photo: Photographic Studio, Natural History Museum, London.)

specimen under this name, but Lele and Walton (1962b) note that it differs markedly from Lindley and Hutton's specimen in its nervation and the outline of the pinnules. Lele and Walton therefore nominated one of the Puddlebrook specimens as 'lectotype' (in fact a neotype), but it is far from clear that it is conspecific with Lindley and Hutton's original concept of the species.

Thomas and Purdy (1982) describe some apparently radiospermic (i.e. radially symmetrical) seeds or ovules as *Carpolithus puddlebrookense*. They had an integument fused to the nucellus except at the apex, where it formed four apical lobes. The nearest comparison seems to be with the Tournaisian petrified seeds/ovules *Eurystoma angulare* Long from the Whiteadder (p. 124). However, *Eurystoma* was borne in *Alcicornopteris* cupulate structures, of a type not so far reported from Puddlebrook. Furthermore, *Eurystoma* is thought to have calamopityalean affinities, and none of the foliage found at Puddlebrook is of a type normally associated with that order (e.g. *Triphyllopteris*, *Spathulopteris*).

Two fragmentary Puddlebrook specimens were identified by Lele and Walton (1962b) as *Archaeopteridium tschermakii*. Better specimens have been since described by Rowe (1992), who also found pre-pollen organs which confirm that the species belongs to the pteridospermous class Lagenostomopsida. Although generally rare, this is a widely occurring species, having been reported from several localities in Scotland, Germany and Poland. The Puddlebrook specimens are the only examples known from England or Wales.

Although plant fossils have been reported from elsewhere in the Drybrook Sandstone (e.g. Cleal, 1986a), this is by far the most diverse assemblage from the formation. Five of the taxa listed at the beginning of this section have been reported only from the Drybrook Sandstone, and four of these only from Puddlebrook. There is some overlap in composition with other British Visean assemblages, particularly those from North Wales (Teilia and Moel Hiraddug – see p. 175). However, the overall balance of species separates Puddlebrook from most other palaeobotanical sites of this age. This presumably represents its spatial isolation, being separated from these other, more northerly localities by the Wales–Brabant 'landmass'.

Conclusion

This is the best site for Lower Carboniferous plant fossils in southern Britain. They represent the vegetation growing here about 330 million years ago, which consisted mainly of shrubby club-mosses and primitive seed plants. They include fossils that demonstrate the connection between vegetative and reproductive structures, which allows some of the species to be viewed more as whole, living plants, rather than just as disarticulated organs. Several of the species are unique to this locality, including *Diplopteridium holdenii* Lele and Walton, one of the most completely reconstructed early seed plants.

MOEL HIRADDUG

Highlights

Moel Hiraddug is the best available locality for plant fossils in the Visean Foel Formation of North Wales. A number of taxa are unique to here, including *Lepidodendropsis jonesii*, *Archaeosigillaria stobbsii*, *Rhacopteris weissii* and *Calathiops dysertbensis*. It is also one of the few Visean localities where the plant fossils have cuticles preserved.

Introduction

This Lower Carboniferous site consists of two small quarries south of Dyserth, North Wales (SJ 061783) (Figure 5.38). Some authors have referred to it as 'Dyserth' (e.g. Lacey, 1962). There is a Dyserth Quarry *c.* 0.5 km further north, however, and so the alternative name Moel Hiraddug Quarries is used here (named after the hill on the side of which they occur). Plant fossils were first recorded by Morton (1871, 1886, 1898), who noted similarities with Bowman's (1837) assemblage from a similar stratigraphical interval on the opposite side of the Vale of Clwyd, at Craig-y-Forwen near St Asaph. Fossils from Moel Hiraddug were also mentioned by Hind and Stobbs (1906) and Hind (1907), although the first detailed description with illustrations was Walton's (1926) analysis of *Rhacopteris weissii* Walton. Walton (1928), Neaverson (1930) and Hirmer (1939) all briefly mentioned the Moel Hiraddug assemblage, but it was not until Lacey made extensive collections here between 1946 and 1960 that its full diversity could be assessed. Provisional taxonomic lists were given by Lacey (1952a, b) who later published a full monographic treatment (Lacey, 1962).

Description

Stratigraphy

There have been numerous geological accounts of this area (e.g. Morton, 1871, 1886; Strahan, 1885a; Hind and Stobbs, 1906; Neaverson, 1930, 1945; Somerville *et al.*, 1989). The strata exposed at Moel Hiraddug Quarries are about 17 metres of brown limestones, with lenticular shale and sandstone bodies, and they belong to the Foel Formation (traditionally called the Lower Brown Limestones). Somerville *et al.* (1989) have placed this formation in the upper Chadian, and suggest that it represents shallow marine deposits.

Palaeobotany

The fossils are mainly compressions, sometimes with cuticles still preserved. The assemblage comprises the following taxa:

Algae (division unknown):
- *Koninckopora inflata* (de Koninck) Wood
- *Bythotrepis plumosa* Kidston
- *B. nodosa* Lacey

Lycopsida:
- *Archaeosigillaria stobbsii* Lacey
- *Clwydia decussata* Lacey
- *Lepidodendropsis jonesii* Lacey
- *Lepidostrobophyllum fimbriatum* (Kidston) Allen
- *Lepidodendron* sp.
- *Stigmaria ficoides* (Sternberg) Brongniart
- *Stigmaria* sp.
- *Knorria acicularis* Göppert
- ?*Halonia* sp.

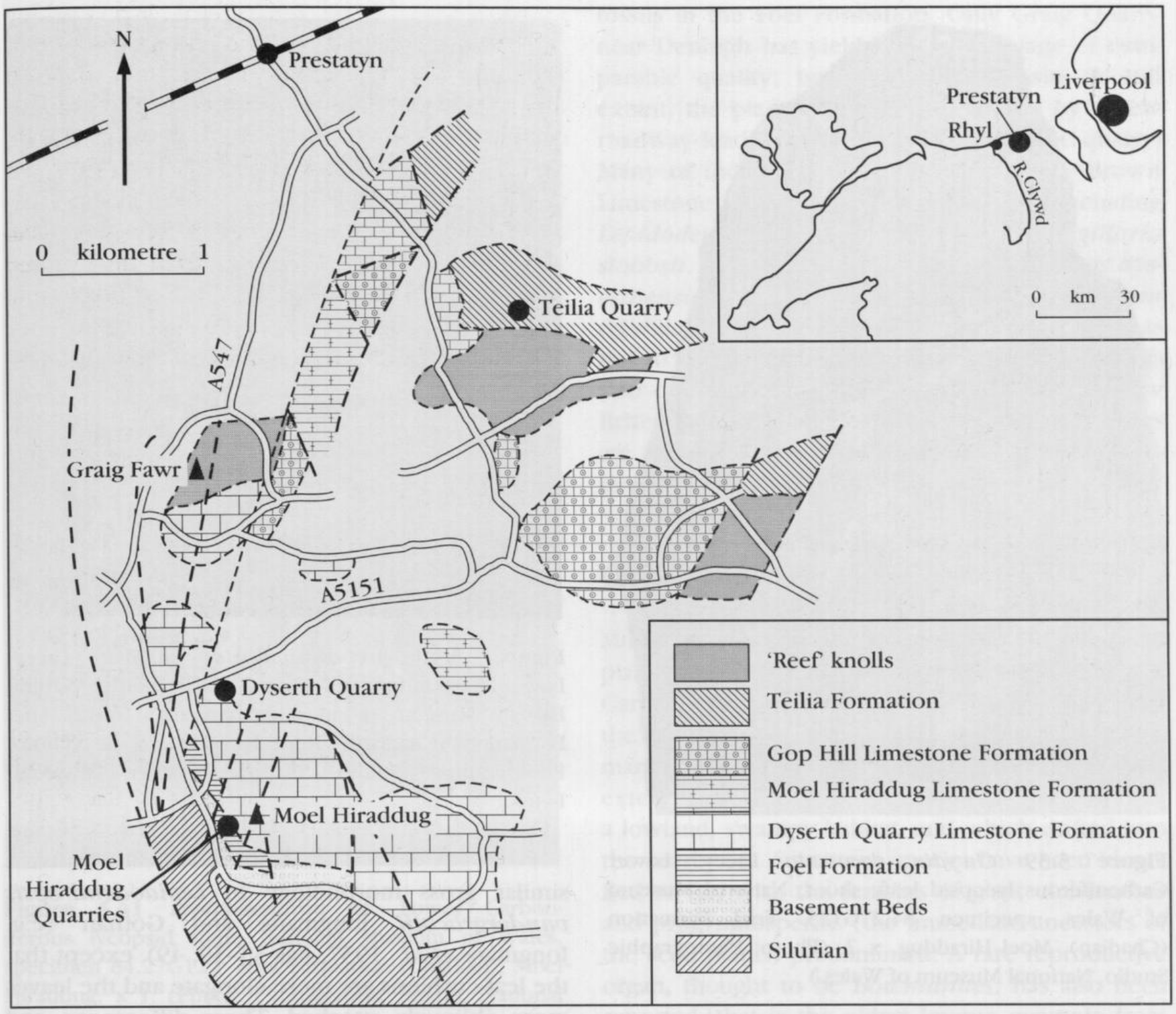

Figure 5.38 Lower Carboniferous geology of the area south of Prestatyn, showing the position of the quarries at Moel Hiraddug and Teilia. Based on Somerville *et al.* (1989, figure 1).

Equisetopsida:
- *Archaeocalamites radiatus* (Brongniart) Stur
- *Bowmanites tenerrimus* (Ettingshausen) Hoskins and Cross

Progymnospermopsida(?):
- *Rhacopteris weissii* (Walton) Hirmer
- *R. subcuneata* Kidston

Lagenostomopsida:
- *Calathiops dysertbensis* Lacey

Interpretation

This is the type locality for *Archaeosigillaria stobbsii* (Figure 5.40), and has yielded information on both gross morphology and epidermal structure. It is very similar in gross morphology to *Archaeosigillaria kidstonii* Krausel and Weyland from the Carboniferous Limestone of Cumbria (Kidston, 1885a, 1901b; Crookall, 1966; Chaloner *in* Boureau *et al.*, 1967). However, since the epidermal structure of *A. kidstonii* is unknown, Lacey (1962) opted to place the better-preserved Moel Hiraddug specimens in a new species.

Associated with the *Archaeosigillaria* stems are slender leafy shoots. Lacey (1962) noted that they had a different phyllotaxis and epidermal structure to *A. stobbsii*, and so assigned them to a different species, *Clwydia decussata* (Figure 5.39). However, similar leafy shoots have been

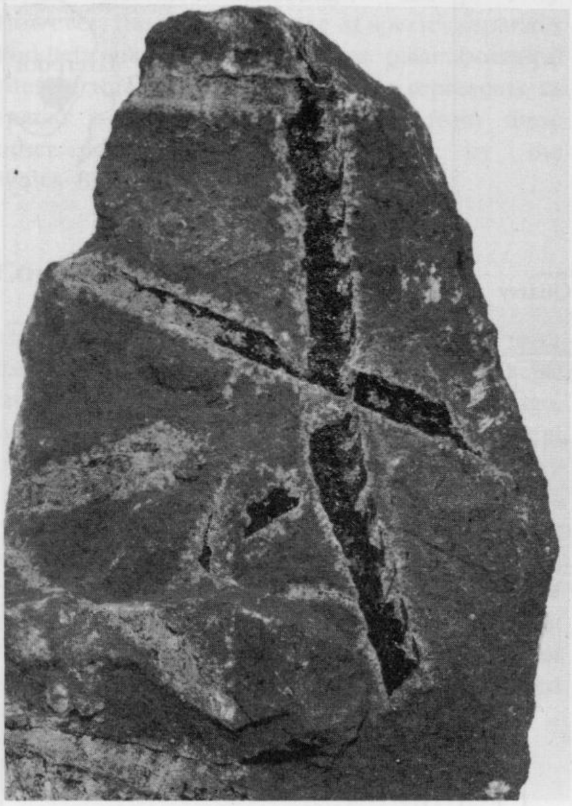

Figure 5.39 *Clwydia decussata* Lacey. Lower Carboniferous lycopsid leafy shoot; National Museum of Wales, specimen 84.27G125. Foel Formation (Chadian), Moel Hiraddug. x 2. (Photo: Photographic Studio, National Museum of Wales.)

Figure 5.40 *Archaeosigillaria stobbsii* Lacey. Lower Carboniferous lycopsid leafy shoots; Natural History Museum, London, specimen V.16012. Foel Formation (Chadian), Moel Hiraddug. x 1. (Photo: Photographic Studio, Natural History Museum, London.)

reported in association with *Archaeosigillaria* at other Visean localities (e.g. Kidston, 1885a), and many workers consider them to be parts of the same plant. Central to the debate is the interpretation of two of Kidston's specimens (Chaloner *in* Boureau *et al.*, 1967, fig. 340 c, d) as showing the attachment of such leafy shoots to *Archaeosigillaria* stems. Rowe (1988a) has recently concluded that these specimens are too poorly preserved for the case to be proved, and that the taxonomic separation of the stems and shoots is best retained, at least until the group as a whole can be revised in detail.

Lacey (1952a) identified a single stem fragment as *Lepidophloios* cf. *laricinus* Sternberg, but, in a footnote to the paper, Jongmans suggests that it might be a *Lepidodendropsis*. Lacey (1962) later demonstrated that the stem was eligulate, thus tending to confirm Jongmans' view. It has a very similar gross morphology to *Lepidodendropsis vandergrachtii* Jongmans and Gothan (e.g. Jongmans *et al.*, 1937, figs 33–39, 49), except that the leaf cushions are more elongate and the leaves more obliquely attached. These differences, and the absence of information on the *L. vandergrachtii* epidermal structure, caused Lacey to refer the Moel Hiraddug specimen to *Lepidodendropsis jonesii*.

The lycopsid sporophylls *Lepidostrobophyllum fimbriatum* occur commonly here. Elsewhere, they are often associated with *Eskdalia* stems (e.g. Puddlebrook – see p. 169), but there is no evidence of such stems at Moel Hiraddug. However, at another Foel Formation exposure, at Graig Quarry, stems were identified by Lacey (1962) as *Lepidodendron perforatum* Lacey, which Rowe (1988c) considers to belong to *Eskdalia* (although he makes no formal transfer of the species).

Equisetopsids are mainly represented by *Archaeocalamites radiatus* stems, without any evidence of the foliage. In addition, Lacey (1962) described a single sphenophyllalean strobilus with incised sporophylls, under the name *Bowmanites*

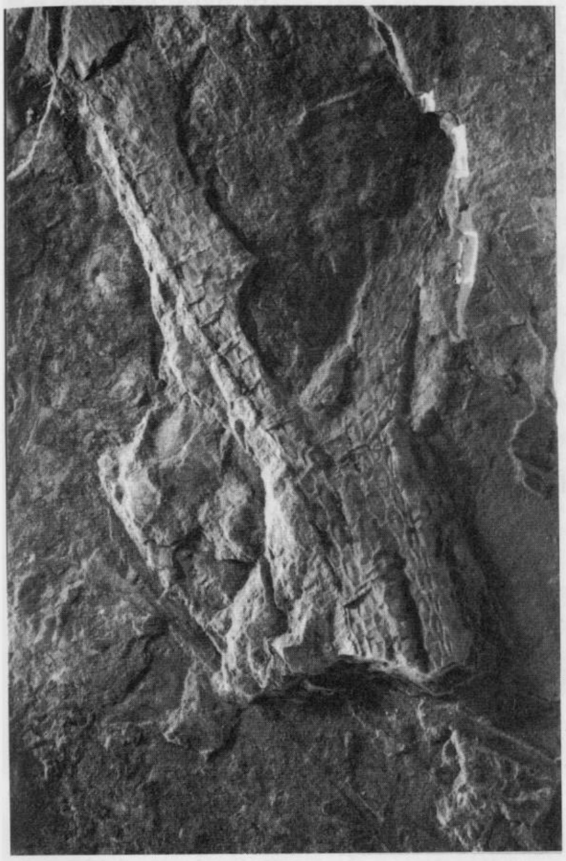

Figure 5.41 *Lepidodendron* sp. Lower Carboniferous lycopsid stem; National Museum of Wales, specimen 84.27G122. Foel Formation (Chadian), Moel Hiraddug. x 1. (Photo: Photographic Studio, National Museum of Wales.)

tenerrimus; but again there is no evidence of the foliage.

The only unequivocal evidence of pteridosperms is the fructification *Calathiops dysertbensis*. This form-genus is usually regarded as having been attached to lagenostomalean fronds such as *Diplopteridium* and *Diplothmema*, but no such fronds have so far been reported from Moel Hiraddug.

Two species of the ?progymnosperm *Rhacopteris* have been reported, *R. weissii* and *R. subcuneata* (Walton, 1926; Lacey, 1962). The former is only known from this locality and is of interest in being one of the few rhacopterid species from which cuticles have been prepared (Lacey, 1962). This may eventually help resolve the taxonomic position of these leaves.

This is easily the best available locality for plant fossils in the Foel Formation. Only Graig Quarry near Denbigh has yielded an assemblage of comparable quality; but, although this site is still extant, the plant bed is now obscured by a new roadway leading to the upper part of the quarry. Many of the species found in the Lower Brown Limestone are unique to the formation, including *Lepidodendropsis jonesii*, *Archaeosigillaria stobbsii*, *Rhacopteris weissii* and *Calathiops dyserthensis*; also *'Lepidodendron' perforatum* (?*Eskdalia* sp. – Rowe, 1988c), although this has not so far been reported from Moel Hiraddug. It is also of particular significance as one of the few British Visean palaeobotanical sites where cuticles are still preserved, allowing details of the epidermal structure to be observed.

Conclusion

Moel Hiraddug has yielded a diverse assemblage of plant fossils, dating from the early part of the Carboniferous period, about 330 Ma. It represents the remains of vegetation growing on the northern margins of St George's Land (an island that extended over parts of central Britain), probably in a lowland, swampy habitat, and which drifted into the nearby sea. Seventeen species have been identified so far, with the remains of giant club-mosses and progymnosperms (the immediate ancestors of the seed plants) predominant. A rare reproductive organ, thought to be *Bowmanites*, has also been reported, that is the oldest known example from Britain of this particular group of horsetails, which, in the Late Carboniferous, were important members of the tropical swamp vegetation. Of special interest is that many of the fossils still have their outer protective 'skin' (known as the cuticle). Plant cuticles have been widely studied in younger fossil floras and have proved of considerable value, as they are often the only source of anatomical detail still preserved. For reasons that are not clear, however, cuticles are extremely rare in the Lower Carboniferous, which makes their presence at Moel Hiraddug of considerable potential importance.

TEILIA QUARRY

Highlights

Teilia Quarry is the only locality to yield plant fossils from the Gronant Group of North Wales, and includes a number of endemic taxa. It is particularly important for the putative progymnosperm *Rhacopteris*, yielding the only known British example with fructifications. It has also yielded some of the best known examples of lagenostomalean fronds from Britain, including *Diplopteridium* and *Sphenopteridium*, and what may be the earliest evidence of the order Trigonocarpales. It is a site of outstanding palaeobotanical significance.

Introduction

Lower Carboniferous plant fossils were first collected from this disused quarry north-east of Gwaenysgor, near Prestatyn, North Wales (SJ 080814), by the amateur geologist J.B. Shone, during the mid-nineteenth century. Morton (1886) published the earliest species list based on Shone's material, although many of his identifications were wrong. The first reliable account of the assemblage was by Kidston (1889a), who also later included a number of Teilia specimens in his classic monograph on Carboniferous plant fossils (Kidston, 1923–1925). Further material was collected during the 1920s, and resulted in a revision of the assemblage by Walton (1926, 1928, 1931); Walton's identifications were also quoted by Neaverson (1930), Crookall (1932) and Hirmer (1939). Most recently, Benson (1935a, b) has given brief accounts on fructifications.

Description

Stratigraphy

Morton (1886) and Walton (1931) have provided accounts of the geology at Teilia. The sequence exposed consists of about 8 metres of thinly-bedded, dark grey limestones belonging to the Gronant Group (previously the Upper Black Limestone Group). In these sedimentary rocks, land-plant fossils are closely associated with fossils of marine animals, and Walton regarded this as evidence that the strata were lagoonal or shallow marine. The fauna mentioned by Morton (1886), Hind and Stobbs (1906), Jackson *in* Walton (1928) and Neaverson (1930) all clearly point to an early Brigantian age (George *et al.*, 1976).

Palaeobotany

The plant fossils are preserved here mainly as adpressions, but no evidence of cuticles has so far been reported. The following taxa have been described:

Lycopsida:
cf. *Lepidodendron* spp.

Equisetopsida:
Archaeocalamites radiatus (Brongniart) Stur

Filicopsida(?):
cf. *Rhodeopteridium tenue* (Gothan) Purkynová

Progymnospermopsida(?):
Rhacopteris circularis Walton
R. robusta Kidston
R. petiolata (Göppert) Schimper
R. fertilis Walton

Lagenostomopsida:
Diplopteridium teilianum (Kidston) Walton
Sphenopteridium capillare Walton
S. pachyrrachis (Göppert) Schimper
Lyginopteris bermudensiformis (Sternberg) Patteisky
Adiantites antiquus (Ettingshausen) Kidston
A. machanekii Stur
Sphenopteris obfalcata Walton
Spathulopteris ettingshausenii (Feistmantel) Kidston
S. clavigera (Kidston) Walton
Calathiops acicularis Göppert
C. glomerata Walton
C. renieri Walton

Cycadopsida:
Neuropteris antecedens Stur
Holcospermum ellipsoideum (Göppert) Walton
Carpolithus sp.

Interpretation

Lycopsida

The lycopsids are represented at Teilia by a few stem fragments, described by Walton (1931). Most belong to a *Lepidodendron*, which Walton compared with *L. obovatum* Sternberg based on a suggestion by Jongmans. However, *L. obovatum* is a confused taxon whose types probably fall in synonymy with *Lepidodendron aculeatum* Sternberg (Thomas, 1970), a species quite different from the Teilia specimens. A single specimen was compared by Walton with *L. calamitoides* Nathorst, but the leaf cushions are poorly preserved and the leaf scar not distinguishable. Considering the poor preservation of this material, it is best recorded for the time being merely as cf. *Lepidodendron* spp.

A single small fragment of a third type of lycopsid was illustrated by Walton in a rather sketchy line diagram. He referred it to *Sigillaria* sp., but the available evidence is inadequate to justify this assignment. Crookall (1966) does not refer to it in his monograph on British *Sigillaria* species.

Equisetopsida

At Teilia, as in most Visean assemblages, equisetopsids are represented by *Archaeocalamites radiatus*. Walton (1931, pl. 26, fig. 39) shows a stem with the characteristic forked leaves of this species.

Filicopsida(?)

The frond fragments assigned to *Rhodeopteridium* have much smaller pinnules with very slender lobes. It is possible that they are parts of small pteridosperm fronds, but their small size rather suggests that they are filicopsid fronds. Walton (1931) assigned the Teilia specimens of this type to *Rhodeopteridium tenue* (syn. *Rhodea tenuis* Gothan), a species first described from the lower Namurian of Silesia (Gothan, 1913). However, Gothan's diagnosis mentions that the rachises are 'winged', a feature not yet demonstrated in the Teilia specimens.

Progymnospermopsida(?)

Among the commoner plant fossils found at Teilia is foliage belonging to the form-genus *Rhacopteris*. Although there is some evidence available on the fructifications of this form-genus, including one specimen described by Walton (1926) from Teilia, its affinities have never been firmly established. On balance, however, it seems most likely that it belongs to the progymnosperms (Archangelsky and Arrondo, 1966; Beck, 1976). It was initially established for Upper Carboniferous species (Schimper, 1869–74), but a number of Lower Carboniferous species were later included (Stur, 1875). Oberste-Brink (1913) placed these Lower Carboniferous species in a separate section, *Rhacopteris (Anisopteris)*, based partly on their stratigraphical position, and partly on the greater asymmetry of the pinnules (some authors have gone as far as raising it in rank to form-genus – Hirmer and Guthörl, 1940; Boureau and Doubinger, 1975). However, this division is probably artificial (Walton, 1926) and the Lower Carboniferous species are best referred to simply as *Rhacopteris*.

The commonest *Rhacopteris* species found at Teilia, *R. circularis*, has round, fairly symmetrical pinnules and a radiating nervation. There have also been tentative records of this species from France (Corsin and Dubois, 1932), the Sahara (Boureau, 1953), Nova Scotia (Bell, 1960) and the Himalayas (Høeg *et al.*, 1955; Pal and Chaloner, 1979), but they are all based on poorly preserved fragments. Somewhat better material has been described from Argentina by Frenguelli (1944) and Peru by Doubinger and Alvarez Ramis (1980), but it is closely associated with *Pseudorhacopteris ovata* (McCoy) Archangelsky, an Upper Carboniferous species from Gondwanaland with very similar shaped pinnules to *R. circularis*. Teilia is the only known locality to yield undoubted examples of *R. circularis*.

The specimens from Teilia identified by Kidston (1889a) as *Rhacopteris inaequilaterata* (Göppert) Stur were included within the synonymy of *R. circularis* by Walton (1926).

A second species from Teilia is *Rhacopteris robusta* (syn. *R.* cf. *petiolata* Walton, 1926, non Göppert). It has asymmetrical pinnules with an incised distal margin, and is thus readily distinguishable from the commoner *R. circularis*. The Teilia specimens have rather smaller pinnules than the types of *R. robusta* from Scotland (Kidston, 1923c, pl. 51, figs 5–7) but compare closely with specimens from Silesia figured by Patteisky (1929, pl. 6, fig. 1).

Walton (1931, pl. 25, fig. 20) figured a single specimen as *Rhacopteris machanekii*, a species based on just one specimen from Moravia (Stur, 1875). Walton implied that it might be a small form of *R. robusta*, a view which is accepted here.

A third species present at this site is *R. petiolata*, which has deeply digitate pinnules. Only one undoubted specimen has been documented (Kidston, 1923c, pl. 53, fig. 5), although some other more fragmentary examples may also belong here (Kidston, 1923c, pl. 53, fig. 3; Walton, 1926, pl. 16, fig. 11).

The fertile specimen of a *Rhacopteris* described by Walton (1926) was essentially similar to the only other example then known (*R. paniculifera* Stur, 1875, pl. 8, fig. 3), in that it showed a dichotomous axis bearing clusters of sporangia. However, unlike Stur's specimen, the one from Teilia has no sterile pinnules attached and so Walton assigned it to a separate species, *R. fertilis*. This remains the only known British example of a *Rhacopteris* bearing fructifications, and has an important bearing on determining the taxonomic position of this group of leaves, which form such an important component of Lower Carboniferous adpression floras. It suggests that they may be progymnosperms, as they appear similar to *Archaeopteris* fructifications (cf. Phillips *et al.*, 1972). However, the fertile rhacopterids were described before the progymnosperms had been recognized as a major taxon, and they have not been subsequently re-assessed. Teilia should thus play a significant role in the much needed revision of this widely occurring fossil foliage.

Lagenostomopsida

Dominating the assemblage are pteridosperm frond fragments, most probably belonging to the Lagenostomales. The most completely known is *Diplopteridium teilianum*, following the work of Walton (1926, 1931). It has an essentially bipartite architecture, with a dichotomy of the main rachis near the base of the frond; it is thus similar in many ways to *Sphenopteridium*. However, it shows no evidence of the transverse bars that typically occur on *Sphenopteridium* racheis, and so the species was for some time referred to the generalized form-genus *Sphenopteris* (Kidston, 1889a, 1923a). However, Walton demonstrated that at least some fronds produced a third branch in the angle of the 'dichotomy', which probably bore the fructifications. Consequently, he assigned it to a new form-genus, *Diplopteridium*. Seeds or sporangia have not been found attached to this third branch, but a number of *Telangium*-like structures were found in close association (that it was a fertile branch has been confirmed in the related species *Diplopteridium holdenii* Lele and Walton from Puddlebrook – see p. 169). Although these *Telangium*-like structures are not well preserved, Benson (1935a) concluded that they were cupules, which originally bore seeds/ovules.

A number of other bipartite fronds found at Teilia have rachises with transverse bars and so are assigned to *Sphenopteridium*. To date, no evidence has been found of their fructifications. Walton (1931) described three forms. *S. capillare* is quite distinctive, having small, deeply incised pinnules packed closely to one another along the rachis; to date it has only been reported from Teilia. The other specimens have larger, more widely spaced pinnules with more extensive lamina. They mostly belong to *S. pachyrrachis*, a well-known species with a wide distribution, known from Scotland (Kidston, 1923b), Bavaria (Lutz, 1933), the Loire (Bureau, 1913–1914) and Moravia (Patteisky, 1929). The third type recognized by Walton is only known from Teilia by one small pinna fragment, and was identified as *S. crassum*. It only differs from *S. pachyrrachis* in having slightly smaller, broader pinnules and Walton argued that it might merely be an extreme form of that species. It has not therefore been included here in the species list for Teilia.

Walton (1931, pl. 24, figs 16, 17) figures two specimens of *Lyginopteris bermudensiformis*. Two forms have been recognized within this species, *Lyginopteris bermudensiformis* fa. *bermudensiformis* (synonyms *Lyginopteris bermudensiformis* fa. *schlotheimii* Stur, 1875 and *Lyginopteris bermudensiformis* fa. *typica* Kidston, 1923c) and *Lyginopteris bermudensiformis* fa. *geinitzii* Stur, 1875. The Teilia specimens are too fragmentary to be certain, but Walton (1931) suggested that they have most in common with *Lyginopteris bermudensiformis* fa. *bermudensiformis*. The specimen figured by Walton (1931, pl. 24, fig. 16) is of particular interest in that it seems to be a 'miniature' version of a *Lyginopteris* frond, complete with dichotomy. There may be a correlation with the bipartite 'mini-fronds' described by Boersma (1972) for *Mariopteris*, thought to represent the small fronds from the most distal part of the plant.

Kidston (1889a, p. 425–6) recorded some poorly preserved fragments as ?*Sphenopteris schlehanii* (Stur) Gothan. This species is now generally included within *Lyginopteris* (Patteisky, 1957) and it is thus likely that Kidston's reported specimens belong to *L. bermudensiformis*.

Associated with these lagenostomalean fronds are a number of fructifications of the *Calathiops*-type (Walton, 1931). None of them show any internal structure, nor are they attached to foliage, and so their affinities must be speculative. However, *C. acicularis* and *C. glomerata* can be compared with the so-called 'micro-cupule' type of lagenostomalean fructification, such as *Telangiopsis* (Kidston, 1924; Long, 1979b). A third type described by Walton as *C. renieri* is nearer to the 'mega-cupule' type of fructification, such as *Megatheca* from the Oil Shale Group of Scotland (Andrews, 1940). Yet another fructification from Teilia, *Calathiops gothanii* Benson, 1935a, seems indistinguishable from *C. glomerata*, to which Benson does not refer.

Other forking fronds in this assemblage belong to *Spathulopteris*, distinguished from *Sphenopteridium* and *Diplopteridium* by the swollen shape of the pinnules, and the absence of pinnae or pinnules attached to the main rachis below the dichotomy. There is no evidence available of fructifications attached to these fronds or of the rachial anatomy (except that there are no transverse bars across the rachises), but it is likely that they belong to the Calamopityales. The commonest species at Teilia is *S. ettingshausenii*, which has relatively slender pinnule-lobes. It is a widely distributed species, having been recorded from the Visean of Scotland (Kidston, 1923b), Moravia (Patteisky, 1929) and Silesia (Gothan, 1937). A single small fragment was also described by Walton (1931) as *S. clavigera*, which has more swollen lobes than *S. ettingshausenii*. However, this specimen shows little evidence as to the frond architecture and is thus included in the species list with a '?'.

A single seed identified by Walton (1931) as *Carpolithes* sp. gives the impression of being platyspermic, similar to *Samaropsis* described from the Tournaisian of Scotland. As remarked in the discussion on the Whiteadder (p. 124), such seed compressions might be correlatives of the petrified *Lyrasperma* seeds, and these in turn may have calamopityalean affinities.

In contrast to most of the other bipartite fronds in the Teilia assemblage, a number have wedge-shaped pinnules with entire margins, and belong to *Adiantites*. They are also distinguished by the more complex branching of the sterile foliage (Walton, 1931, text-fig. 2). Walton (1931) pointed out, however, that there is often a scar at the dichotomy of the main rachis, which might be the origin of a fertile branch, similar to that seen in *Diplopteridium*. If correct, this suggests lagenostomalean affinities. Two species of this type have been recognized from Teilia: *A. machanekii* (Figure 5.42), which is the most abundant, and has slender straight-sided pinnules (Walton, 1931, pl. 23, fig. 6, pl. 24, fig. 12); and *A. antiquus*, with more rounded pinnules (Kidston, 1889a, pl. 1, fig. 1; Kidston, 1923b, pl. 45, fig. 1; Walton, 1931, text-fig. 2). The specimens described by Kidston (1889a) and Walton (1931) as *A. tenuifolius* and *A.* sp. are too small for a positive identification.

Walton (1931) recorded, but did not figure, *Sphenopteris* cf. *filiformis* Kidston from Teilia. He suggested that it was perhaps only a young *Adiantites* frond. It has thus not been included here in the list of species for this locality.

Less completely known types of pteridosperm(?) frond from Teilia have been referred to *Sphenopteris obfalcata* Walton, 1931. It has rather swollen pinnule lobes, similar to the type normally found in *Spathulopteris*, but its frond architecture is too imperfectly known for it to be placed there. To date, this species has only been recorded from Teilia.

Cycadopsida

Two small fragments of *Neuropteris antecedens* were described by Walton (1931) and Crookall (1959), and are the oldest evidence of the cycadopsid order Trigonocarpales (Medullosales of some authors) in the fossil record. This pteridosperm order is of considerable interest, being one of the major components of Late Carboniferous and Early Permian equatorial vegetation. It is also of some evolutionary interest, as it is thought to have been ancestral to the extant group, the cycads. The Teilia specimens are too small to confirm the trigonocarpalean affinities of this species, but the more complete material from the former Czechoslovakia figured by Stur (1875) has a distinctly trigonocarpalean aspect. Also of interest is that the Teilia frond fragments are associated with the seeds *Holcospermum ellipsoideum*, which look remarkably like the trigonocarpalean seeds found in the Upper Carboniferous; a similar association has been reported from slightly younger strata in France by Bureau (1913–1914).

General remarks

Teilia Quarry is the only known locality to yield this distinctive assemblage of plant fossils from the Gronant Group. Many of the other assemblages of similar age, such as from south-east Spain (Jongmans, 1956) and the Loire (Bureau, 1913–1914) are dominated by lycopsids and are thus quite different. More comparable is the assemblage from the Posidonienschiefer of Moravia (Stur, 1875; Oberste-Brink, 1913; Patteisky, 1929; Hartung and Patteisky, 1960). In Britain, the closest

Figure 5.42 *Adiantites machanekii* Stur. Almost complete pteridosperm frond; Natural History Museum, specimen V.2755. Gronant Group (Brigantian), Teilia Quarry. x 0.75. (Photo: Photographic Studio, Natural History Museum, London.)

comparison is found in the upper Oil Shale Group of Scotland, such as at Wardie Shore (see below). There are, however, several of the Teilia species which have not been reported from any of these other areas or localities, including *Rhacopteris circularis*, *Diplopteridium teilianum* and *Sphenopteridium capillare*; also, the Welsh assemblage does not appear to contain certain elements which characterize many other upper Visean assemblages, such as *Archaeopteridium* and *Fryopteris*. Whether this reflects the lagoonal setting for the Gronant Group or some other palaeoecological factor, or is merely a function of collecting and/or taxonomic bias, is as yet unclear.

Conclusion

Teilia Quarry is one of the best known sites in Britain for plant fossils from the Lower Carboniferous, about 330 million years old, and has been studied now for over a century. It is particularly well-known for a type of leaf known as *Rhacopteris*, which occurs very commonly in fossil floras of this age. The Teilia material shows an unusually wide range of shapes of these leaves, as well as including one of only two known specimens bearing reproductive organs. The fossil flora here is also very rich in early seed plant remains, including a number of complete fronds, and several types of fructification. Of especial interest are fragments of the frond known as *Neuropteris*. These are the oldest known remains of an order of plants known as the Trigonocarpales, which later in the Carboniferous and Early Permian became very common in the tropical forests, and which is thought to be ancestral to the living group, the cycads. It is also possibly ancestral to the Bennettitales, a group of plants that became important in the later Mesozoic vegetation, and which may be ancestral to the flowering plants. The only other similar fossil flora has been found in Moravia. Other assemblages of the same age tend either to be dominated by lycopsids ('club-mosses'), such as those found in Spain and France, or, as in the Scottish assemblages, to contain quite different species of seed plants.

WARDIE SHORE

Highlights

Wardie Shore is the best available site for plant fossils from the Visean Wardie Shales (Figure 5.43). It is the type locality for the lycopsid stem *Bothrodendron wardiense* Crookall and the equisete strobilus *Pothocites grantoni* Paterson.

Introduction

Records of Visean plant fossils from this shoreline Oil Shale exposure east of Granton Harbour, on the Firth of Forth (NT 245771), date back to the mid-nineteenth century, the earliest being that of Paterson (1841). Subsequent records include those by Kidston (1883b, c, 1889b, c), but the most comprehensive accounts of the fossils are in the monographs by Kidston (1923b, 1924) and Crookall (1964, 1969). There has been no recent work on the palaeobotany of this site.

Description

Stratigraphy

The geology of this site is described by Peach and Horne (1910). The exposed sequence (Figure 5.44) belongs to the Wardie Shales Formation in the Lower Oil Shale Group. According to Carruthers (1927), these shales were probably laid down under alternating lagoonal and estuarine conditions. Scott (1985) regards them as probably late Holkerian in age.

Palaeobotany

The plant fossils found here are mainly compressions, which are readily separated from the matrix. Their appearance suggests that cuticles should be preserved but, in practice, they have proved impossible to separate from the bituminous carbonized tissue (C.H. Shute, pers. comm., 1989). The following species have been described to date:

Lycopsida:
Lepidodendron veltheimianum Sternberg
Bothrodendron wardiense Crookall

Equisetopsida:
Archaeocalamites radiatus (Brongniart) Stur
Pothocites grantoni Paterson

Lagenostomopsida:
Sphenopteris affine Lindley and Hutton
Spathulopteris dunsii Kidston

Figure 5.43 Wardie Shore. Foreshore exposures of the upper Holkerian Wardie Shales Formation. (Photo: C.J. Cleal.)

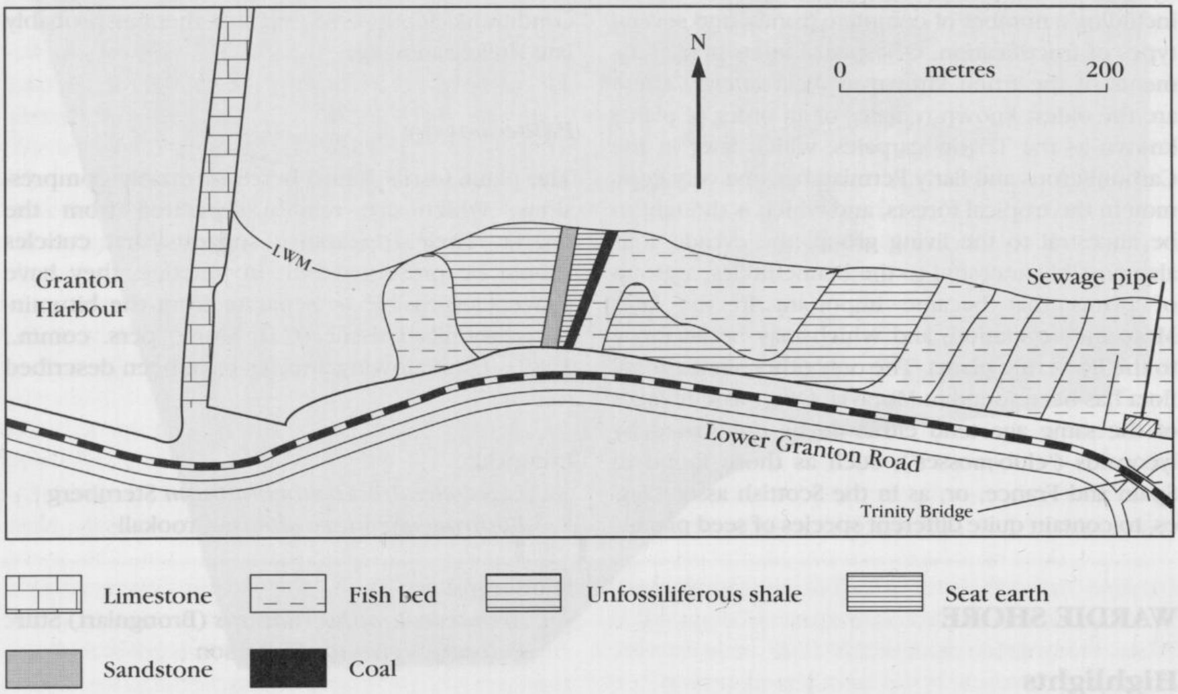

Figure 5.44 Map showing the main lithologies exposed at Wardie Shore. Based on McAdam and Clarkson (1986, Map 7).

Interpretation

Crookall (1964, pl. 64, fig. 1, pl. 71, fig. 1) shows a large specimen of *Lepidodendron veltheimianum* with a row of so-called 'ulodendroid-scars'. Such scars are thought to be the result of branch abscission, and occur commonly in many arborescent lycopsids (Jonker, 1976). A similar specimen from the Burdiehouse Limestone, identified by Carruthers (1870) as *Ulodendron ovale* Carruthers, was transferred to *L. veltheimianum* by Kidston (1885b). *Ulodendron* has been used by many authors as an artificial form-genus for lycopsid axes with such abscission scars; Thomas (1967b) has shown that it in fact represents leafy lycopsid twigs with a distinctive epidermal structure.

This is the only known locality for another species of lycopsid stem, *Bothrodendron wardiense*. It was originally described by Kidston (1889b, c) as *Bothrodendron wiikianum* Heer, but he later recognized that the ligule pit aperture is more distantly placed above the leaf scar (see also Crookall (1964) and Thomas (1980)). Although he proposed an alternative name in manuscript, it was not validly published until after his death, by Crookall (1932). According to Thomas (1980), *Bothrodendron* differs from *Eskdalia*, another lycopsid stem frequently found in the Visean of Britain, in having a clearly marked parichnos mark in the leaf scar; and the Wardie Shore specimen indeed seems to show such a mark. Thomas also notes differences in the epidermal structure, but such information is unavailable at present for *B. wardiense*.

This is also the type locality for the equisete strobilus *Pothocites grantoni* (Paterson, 1841; Kidston, 1883b, c). Unfortunately, however, the type specimens are reported by Chaphekar (1965) as lost, and her re-assessment of the species had therefore to be based on material from Loch Humphrey Burn and Glencartholm (both sites discussed elsewhere in this chapter). Stur (1875) reported similar strobili attached to *Archaeocalamites* stems (see also Chaphekar, 1963), and so it is not surprising to find this type of stem associated with *Pothocites* at Wardie Shore.

Spathulopteris dunsii has only been reported to date from the Oil Shale Group of Scotland (Kidston, 1923b). Kidston lists it as occurring at Wardie Shore, but no specimens from here were illustrated. It is similar to another spathulopterid from the Oil Shale Group of Scotland, *S. decomposita* Kidston, 1923b, but the latter has more closely spaced pinnae and larger pinnules. Clearly, however, it is possible that they are just small and large fronds of a single biological species. The affinities of *Spathulopteris* are at present unproved, but may be with the Calamopityales, one of the two main orders of seed plants found in the Lower Carboniferous.

Kidston (1924) figured a number of specimens of the lagenostomalean frond *Sphenopteris affine* from the Oil Shale Group of Scotland. He mentions Wardie Shore as one of the many sites to yield the species, although none of the figured specimens originated from here. Kidston assigned the species to the form-genus *Telangium*, since he was able to show that the fronds bore *Telangium* fructifications. However, such fructifications are only rarely found attached to such fronds, and it is unwise to use a fructification form-genus for fronds which are normally found in a sterile condition (compare comments by Cleal, 1986b on the combination of form-genera representing different organs of a plant). Since *S. affine* has an essentially similar frond architecture and bore the same fructifications as the type-species of *Sphenopteris* (*Sphenopteris elegans* (Brongniart) Sternberg; synonym *Diplothmema adiantoides* (Schlotheim) Gothan – see Kidston, 1923c), it is best if it is retained in that form-genus.

The Oil Shale Group of Scotland has yielded some of the best preserved Visean plant compressions in Britain. The Burdiehouse Limestone was for many years one of the best stratigraphical horizons for such fossils (e.g. Lindley and Hutton, 1831–37; Miller, 1857), but there are now no suitable exposures of this bed. The oil shales themselves, however, particularly the Wardie Shales, have also produced some remarkably well-preserved specimens. When the matrix dries, the fossil sometimes peels off more or less intact (Kidston, 1923b, c, 1924), and almost has the appearance of a compressed piece of modern plant, albeit blackened (some excellent examples of such isolated fossils are figured by Kidston, 1924, pl. 101 figs 7–10). Plant fossils have been recorded from a number of exposures of the Wardie Shales in Edinburgh and environs, in particular Hailes Quarry and at a number of localities along the Water of Leith (Kidston, 1923a, 1925), but only Wardie Shore now still yields them. The site has only so far yielded the limited assemblage listed above, but this may just reflect the limited amount of collecting that has been done here, especially in recent years. Kidston also lists from other nearby exposures of the Wardie Shales the following taxa, which may also eventually prove to be present at Wardie Shore:

Sphenopteris cuneolata Lindley and Hutton
Sphenopteridium pachyrrachis (Göppert) Potonié
S. crassum (Lindley and Hutton) Kidston
S. speciosum Kidston
Spathulopteris obovata (Lindley and Hutton) Kidston
S. decomposita Kidston
Rhacopteris lindsaeformis (Bunbury) Kidston
R. inaequilaterata (Göppert) Stur
R. geikiei Kidston
Schuetzia bennieana Kidston

Similar British assemblages to that found in the Wardie Shales have been reported from Glencartholm and to a lesser extent Teilia Quarry (see comments elsewhere in this chapter on these sites for details of the comparison). Outside Britain, comparable assemblages are known from Upper Silesia (Patteisky, 1929; Hartung and Patteisky, 1960). Most other Visean assemblages from Europe differ from that of the Wardie Shales in both overall balance and species composition (Hirmer, 1939; Vakhrameev *et al.*, 1978). In particular, the Wardie assemblage has a much higher proportion of lycopsids and equisetes, suggesting a wetter, more swampy environment. According to Raymond and Parrish (1985), a rain-shadow caused by newly formed mountains to the west resulted in much of western Europe having a relatively dry climate during the Early Carboniferous. However, the Scottish sites such as Wardie seem to have avoided its influence, perhaps due to local topographic factors.

Conclusion

Wardie Shore is the only site that still yields abundant plant fossils from the Scottish Oil Shale Group, about 335 million years old. These shales were once a famous source of plant fossils. However, as the shales are no longer a commercial hydrocarbon source, there are now no quarries or mines from which the fossils can be collected. This particular site has yielded a number of club-mosses and early seed plants. One of its main interests, though, is as the type locality for a cone known as *Pothocites grantoni*, which is now known to be an early type of horsetail fructification, and has proved important for establishing the early evolutionary history of this extant class of plants. The general balance of the assemblage, with its predominance of club-mosses and horsetails, suggests a much wetter environment than is represented by the vegetation of this age found elsewhere in Europe.

GLENCARTHOLM

Highlights

Glencartholm has yielded one of the best examples of a *Neuropteris antecedens* Zone fossil flora from Britain. Many of the species found here are widely distributed, but there are a number for which this is the only or best locality, such as *Rhacopteris geikiei*, *Sphenopteridium macconochiei* and *Rhodeopteridium machanekii*. Glencartholm has provided particularly fine examples of *Spathulopteris*. It is a site of considerable palaeobotanical significance.

Introduction

Lower Carboniferous rocks in the bed of River Esk, about 4 km north-west of Canonbie, Dumfries and Galloway (NY 377795), are best known as a site for fish and crustacean fossils. However, they have also yielded a diverse plant fossil assemblage. They were first discovered in 1876 by A. Macconochie, during the mapping of the area by the Geological Survey. Kidston (1883a) made a preliminary report on the assemblage (see also Kidston, 1886), and later published a systematic account (Kidston, 1903b). Specimens from here were extensively used in the Geological Survey monographs on Carboniferous plant fossils (Kidston, 1923–1925; Crookall, 1955–1975). In addition, there have been accounts of individual taxa from here, including *Pothocites* (Kidston, 1882, 1883b, c; Chaphekar, 1965), *Eskdalia* (Thomas, 1968) and *Lycopodites* (Kidston, 1901b). Thomas's *Eskdalia* study is particularly important since it shows that cuticles are preserved in at least some of the Glencartholm fossils.

Description

Stratigraphy

The plant fossils occur in the Glencartholm Volcanic Group, a sequence of tuffs, shales and sandstones near the base of the Upper Border Group (Lumsden *et al.*, 1967). They are interpreted as shallow marine or lagoonal deposits, which were subject to periodic burial from volcanic outfall. Foraminifera from the sequence suggest a position near the Holkerian–Asbian boundary (George *et al.*, 1976).

Palaeobotany

The following taxa have been reported to date:

Algae (divisions unknown):
- *Bythotrepis acicularis* (Göppert) Kidston
- *B. plumosa* Kidston
- *B. simplex* Kidston
- *B. scotica* Kidston

Lycopsida:
- *Eskdalia minuta* Kidston
- *Lepidodendron veltheimianum* Sternberg
- *Lepidostrobus ornatus* Brongniart
- *Lepidostrobophyllum lanceolatum* (Lindley and Hutton) Bell
- *Stigmaria ficoides* (Sternberg) Brongniart
- *L. fimbriatum* (Kidston) Allen
- *Lycopodites stockii* Kidston

Equisetopsida:
- *Archaeocalamites radiatus* (Brongniart) Stur
- *Pothocites grantoni* Paterson

Filicopsida(?):
- *Rhodeopteridium machanekii* (Ettingshausen) Purkyňová

Progymnospermopsida(?):
- *Rhacopteris lindsaeformis* (Bunbury) Kidston
- *R. geikiei* Kidston

Lagenostomopsida:
- *Sphenopteris bifida* Lindley and Hutton
- *Sphenopteridium pachyrrachis* (Göppert) Schimper
- *S. macconochiei* Kidston
- ?*S. crassum* (Lindley and Hutton) Kidston
- *Spathulopteris obovata* (Lindley and Hutton) Kidston
- *S. decomposita* Kidston
- *Cardiopteridium nanum* (Eichwald) Walton
- *Carpolithes* sp.

Interpretation

Algae

Kidston (1883a, 1903b) described a variety of enigmatic fossils from here, which he interpreted as algal remains. He assigned them to four species of the 'artificial' form-genus *Bythotrepis*, but could draw no conclusions about their affinities.

Lycopsida

These are relatively rare at Glencartholm, but the most abundant are the stems *Lepidodendron veltheimianum* and rooting structures *Stigmaria ficoides*. In association are strobili described (Kidston, 1903b) as *Lepidostrobus variabilis* Lindley and Hutton, but which Crookall (1966) later transferred to *Lepidostrobus ornatus* (it should be noted that this is a true *Lepidostrobus* as interpreted by Brack-Hanes and Thomas (1983), i.e. a microsporangiate strobilus). Most *Lepidodendron* species, however, are thought to have borne *Flemingites* strobili, and so there must be some doubt as to whether *L. ornatus* was attached to *L. veltheimianum*.

A second lycopsid plant represented at Glencartholm had stems belonging to the form-genus *Eskdalia*. Kidston (1883a, 1903b) interpreted it as a fern stem, but Thomas (1968) demonstrated that it was a ligulate lycopsid (see also Chaloner *in* Boureau *et al.*, 1967; Thomas and Meyen, 1984; Rowe, 1988c). A key aspect of Thomas's study was the preparation of cuticles, which yielded evidence of the ligule, stem stomata and 'resistant excrescences'. However, no evidence of a parichnos was found. It appears to be a wide-ranging form-genus, having been reported from Puddlebrook (see above), and from several localities in Siberia (Thomas and Meyen, 1984). It is also very similar to the '*Lepidodendron*' *perforatum* Lacey, 1962 from North Wales (Rowe, 1988c). Nevertheless, Glencartholm remains one of the most important localities for this form-genus.

There seems to be a consistent association between *Eskdalia* and the isolated sporophylls *Lepidostrobophyllum fimbriatum* (cf. also Puddlebrook Quarry – see above). However, the only species of *Eskdalia* to which strobili have been found attached have sporophylls of a different type (*E. variabilis* (Lele and Walton) Rowe, 1988c). This problem has been discussed under Puddlebrook Quarry (p. 169).

A poorly preserved specimen of an herbaceous lycopsid was described by Kidston (1884, 1901b) as *Lycopodites stockii*. It shows a leafy shoot with sporangia arranged both in a terminal strobilus and amongst the leaves. Bower (1908) argued that this arrangement of sporangia points to it belonging to the subsection *Phlegmaria*, in the classification established for extant species. It is one of the earliest known examples of a fossilized lycopodiacean with fructifications preserved.

Equisetopsida

The equisetes are represented here by the ubiquitous (in the Lower Carboniferous) *Archaeocalamites radiatus*. Strobili found in close association were identified by Kidston (1882) as *Pothocites calamopsoides* Kidston (Figure 5.45), but he later recognized that they were indistinguishable from *P. grantoni* (Kidston, 1883b, c).

Filicopsida(?)

Glencartholm is the best known locality for *Rhodeopteridium machanekii*. It has yielded several large specimens, showing the distinctive large, deeply incised pinnules. Relatively little is known of the branching architecture or pinnule variation in these fern-like plants, and so large specimens such as those found here have considerable significance.

Progymnospermopsida(?)

The commonest type of foliage which probably belongs to this group is *Rhacopteris lindsaeformis*. Kidston (1903b) initially identified it as *Rhacopteris inaequilaterata* (Göppert) Stur. However, he later revised this identification (Kidston, 1923c), although he still listed Glencartholm as a locality yielding *R. inaequilaterata*; this was probably just a clerical error.

Glencartholm is the type and best known locality for a second species of ?progymnosperm foliage, *R. geikiei*. It has very distinctive pinnules, which are deeply incised with slender lobes, but not markedly asymmetrical, as in most other deeply incised rhacopterid species.

Lagenostomopsida

The most abundant pteridosperm fossils found here to date are fronds. The most abundant belong to the Lagenostomales. Three species of *Sphenopteridium* have been recorded. *S. pachyrrachis* is by far the most common (Figure 5.46). ?*S. crassum* has never been illustrated, but there must be a strong possibility that the ?*S. crassum* is merely a small form of *S. pachyrrachis*. The third, *S. macconochiei*, is only known from Glencartholm. Details of the venation and rachis ornamentation appear to support its inclusion in *Sphenopteridium*, but, compared with the other known species of the genus, it has more robust, subrhomboidal, entire-margined pinnules.

Kidston (1924) figured a fructification from here as *Sphenopteris bifida*, but details of the

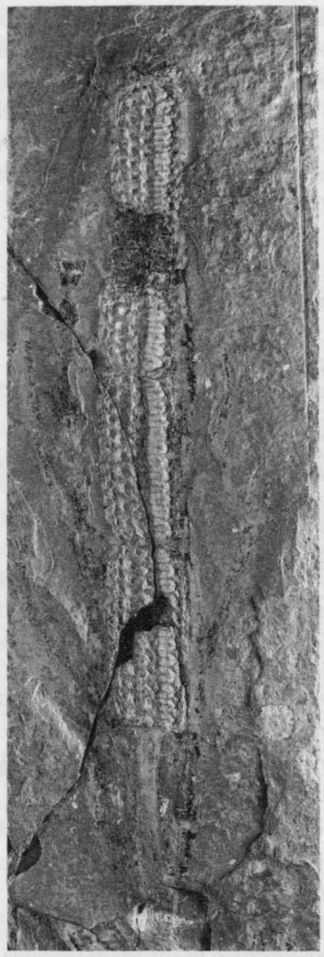

Figure 5.45 *Pothocites grantoni* Paterson. Cone of archaeocalamitid equisetopsid; Natural History Museum, London, specimen V.195. Glencartholm Volcanic Group (Holkerian–Asbian), Glencartholm. × 1. (Photo: Photographic Studio, Natural History Museum, London.)

Figure 5.46 *Sphenopteridium pachyrrachis* (Göppert) Schimper. Almost complete pteridosperm frond; Natural History Museum, London, specimen V.186. Glencartholm Volcanic Group (Holkerian–Asbian), Glencartholm. x 1. (Photo: Photographic Studio, Natural History Museum, London.)

sterile part of the frond were not given to support the identification.

A number of relatively large portions of *Spathulopteris* fronds has been illustrated from here (Kidston, 1924). Neither of the recorded species (*S. obovata* and *S. decomposita*) is rare or particularly distinctive. Nevertheless, the Glencartholm material is of interest as providing some of the best examples of this form-genus to be recorded in the literature. Fructifications or stem/rachis anatomy are unknown, but the fronds are believed to belong to the Calamopityales (see discussion on Loch Humphrey Burn, above).

Two small specimens of *Cardiopteridium nanum* have been found here. The taxonomy of this species has had a complex history (Walton, 1941), but it is now generally assumed that a range of species names used in the past in fact just reflects a marked degree of infra-specific variation in this taxon. Walton retained a distinction at the rank of forma between the large and small types of pinnules, but this seems to be an artificial division of doubtful utility.

General remarks

The occurrence together at Glencartholm of *Spathulopteris* and *Cardiopteridum* clearly indicates that the assemblage belongs to the lower part of the *Neuropteris antecedens* Zone (*Diplopteridium* Subzone) of Cleal (1991). There is some comparison with the Wardie Shales assemblage (p. 181), which has a number of species in common, such as *Rhacopteris lindsaeformis*, *Pothocites grantoni* and *Lepidodendron veltheimianum*. The Wardie assemblage, however, has a higher proportion of lycopsids. There are also differences in the pteridosperm composition, such as the presence at Wardie of *Sphenopteris affinis* instead of the closely related *S. bifida*. Also comparable among the British Visean assemblages is that from Teilia Quarry (p. 175), but the similarity here seems to be mainly at the rank of form-genus, the only species in common being *Archaeocalamites radiatus* and *Sphenopteridium pachyrrachis*.

Outside of Britain, the nearest comparison is with assemblages reported from the Pollak Stollen Formation of Upper Silesia (Patteisky, 1929; Hartung and Patteisky, 1960), which includes among others *Lepidodendron velthiemianum*, *Rhodeopteridium machanekii* and *Sphenopteridium pachyrrachis*. However, most of the other Lower Carboniferous assemblages from central Europe differ markedly from that found at Glencartholm, both in overall balance and in species composition (for reviews of these assemblages see Hirmer, 1939 and Vakhrameev *et al.*, 1978). The reason for these differences has not been properly investigated, and it is not clear whether it reflects palaeoecological or biostratigraphical variation, or even just taxonomic and/or collecting bias. However, as one of the best documented fossil floras of the Upper Visean of Europe, Glencartholm will clearly play a central role in unravelling the patterns of vegetational distribution within the palaeoequatorial belt.

Conclusion

Glencartholm has yielded one of the best documented fossil floras from the upper part of the Lower Carboniferous of Britain, representing vegetation growing some 330 million years ago. Only two species have been found here, the possible fern *Rhodeopteridium machanekii* and the seed plant *Sphenopteridium macconochiei*. It has also yielded some exceptionally complete examples of leaves of the ?progymnosperm (i.e. probably belonging to the immediate ancestors of seed plants) *Rhacopteris*, and of the early seed plant *Spathulopteris*, which have proved important for understanding the affinities of these plants. The club-mosses here include a small, leafy form (*Lycopodites*) very similar to the living *Lycopodium*. In contrast to many other fossil floras of this age from northern Britain, however, club-mosses are relatively rare and probably represent vegetation growing in drier habitats. A much closer comparison can be made with fossil floras found in continental Europe, in particular from Upper Silesia (Poland).

VICTORIA PARK

Highlights

Victoria Park has the best known examples of *in situ* stumps of arborescent lycopsids in the Lower Carboniferous, providing a unique insight into the forests which were starting to dominate the palaeoequatorial regions at that time (Figure 5.47).

Figure 5.47 Victoria Park. *In situ* fossilized tree stumps in the Limestone Coal Group (lower Pendleian). (Photo: B.A. Thomas.)

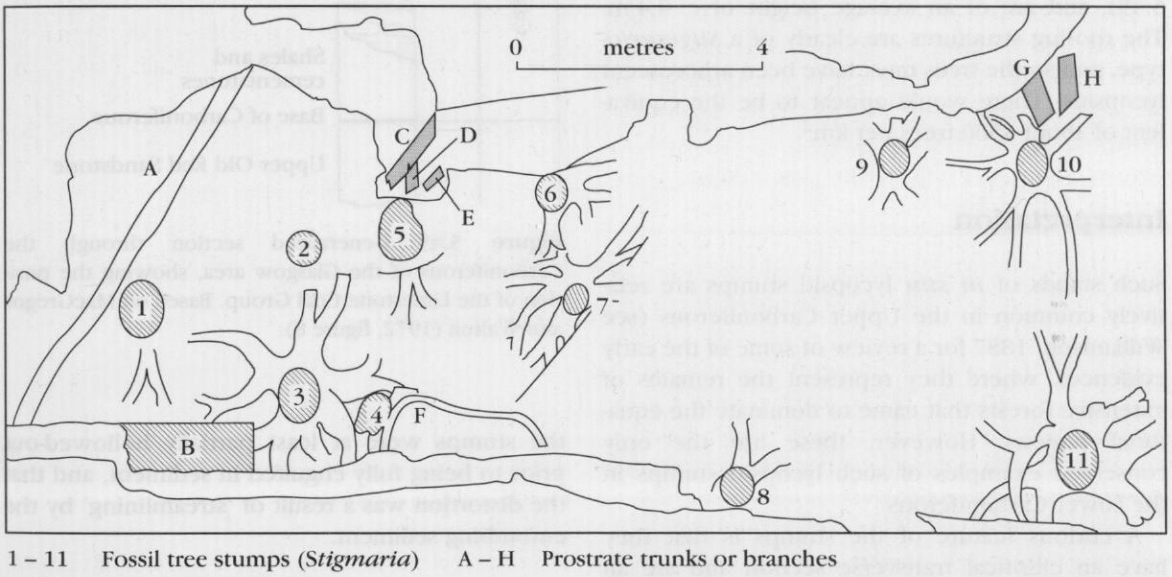

Figure 5.48 Plan of the Fossil Grove at Victoria Park, showing distribution of *in situ* lycopsid stumps. Based on MacGregor and Walton (1972, figure 1).

Introduction

This famous locality is under a covered enclosure in Victoria Park, Glasgow (NS 541673), and shows a cluster of *in situ* Namurian lycopsid stumps, sometimes called the 'Fossil Grove' (Figure 5.48). In addition to its palaeobotanical interest, it is significant as one of the earliest examples of a conserved earth science site (Black, 1988). The stumps were discovered in 1887 (Kidston, 1888), but were not described in detail until MacGregor and Walton (1948, 1972; see also Mclean, 1973; Lawson and Lawson, 1976). The most comprehensive account to date is by Gastaldo (1986).

Description

Stratigraphy

The stumps lie within the Limestone Coal Group, of early Pendleian age (Figure 5.49). They are rooted in a silty mudstone, which Gastaldo (1986) interpreted as a palaeosol, and the aerial parts were originally entombed in sandstones, which were probably crevasse-splay deposits.

Palaeobotany

Eleven stumps are preserved *in situ* here (Figure 5.49), and are of an average height of *c.* 0.4 m. The rooting structures are clearly of a *Stigmaria*-type, and so the trees must have been arborescent lycopsids. There would appear to be the equivalent of about 4500 trees per km^2.

Interpretation

Such stands of *in situ* lycopsid stumps are relatively common in the Upper Carboniferous (see Williamson, 1887 for a review of some of the early evidence), where they represent the remains of extensive forests that came to dominate the equatorial regions. However, these are the only conserved examples of such lycopsid stumps in the Lower Carboniferous.

A curious feature of the stumps is that they have an elliptical transverse section and are all aligned in about the same direction. MacGregor and Walton (1972) interpreted this as due to tectonic distortion, but Gastaldo (1986) has pointed out that there is little other evidence of tectonic deformation here. Instead, Gastaldo argued that the stumps were at least partially hollowed-out prior to being fully engulfed in sediment, and that the distortion was a result of 'streamlining' by the entombing sediment.

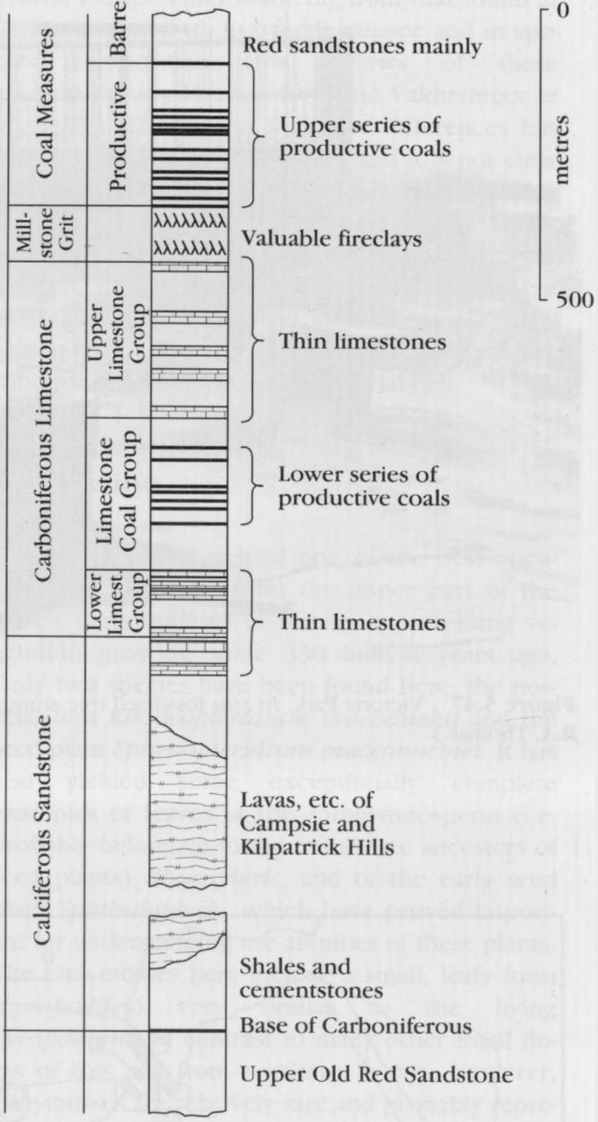

Figure 5.49 Generalized section through the Carboniferous of the Glasgow area, showing the position of the Limestone Coal Group. Based on MacGregor and Walton (1972, figure 8).

Conclusion

Victoria Park has the only preserved examples of *in situ* stumps of giant club-mosses in the Lower

Carboniferous, some 325 million years old. They allow us to estimate the tree density in the forests growing at this time in Britain as about 4500 per km^2. Most localities containing plant fossils only yield fragments of stems, leaves or reproductive organs, that were washed from the site where they grew. This makes localities such as Victoria Park all the more remarkable.