Palaeozoic Palaeobotany of Great Britain

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

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Chapter 4

Devonian

During the Devonian, there was a dramatic change in terrestrial vegetation. From the humble stock of rhyniophytes, rhyniophytoids and primitive lycopsids in the Silurian, there was a rapid radiation of plant groups, as vegetation evolved to fill the newly-available, terrestrial ecological niches (Figure 4.1). This new plant cover included the first appearance of equisetes, 'advanced' lycopsids (e.g. protolepidodendrids), trimerophytes, fern-like plants (e.g. rhacophytids, cladoxylids), progymnosperms and, eventually, fully gymnospermous plants. By the end of the period, all of the major groups of vascular plants except the angiosperms were present. During the period, there was also a number of major morphological innovations in the Plant Kingdom, including laminate foliage, the seed as a means of propagation, and the arborescent habit (Figure 1.1). Together, these phylogenetic and morphological developments provided the spring-board from which the luxuriant Carboniferous floras could develop.

The Devonian plant fossil record is particularly good in Britain, especially in the lower part of the system. The flora found at Rhynie stands pre-eminent, but there are also a number of other key sites in southern Scotland, Wales and the Welsh Borders. As a consequence, British Devonian palaeobotany has played a central role in developing our ideas on early land plant evolution.

PALAEOGEOGRAPHICAL SETTING

During the Devonian, most of Britain was on the south-east margins of Laurussia and thus very near the equator (Figure 4.2). Apart from the marine environments of south-west England, sedimentation was mainly non-marine, in fluvio-deltaic or lacustrine environments (Allen, 1979; Trewin, 1985), and resulted in red-beds of the Old Red Sandstone 'magnafacies' (Erben, 1964). The proximity of Britain to the equator indicates tropical temperatures but the evidence for precipitation rates is equivocal. Clearly, in the upland regions there must have been considerable precipitation, in order to produce large enough rivers to generate the extensive deltas. On the deltas themselves, however, there is little direct sedimentological evidence of precipitation, and there is indication that, at least periodically, the climate was comparatively dry (e.g. the '*Psammosteus* Limestone' in the Welsh Borders – Allen, 1985).

The geographical distribution of Devonian plant fossils has been discussed by Edwards (1973, 1990), Raymond *et al.* (1985), Raymond (1987), Allen and Dineley (1988), and Edwards and Berry (*in* Cleal, 1991). Through much of the Devonian, the general pattern seen in the Silurian continues to be recognizable. Devonian plant fossils have been most widely found in the low palaeolatitudes, particularly in Laurussia (which includes the British localities) and thus represent tropical and subtropical vegetation. Within these low palaeolatitudes, some provincialism can be recognized, such as in northern Gondwana (e.g. Malone, 1968; Tims and Chambers, 1984), Kazakhstania (Yurina, 1969; Senkevich, 1975) and Cathaysia (Li and Cai, 1978; Li and Edwards, 1992).

Northern high palaeolatitudes, as represented in present-day Siberia, had a quite distinctive vegetation throughout the Devonian (Petrosyan, 1968; Stepanov, 1975). However, the plant fossils from here have not been studied to the same extent as those of the low palaeolatitudinal Laurussia, and a detailed comparative analysis will be needed to establish the exact extent of the differences.

Fossils representing the southern high palaeolatitude vegetation occur in South Africa, South America and Antarctica. Their stratigraphically lowest occurrence is in the Middle Devonian (Anderson and Anderson, 1983). In contrast to the low palaeolatitude vegetation, especially of Laurussia, lycopsids such as *Archaeosigillaria* and *Leptophloeum* predominated, and this remained the situation through into the Early Carboniferous.

Edwards (1973) argued that, in the Upper Devonian, plant fossil provincialism is much less extreme, and that most assemblages are dominated by taxa such as *Archaeopteris*, *Cyclostigma* and *Rhacophyton* (see also Edwards and Berry *in* Cleal, 1991). However, the Upper Devonian palaeobotanical record (especially in the Frasnian) is much poorer than that of the Lower and Middle Devonian (Banks, 1980), and this may be the real reason for the apparent reduction in provincialism. That the reduction is artificial is supported by the similarity of the palaeophytogeography of the Middle Devonian and the Lower Carboniferous, suggesting that there was an essential floristic continuity from the Middle Devonian to Early Carboniferous.

There has been disagreement as to the degree of global provincialism in Devonian plant fossil assemblages. Raymond (1987), using statistical techniques, such as polar ordination analysis, claims to recognize considerable differentiation,

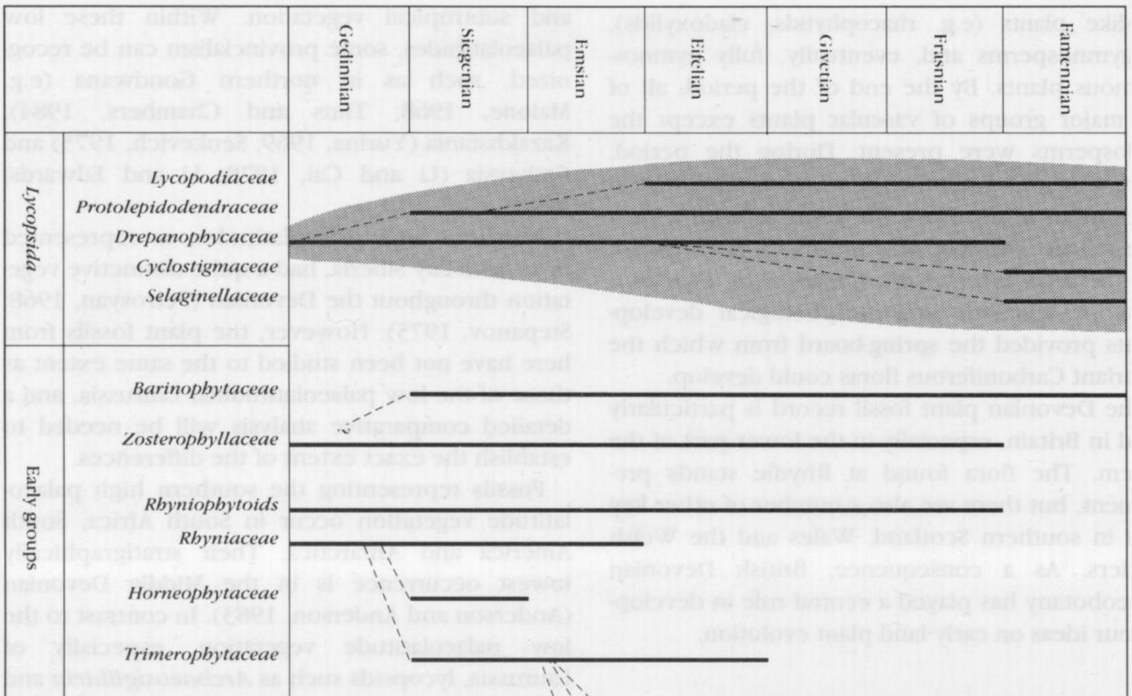

Figure 4.1 The distribution of families of vascular plants in the Devonian. Based on data from Cleal (1993).

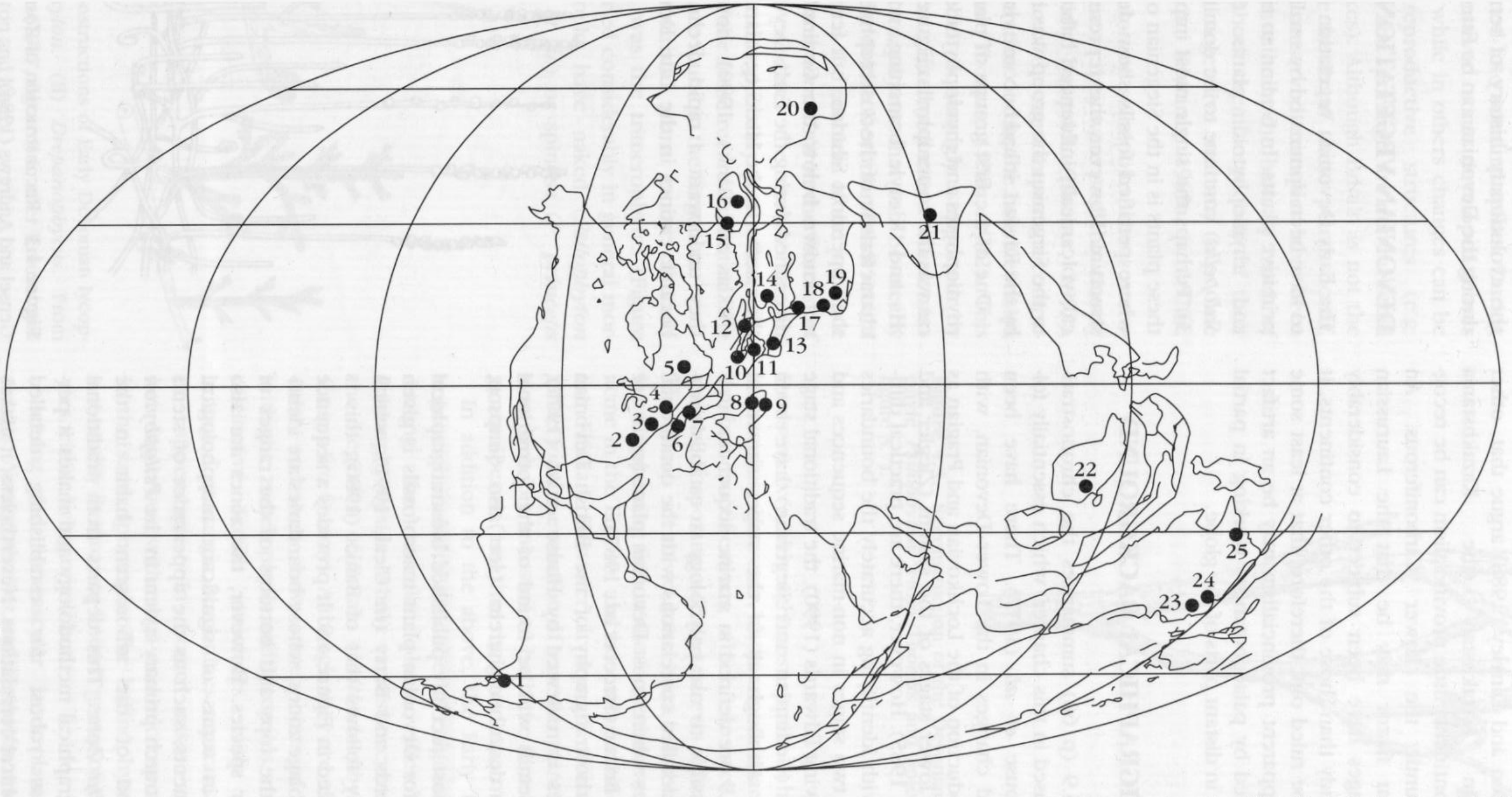

Figure 4.2 The palaeogeography of the Devonian, showing the location of the major fossil floras of this age. 1 – North Argentina; 2 – West Virginia; 3 – Pennsylvania; 4 – Maine; 5 – Quebec; 6 – New York State; 7 – New Brunswick; 8 – Rhineland; 9 – Bohemia; 10 – Ireland; 11 – Wales and the Welsh Borderland; 12 – Scotland; 13 – Belgium; 14 – Norway; 15 – Bear Island; 16 – Spitsbergen; 17 – Poland; 18 – Moldavia; 19 – Ukraine; 20 – Kuzbass; 21 – Kazakhstan; 22 – Yunnan; 23 – Victoria; 24 – New South Wales; 25 – Queensland. Based on Scotese and McKerrow (1990).

especially in the upper Lower Devonian. In contrast, Allen and Dineley (1988) argue that, other than in Kazakhstan (the Kazakhstania Palaeocontinent) little provincialism can be recognized until the Lower Carboniferous. An important factor may be that the Laurussian assemblages have been subject to considerably more study than those of the other continents. It cannot be ruled out, therefore, that at least some of the apparent provincialism may be an artifact introduced by palaeobotanists working in partial isolation in distant parts of the globe.

STRATIGRAPHICAL BACKGROUND

Figure 4.9 (p. 60) summarizes the chronostratigraphy used in this chapter, which essentially follows House *et al.* (1977). There have been proposed changes in the Lower Devonian, with the introduction of the Lochkovian and Pragian as the two lower stages of the system (Ziegler and Klapper, 1985). However, there are practical difficulties with identifying accurately the boundaries of these two stages in non-marine sequences and so, following Edwards (1990), the traditional stage divisions (Gedinnian and Siegenian) have been retained. Although all of the stages shown in Figure 4.9 are defined in marine sequences, it is now possible to use palynology to establish reasonably detailed correlations with the continental sequences where most Devonian plant fossils are found in Britain (Streel *et al.*, 1987).

The lithostratigraphy of the British Devonian sequences is reviewed by House *et al.* (1977), where details will be found of the formational intervals described herein (see also Simpson, 1959).

The most recently published biostratigraphical scheme for Devonian plant macrofossils is given by Edwards and Berry (*in* Cleal, 1991), which essentially follows that of Banks (1980); this is summarized in Figure 4.9. It provides a sequence of assemblage zones, whose boundaries are identified by the tops and bottoms of the ranges of particular species. However, the zones are also defined in terms of significant morphological developments, such as the appearance of stems with centrarch primary xylem in the *Psilophyton* Zone and of the arborescent habit in the *Svalbardia* Zone. This departs from traditional biostratigraphical methodology and makes it perhaps less robust for establishing detailed stratigraphical correlations. Nevertheless, it makes it a particularly useful framework around which the evolutionary history of terrestrial vegetation during the Devonian can be fitted.

DEVONIAN VEGETATION

The Early Devonian vegetation of Britain appears to have been dominated by small, morphologically primitive plants. In Gedinnian times, rhyniophyte and rhyniophytoid plants (e.g. *Cooksonia*, *Salopella*) continue to be dominant (see Chapter 3). Perhaps the single most important locality for these plants is in the Siegenian of Britain (Rhynie), where petrified fossils show details of their cell structure. However, this represents a rather atypical, volcanically-influenced habitat and elsewhere in the Siegenian the group was in serious decline; by the Emsian, it had become virtually extinct.

One of the first groups of plants to replace the rhyniophytes and rhyniophytoids in the British floras was the zosterophylls (Figure 4.3). Evidence of 'H'- and 'K'-style branching, widely regarded as characteristic of the zosterophylls, is known from the uppermost Silurian, but fertile specimens are not known below the Gedinnian. They rapidly diversified during the Early Devonian and reached their acme in the late Siegenian and early Emsian (Niklas and Banks, 1990); however, soon after they underwent a rapid decline and eventually became extinct in the Late Devonian. The early

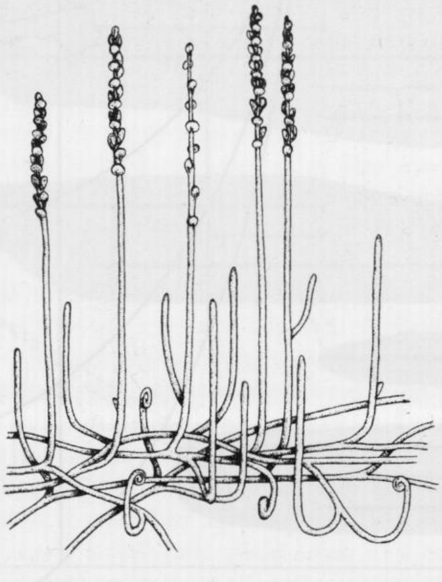

Figure 4.3 Reconstruction of *Zosterophyllum*. From Gensel and Andrews (1984).

forms (e.g. *Zosterophyllum*) had naked axes with sporangia aggregated into terminal spikes. During the Siegenian, however, some developed leaves (e.g. *Sawdonia*), while in others changes can be seen in the reproductive structures (e.g. *Gosslingia*, where the sporangia are not clustered into terminal spikes). Although Britain is not the only place where fossils of these plants occur, some of the best preserved examples have been found here and have been the basis of much of what we know about them, especially of their reproductive and vegetative anatomy (e.g. Lele and Walton, 1962a; Edwards, 1969a, b, 1970a, 1972, 1975).

From an evolutionary standpoint, the zosterophylls are important as they were probably closely related to the early lycopsids (Hueber, 1992), which became one of the most important components of land vegetation during the Late Devonian and Carboniferous (Thomas, 1978a, 1992). This phylogenetic model is strongly supported by the sequence of intermediaries *Sawdonia–Asteroxylon–Drepanophycus* that can be clearly demonstrated in the British Devonian fossil record (Figure 4.4). There is the problem of the presence of the lycopsid *Baragwanathia* in the Silurian of Australia, which pre-dates the earliest known zosterophylls, but this probably just reflects the incompleteness of the fossil record. In Britain, the earliest lycopsids are found in the Siegenian.

Another characteristic plant group of Early Devonian Britain was the trimerophytes (Figure 4.5). The taxa varied considerably in general morphology, and could have naked (*Psilophyton dawsonii* Banks *et al.*) or spinose (*P. princeps* Dawson) axes, although most appear to have been herbaceous. However, they are all characterized by their fructifications, which consisted of loose trusses of sporangia (e.g. Andrews *et al.*, 1977). The group seems to have been relatively short-lived, appearing first in the Siegenian, reaching its acme in the Emsian, and becoming extinct during the Eifelian. However, it was of critical importance for the evolution of vascular plants, since it was probably ancestral to both the ferns and progymnosperms (and thus the gymnosperms).

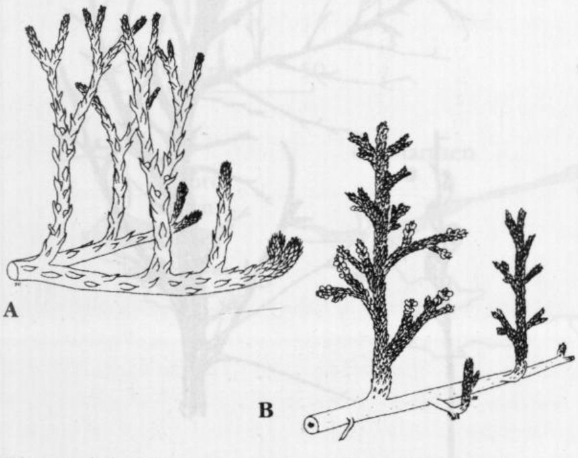

Figure 4.4 Reconstructions of Early Devonian lycopsids. (A) *Asteroxylon*. (B) *Drepanophycus*. From Thomas and Spicer (1987, figure 3.6; after Kräusel and Weyland, and Kidston and Lang).

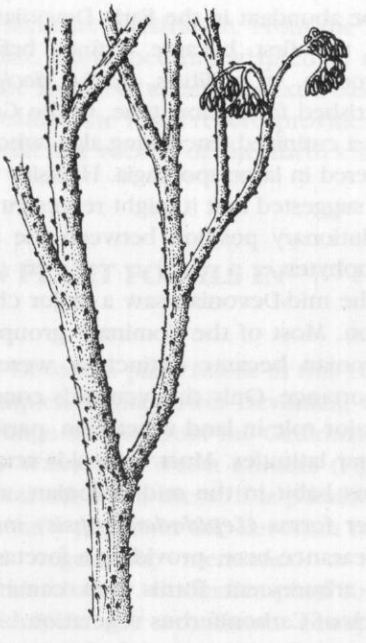

Figure 4.5 Reconstruction of the Devonian trimerophyte *Psilophyton*. From Thomas and Spicer (1987, figure 3.7).

In addition to the above, the Early Devonian vegetation included a number of enigmatic plants. Among the vascular plants, there is the Barinophytopsida, whose earliest occurrence is in the Siegenian of Britain (*Krithodeophyton* from Craig-y-Fro Quarry). Although they are clearly vascular, and even show some points of similarity with the zosterophylls and lycopsids, many have distinctive fertile structures with pinnately arranged sporangia, sometimes separated by sterile appendages. In some cases they are heterosporous, with mega- and microspores borne in the same sporangia. The barinophytopsids do not readily fit into any known group of pteridophytes, either living or extinct.

Among the non-vascular land plants, *Prototaxites*, *Nematothallus* and *Pachytheca* continued to be abundant in the Early Devonian, although all but the first became extinct before the mid-Devonian. In addition, *Parka decipiens* Fleming flourished for a short time, in the Gedinnian. This was a cutinized, encrusting alga, whose thallus was covered in large sporangia. Hemsley (1989, 1990a) has suggested that it might represent an immediate evolutionary position between the algae and the bryophytes.

The mid-Devonian saw a major change in vegetation. Most of the dominant groups of the Early Devonian became extinct or were declining in importance. Only the lycopsids continued to play a major role in land vegetation, particularly in the higher latitudes. Most lycopsids retained a herbaceous habit in the mid-Devonian, although some larger forms (*Lepidodendropsis*) made their first appearance here, providing a foretaste of some of the arborescent forms that came to dominate much of Carboniferous vegetation.

The characteristic rhyniophyte/zosterophyll/trimerophyte complex of the Early Devonian was gradually replaced in mid-Devonian times by early, fern-like plants and progymnosperms (Figure 4.1). Both groups probably evolved from the trimerophytes. The fern-like plants include representatives of the Cladoxylales, Iridopteridales and Coenopteridales, and can be recognized to be allied with the ferns mainly on the basis of their stem anatomies (Scheckler, 1974). However, they were quite different in outward appearance from recent ferns, most noticeably in not having laminate fronds. The foliage instead consisted of three-dimensionally branching systems of terete axes, which would often bear terminal trusses of sporangia. All known forms were herbaceous, although some could be up to one metre or more high (e.g. *Pseudosporochnus*, Figure 4.6).

The earliest and most primitive progymnosperms are found in Britain (*Protopteridium*, Figure 4.7). Like their presumed ancestors, the trimerophytes, these early progymnosperms did not have fully laminate foliage, and are distinguished mainly by the presence of secondary wood in the stems, and the greater complexity of the protoxylem (Beck, 1976). The first of these features is of great significance, as it allowed the evolution of the arboreal habit and thus of forest habitats. The size of these earliest progymnosperms is still a matter of conjecture, although they were probably at least several metres high.

The Late Devonian saw the extinction of the typical Early Devonian forms, while the lycopsids,

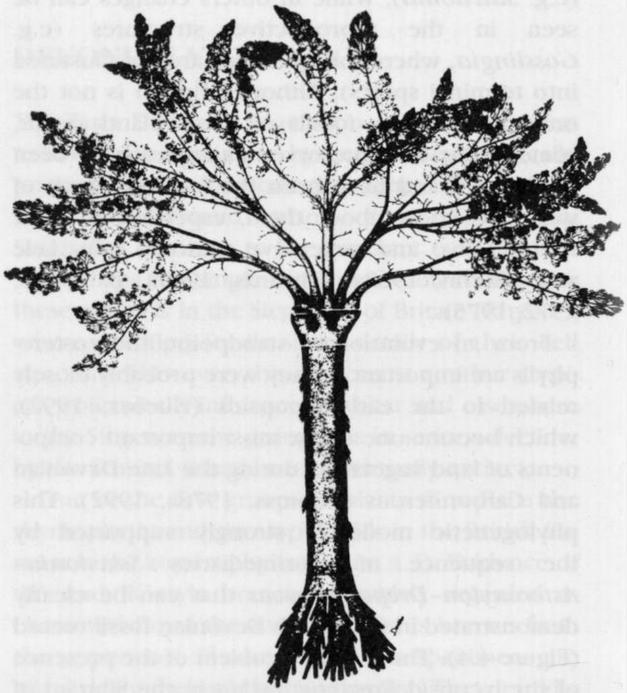

Figure 4.6 Reconstruction of the Devonian fern-like plant *Pseudosporochnus*. Based on Leclercq and Banks (1962).

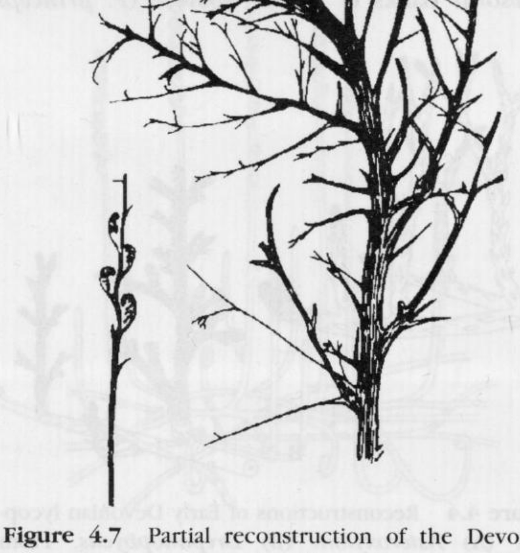

Figure 4.7 Partial reconstruction of the Devonian progymnosperm *Protopteridium*. Based on Meyen (1987, figure 38M).

progymnosperms and fern-like plants continued to diversify. The arborescent habit became fully developed, with trees growing to over 20 metres high (Beck, 1962).

Equisetes, in the form of the Bowmanitales and Pseudoborniales, also made their first appearances in the Late Devonian (Figure 4.1). It was once thought that equisetes first appeared in the mid-Devonian, represented by fossils such as *Hyenia*. However, the latter are now generally thought to belong to the cladoxylaleans.

The earliest British examples of seed plants are found in the Famennian of Devon (Arber and Goode, 1915), and are only just pre-dated by examples from North America (Rothwell *et al.*, 1989). Little is still known about the Devonian gymnosperms, although they seem mostly to have been herbaceous and probably belonged to the lagenostomalean pteridosperms. The development of seeds was of critical importance for the evolution of terrestrial vegetation, as it finally freed plants from the constraint of requiring moist conditions to facilitate fertilization. From the end of the Devonian, plants became adapted to take advantage of the so-called 'upland' or extra-basinal habitats. Thereafter, the fossil record provides an increasingly selective record of the Earth's total vegetation.

DEVONIAN PLANT FOSSILS IN BRITAIN

The record of Devonian plant fossils in this country is most complete in the Lower Devonian, with an extensive range of sites from the Gedinnian to the Emsian in Wales, the Welsh Borders (Figure 4.8) and in Scotland. From these, it is possible to document the early phases in the Devonian radiation of land vegetation, mentioned at the beginning of this chapter. Gedinnian plant fossils are found widely in the Arbuthnott Group of Tayside, Scotland, although there are also a number of sites in the Ditton Group of Shropshire and

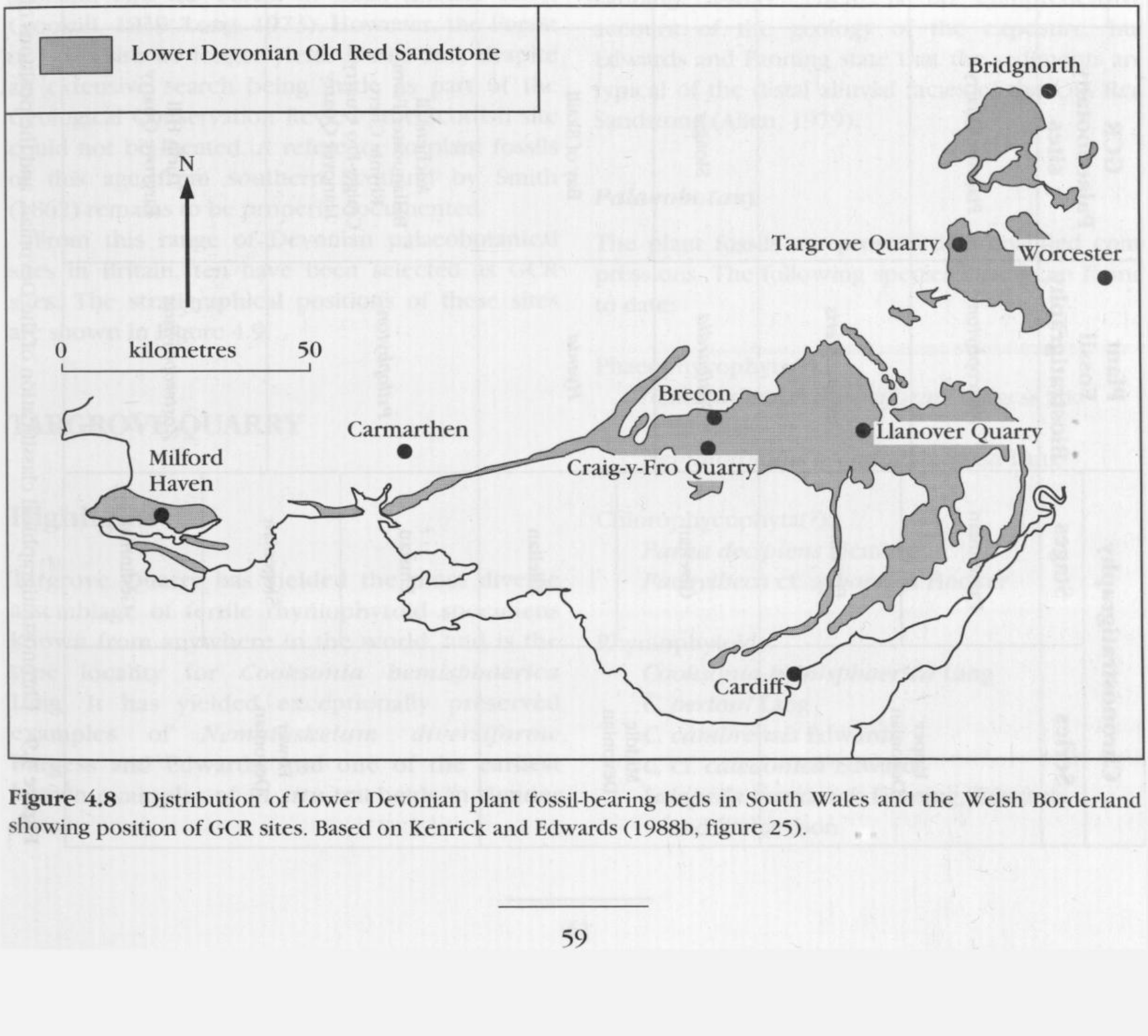

Figure 4.8 Distribution of Lower Devonian plant fossil-bearing beds in South Wales and the Welsh Borderland showing position of GCR sites. Based on Kenrick and Edwards (1988b, figure 25).

Chronostratigraphy		Plant Fossil Biostratigraphy	GCR Palaeobotany sites	Main areas outside Britain				
Series	**Stages**			**Western Europe**	**Eastern Europe**	**Asia**	**Southern Continents**	**North America**
Upper Devonian	Famennian	*Rhacophyton*	Plaistow Quarry	Bear Island Belgium Ireland	Ukraine	Kazakhstan Kuzbass	New South Wales	Pennsylvania New York St. West Virginia
	Frasnian	*Archaeopteris*		Bear Island	Ukraine	Kazakhstan Kuzbass	New South Wales	New York St. Quebec
Middle Devonian	Givetian	*Svalbardia*	Sloagar	Spitsbergen Belgium Rhineland	Bohemia Ukraine	Kazakhstan Kuzbass Yunnan	Queensland	New York State
	Eifelian	*Hyenia*	Bay of Skaill	Spitsbergen Belgium Rhineland	Bohemia Ukraine	Kazakhstan Kuzbass		New Brunswick
Lower Devonian	Emsian	*Psilophyton*	Auchensail Ballanucater Farm Rhynie Chert Craig-y-Fro Quarry Llanover Quarry	Spitsbergen Norway Belgium Rhineland	Poland Ukraine Moldavia	Kuzbass Yunnan	Victoria N. Argentina	New Brunswick Maine
	Siegenian							
	Gedinnian	*Zosterophyllum*	Turin Hill Targrove Quarry	Spitsbergen Belgium Rhineland	Bohemia	Kazakhstan Kuzbass Yunnan	Victoria	

Figure 4.9 Chronostratigraphical classification of the Devonian, and the positions of the GCR and other major palaeobotanical sites in this system.

the St Maughan's Group of South Wales (Edwards, 1990). Siegenian plant fossils are best represented in the Senni Beds and its equivalents in South Wales and the Welsh Borders (Croft and Lang, 1942). There is also the world-famous Rhynie Chert in the Grampians of Scotland, which is now thought to be Siegenian in age. The Strathmore Group of central Scotland, provides the most abundant Emsian plant fossils in this country (Henderson, 1932; Rayner, 1983, 1984).

Middle Devonian plant fossils are mainly found in the fossil fish beds of northern Scotland, ranging from Cromarty north to the Shetlands. There are also records of poorly-preserved fossils from Cornwall (Fox, 1900, 1901, 1904; Lang, 1929; Hendriks, 1935, 1966; Hendriks *et al.*, 1971).

For reasons which are still far from clear, Upper Devonian plant fossil occurrences are rare throughout the world, and Britain is no exception to this. The best British examples are found in the Baggy Formation and its lateral equivalents in north Devon (Arber and Goode, 1915). In Ireland, the Kiltorcan assemblage is of about the same age, and has yielded well-preserved examples of *Archaeopteris* and *Cyclostigma* (Chaloner, 1968). Comparable assemblages have also been found in Scotland and the Forest of Dean (Miller, 1857; Crookall, 1939; Long, 1973). However, the Forest of Dean site no longer yields fossils and, despite an extensive search being made as part of the Geological Conservation Review, the Scottish site could not be located. A reference to plant fossils of this age from southern Scotland by Smith (1862) remains to be properly documented.

From this range of Devonian palaeobotanical sites in Britain, ten have been selected as GCR sites. The stratigraphical positions of these sites are shown in Figure 4.9.

TARGROVE QUARRY

Highlights

Targrove Quarry has yielded the most diverse assemblage of fertile rhyniophytoid specimens known from anywhere in the world, and is the type locality for *Cooksonia hemisphaerica* Lang. It has yielded exceptionally preserved examples of *Nematasketum diversiforme* Burgess and Edwards, and one of the earliest known examples of *in situ* tracheids in slender axes.

Introduction

This Gedinnian-age locality is a small sandstone quarry in the grounds of Downton Hall, near Ludlow, Shropshire (SO 525780) and is Locality 105 in Ball and Dineley (1961). The first plant fossils were recorded by Marston (1870), who interpreted what were *Parka* specimens as eurypterid egg-packets. More specimens were described by Lang (1937), who also illustrated *Cooksonia* and *Nematothallus* material. However, the most complete accounts are by Edwards and Fanning (1985) and Fanning *et al.* (1992).

Description

Stratigraphy

Lang (1937) stated that this exposure was in the upper Downton Group, but Ball and Dineley (1961) map it as *c.* 60 metres above the main *Psammosteus* Limestone, thus placing it in the lower Ditton Group. On the basis of the spores and fish fossils found here, the sequence is Gedinnian in age (Richardson *in* Edwards and Fanning, 1985). There is no comprehensive account of the geology of the exposure, but Edwards and Fanning state that the sediments are typical of the distal alluvial facies of the Old Red Sandstone (Allen, 1979).

Palaeobotany

The plant fossils are preserved as coalified compressions. The following species have been found to date:

Phaeophycophyta(?):
Nematasketum diversiforme Burgess and Edwards
Nematothallus pseudovasculosa Lang

Chlorophycophyta(?):
Parka decipiens Fleming
Pachytheca cf. *sphaerica* Hooker

Rhyniophytoids:
Cooksonia hemisphaerica Lang
C. pertoni Lang
C. cambrensis Edwards
C. cf. *caledonica* Edwards
Salopella marcensis Fanning, Edwards and Richardson

Tortilicaulis transwalliensis Edwards
Uskiella reticulata Fanning, Edwards
and Richardson
cf. *U.reticulata*
Tarrantia salopensis Fanning, Edwards
and Richardson

Zosterophyllopsida:
Zosterophyllum cf. *fertile* Leclercq

There is also a number of unnamed rhyniophytoid fructifications described from here by Edwards and Fanning (1985), and Fanning *et al.* (1992).

Interpretation

This site yielded some of the specimens used by Lang (1937) in his description of *Nematothallus*. They show that it had a pseudoparenchymatous structure surrounded by a cuticle. Lang (1945) and Edwards and Rose (1984) suggested that there was an outer epidermal layer, but the Targrove Quarry specimens do not seem to show this. Lang (1937) also noted some cutinized spores in the Targrove Quarry specimens, although no evidence of the fruiting bodies was found.

Lang (1937) implied that *Prototaxites* occurs here, but he neither figured nor described any specimens. It is also listed by Edwards and Fanning (1985). Burgess and Edwards (1988) subsequently identified the Targrove specimens as *Nematasketum diversiforme* Burgess and Edwards, although again none from here is figured. This species and genus are briefly discussed further in Chapter 3, in the section dealing with Perton Lane.

The most significant vascular plant found here, at least from a stratigraphical standpoint, is *Zosterophyllum*. The record is based on one specimen showing the characteristic branching pattern of the form-genus, and a poorly-preserved fertile spike, neither of which has been figured (Edwards and Fanning, 1985). Its presence indicates that the flora belongs to the *Zosterophyllum* Zone of Banks (1980), and thus is probably Early Devonian in age.

Far commoner at Targrove Quarry are rhyniophytoid species. Lang (1937) initially described only *Cooksonia hemisphaerica* Lang from here, for which it is the type locality. Further collecting, however, has yielded a much wider variety of fertile rhyniophytoid specimens, which have been assigned to various other species of *Cooksonia*, as well as *Salopella*, *Tortilicaulis*, *Uskiella* and *Tarrantia* (Fanning *et al.*, 1992). There were also numerous other forms of sporangia described by Edwards and Fanning, including ellipsoidal and bifurcating types, which belong to so far undescribed form-genera. Thus it comprises by far the most diverse assemblage of fertile rhyniophytoid taxa known from anywhere in the world.

Lang (1937) was also able to demonstrate *in situ* tracheids in a slender axis from here. This was the first direct evidence of vascular tissue in these very early land plants and, until the discovery of similar specimens in the Silurian of Capel Horeb, was the oldest known evidence of *in situ* tracheids in the fossil record. Since the only fertile rhyniophytoid reported from here by Lang was *C. hemisphaerica* Lang, he concluded that *Cooksonia* must have been a vascular plant. However, the discovery by Edwards and Fanning of a much more diverse rhyniophytoid assemblage here must now cause this argument to be doubted, since it is impossible at this stage to be certain which of the species had vascular tissue and which (if any) had not.

Similar *Zosterophyllum* Zone assemblages have been reported from Caldy Island, Dyfed (Lang, 1937) and Newton Dingle, Shropshire (Edwards and Richardson, 1974), although this is not as diverse. A comparable flora comes from the Arbuthnott Group of Scotland, such as found at Turin Hill (see below), but that flora is dominated by zosterophylls and has only subsidiary rhyniophytoid elements. From outside of Britain, *Zosterophyllum* Zone floras have been described from Belgium (Leclercq, 1942), Spitsbergen (Høeg, 1942) and Czechoslovakia (Obrhel, 1968), but they differ from the Targrove Quarry assemblage by the presence of *Taeniocrada* and the more restricted rhyniophytoid composition. The assemblage from Kuznetsk in Siberia described by (Stepanov, 1975), although sharing a number of genera with the Targrove Quarry assemblage, also contains several enigmatic endemics such as *Juliphyton*, *Uksunaiphyton*, *Pseudosajania* and *Salairia*, all of unknown affinities.

The assemblage of plant fossils found at Targrove Quarry is thus unique in both a national and international sense. It is transitional between the more primitive Silurian assemblages such as are found at Perton Lane and Freshwater East (see Chapter 3) and the slightly more advanced floras of Turin Hill (see below). It is thus of key importance for understanding the earliest phases in the diversification of land vegetation in the earliest part of the Devonian.

Conclusion

Nowhere else in the world has yielded such a diverse assemblage of rhyniophytoid plants than Targrove Quarry. They are thought to represent the most primitive type of land plants. The rhyniophytoids first appeared about 425 million years ago in the Silurian (see previous chapter) and flourished in the earliest Devonian, such as represented by the Targrove fossils. After some 35 million years, they declined and became extinct, as more advanced plants evolved to take advantage of the land habitats. The Targrove fossils are about 410 million years old and thus represent the acme of this highly significant group of plants which, although of only very simple form, represent a key phase in the evolution of land vegetation.

TURIN HILL

Highlights

Turin Hill is the best site for plant fossils from the Lower Devonian Arbuthnott Group flora, the most typical *Zosterophyllum* Zone flora in Britain, and one of the best examples of its type in the world (Figure 4.10). It has yielded abundant specimens of *Parka* and fertile *Zosterophyllum* and is the type locality for *Cooksonia caledonica* Edwards. It is of international significance for the study of

Figure 4.10 Turin Hill, Aberlemno Quarry. Strike section along flaggy deposits of the Gedinnian Dundee Formation. (Photo: C.J. Cleal.)

the *Zosterophyllum*-dominated vegetation of the earliest Devonian.

Introduction

The famous Old Red Sandstone palaeontological sites on Turin Hill, which lie near Forfar, Tayside Region (NO 493535), were extensively worked during the eighteenth and nineteenth centuries for Arbroath Paving Stones (Mackie, 1980). Two of these quarries are particularly well known plant fossil localities: Clocksbriggs Quarry (also known as Wemyss Quarry) and Aberlemno Quarry. Early records of the plant fossils concentrated mainly on the non-vascular species (Miller, 1855, 1857; Peach, 1877; Powrie *in* Warden, 1881; Kidston, 1886, 1893, 1897; Dawson and Penhallow, 1891; Reid, 1895; Reid *et al.*, 1898; see also Niklas, 1976a). Vascular plant fossils were also recorded in some early studies (Peach, 1877; Kidston, 1886; Reid and Macnair, 1899), but were not dealt with in detail until Lang's (1927a) account of *Zosterophyllum*, and subsequently by Lele and Walton (1962a), Walton (1964a) and Edwards (1970b, 1975). In addition to the flora, a diverse freshwater fish and arthropod fauna has been found here (Hickling, 1912; Westoll, 1951).

Description

Stratigraphy

The geology of these quarries is described by Armstrong *et al. in* Friend and Williams (1978). Exposed here are interbedded red fluvial sandstones and grey-green lacustrine siltstones belonging to the Dundee Formation of the Arbuthnott Group (Campbell, 1913; Armstrong and Paterson, 1970; earlier called the Carmyllie Beds by Hickling, 1908). The plant fossils belong to the *Zosterophyllum* Zone of Banks (1980), indicating a Gedinnian or early Siegenian age for these strata. Palynological and fish evidence supports an early Gedinnian age (Edwards and Fanning, 1985, Table 1; Edwards, 1990).

Palaeobotany

The plant fossils are found mainly in the laminated, lacustrine siltstones. Commonest are impressions picked out by iron staining, but some coalified compressions and petrifactions also occur. The following assemblage has been reported to date:

Phaeophycophyta(?):
  Prototaxites forfarensis (Kidston) Pia

Chlorophycophyta(?):
  Parka decipiens Fleming
  Pachytheca sp.

Rhyniophytoids:
  Cooksonia caledonica Edwards

Zosterophyllopsida:
  Zosterophyllum myretonianum Penhallow

Interpretation

Although *Parka decipiens* (Figure 4.11) was first described from the Lower Devonian of Fife

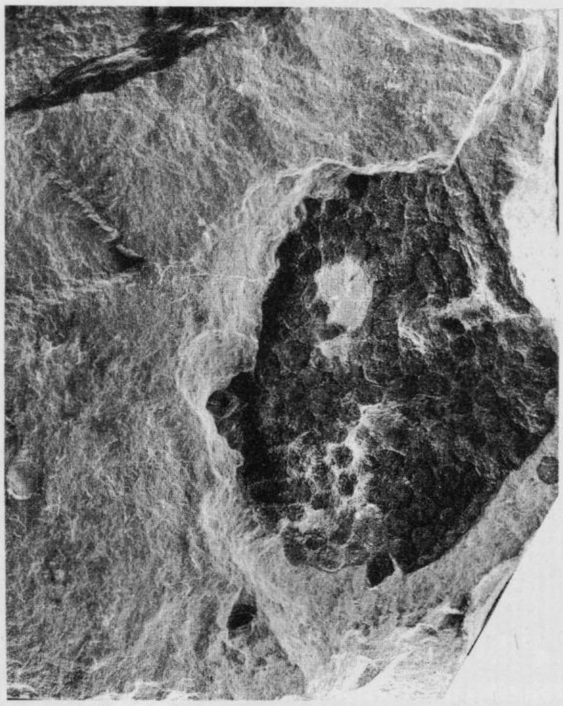

Figure 4.11 *Parka decipiens* Fleming. Enigmatic, possible early land plant, consisting of a cutinized thallus covered with discoid sporangia; Natural History Museum, London, specimen V.24951. Dundee Formation (Gedinnian), Carmylie, Tayside. × 2. (Photo: Photographic Studio, Natural History Museum, London.)

(Fleming, 1831), Turin Hill is probably the best known locality for this species and much of the early debate about its affinities was based on specimens from here (summarized by Dawson and Penhallow, 1891 and Don and Hickling, 1917). It has been variously argued to be of animal origin (Mantell, 1852; Lyell, 1865; Woodward, 1866–1878), to be the seeds of a rush or bur-reed (Fleming, 1831), or the fruiting body of some other enigmatic plant (Dawson and Penhallow, 1891; Reid *et al.*, 1898; Edwards, 1921). However, it is now believed to have been a thalloid plant attached to the substrate by a basal holdfast, and probably spending at least part of its life out of water (Niklas, 1976a, 1976c). Possible affinities with the green algae (Niklas (1976a) and the liverworts (Neuber, 1979) have been suggested. Most recently, Hemsley (1989, 1990a) has suggested that it might have been an evolutionary intermediary between the algae and the bryophytes.

Peach (1877) identified a specimen from here as *Cyclopteris* (photographically re-figured by Høeg, 1942, pl. 46, figs 10 and 11). This form-genus is usually applied to the basal pinnules of certain Upper Carboniferous medullosan fronds, which is clearly out of the question here. More likely is that it is a specimen of *Parka* viewed from the lower surface (cf. Don and Hickling, 1917, pl. 54, fig. 9).

Niklas (1976a) described a poorly preserved specimen of *Pachytheca* from Turin Hill, and showed that it had a similar growth pattern to *Parka*. Niklas (1976b) also showed similarities in the chemical composition between the two, but pointed out, that the taxonomic significance of this similarity is uncertain.

A partially permineralized, branched axis, over one metre long, was described by Miller (1855, 1857) as part of a *Lepidodendron* stem. Most of the specimen is now believed to be lost, but Lang (1926) suggested that the holotype of *Cryptoxylon forfarense* Kidston was originally part of it. Kidston (1897) originally described the structure of the stem as being cellular, but Kidston and Lang (1924) later showed that it was pseudoparenchymatous and so transferred it to *Nematophyton* (syn. *Prototaxites*). Lang (1926) described a second species of *Prototaxites* from the Arbuthnott Group as *Nematophyton caledonianum*. To date, it has not been reported from Turin Hill but its presence might well be anticipated.

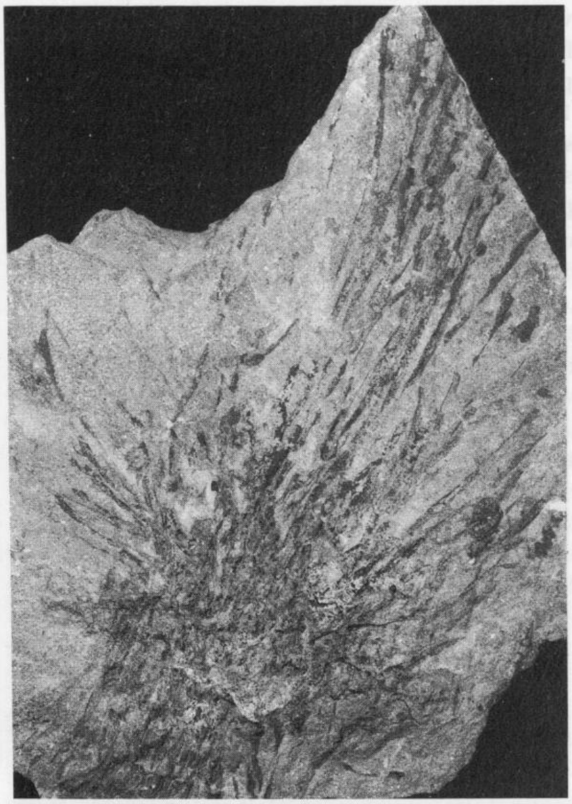

Figure 4.12 *Zosterophyllum myretonianum* Penhallow. Tangled mass of axes at the base of the plant that gave rise to the vertical shoots; Natural History Museum, London, specimen V.58041. Dundee Formation (Gedinnian), Balgavies Quarry, near Forfar, Tayside. × 0.5. (Photo: Photographic Studio, Natural History Museum, London.)

Slender branching axes occur commonly in the Arbuthnott Group (Figure 4.12), and were initially believed to be either part of an eel-grass type plant (Miller, 1857), or the vegetative part of a plant which bore *Parka* as its fruiting body (Dawson and Penhallow, 1891). Miller described rounded bodies attached laterally to some of these axes and argued that they might be leaves. Penhallow (1892) recognized them to be sporangia, however, and erected the name *Zosterophyllum myretonianum*. The Turin Hill specimens have not yielded such well-preserved cuticles as have been described from Myreton Quarry (Lele and Walton, 1962a), but they have included some exceptionally complete specimens which have allowed the gross morphology of the plant to be reconstructed (Lang, 1927a; Lele and Walton, 1962a; Walton, 1964a). Numerous fertile specimens have also been found here (e.g. Figure

4.13) and formed the bulk of the material used by Edwards (1975) in her study on the morphological variation of the species. Although several species from other localities have been subsequently placed in *Zosterophyllum* (reviewed by Edwards, 1975), *Z. myretonianum* remains the best understood. The form-genus is of particular importance since it is the effective type of the Zosterophyllopsida, an important class of early land plants, probably related to the lycopsids ('club-mosses'). This subdivision is generally accepted to be the evolutionary precursor that played such an important role in the later Palaeozoic floras.

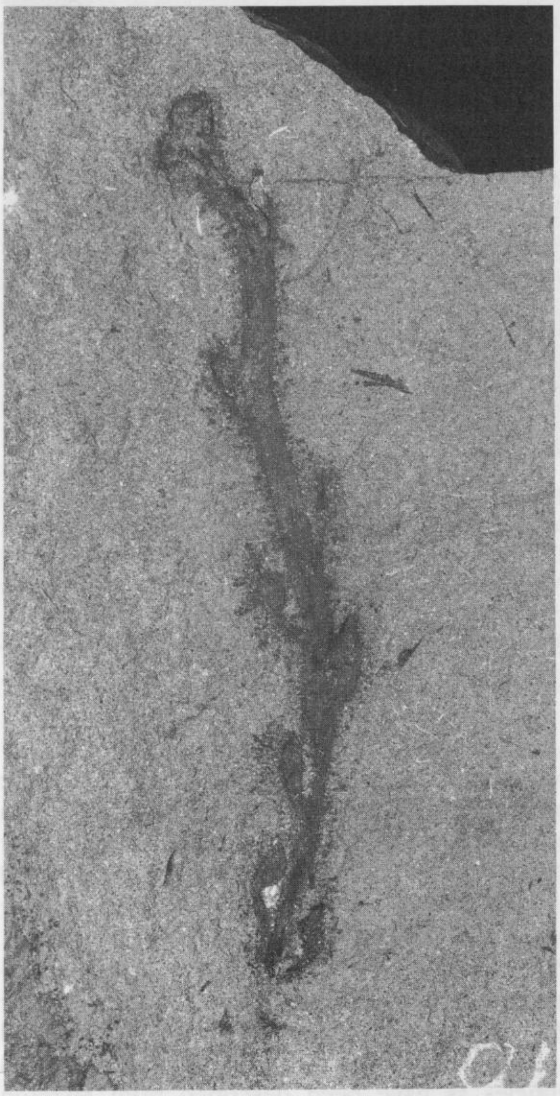

Figure 4.13 *Zosterophyllum myretonianum* Penhallow. A fertile spike with sporangia arranged around the axis; Natural History Museum, London, specimen V.58047. Dundee Formation (Gedinnian), Clocksbriggs Quarry, Turin Hill. × 2. (Photo: Photographic Studio, Natural History Museum, London.)

Edwards (1972) described a second zosterophyll, *Z. fertile* Leclercq, from the Arbuthnott Group near Arbroath (probably Kelly Den, but locality details are not clearly recorded), but it has not so far been reported from Turin Hill.

For many years, *Zosterophyllum* was the only type of vascular plant known from the Arbuthnott Group. More recently, however, Edwards (1970b) has described specimens from Aberlemno Quarry as *Cooksonia caledonica*. These show naked, dichotomous axes with terminal, globose sporangia, typical of *Cooksonia*, but the sporangia often have a marginal rim. The latter may only be a preservational feature, but may alternatively be the remains of a dehiscence mechanism (Edwards and Edwards, 1986). If the latter eventually proves to be correct, then the generic position of this species may have to be revised.

Several localities in the vicinity of Forfar and Arbroath have yielded the Arbuthnott Group flora (Kidston and Lang, 1924; Lang, 1926, 1927a; Lele and Walton, 1962a; Edwards, 1970b, 1975). Many of these have, however, been subsequently infilled or flooded. In particular, Myreton Quarry, from where Lele and Walton (1962a) obtained cuticles of *Zosterophyllum*, has been landscaped. Of the sites still remaining, the Turin Hill quarries yield easily the most abundant and well-preserved plant fossils.

The Arbuthnott Group flora is the most typical *Zosterophyllum* Zone assemblage (*sensu* Banks, 1980) known from Britain. Other assemblages from this zone have been recorded from Caldy Island, Dyfed (Lang, 1927a, 1937), Newton Dingle, Shropshire (Edwards and Richardson, 1974) and Targrove Quarry (see above). However, these all contain a much lower proportion of zosterophylls. *Zosterophyllum* Zone assemblages also occur in Spitsbergen (Høeg, 1942), the former Czechoslovakia (Obrhel, 1968) and Kuznetsk (Stepanov, 1975), but none has been reported to yield such well-preserved specimens. Turin Hill is thus of international importance for the study of the *Zosterophyllum*-dominated vegetation, which seems to have occurred widely in the lowland terrestrial habitats during the earliest Devonian of the northern hemisphere; the radiation of this vegetation marked the first phases of the diversification of the land floras in this part of the world (see Chapter 3 for comments on the more 'advanced' floras found in Gondwana).

Conclusion

Turin Hill yields the best example of a *Zosterophyllum* Zone flora (about 400 million years old) from anywhere in the world. Other floras of this type have been reported from South Wales, the Welsh Borders, Spitsbergen, Czechoslovakia and Siberia, but none have yielded such well-preserved specimens. Most significant here is the presence of well-preserved examples of the unusual alga *Parka*, and of the early vascular plant *Zosterophyllum*. The latter is important as it is regarded as ancestral to the club-mosses which, in the Late Carboniferous (310–300 Ma), formed extensive tropical forests that resulted in thick, economically important coal deposits (see Chapter 6). The site is also important as the type locality for *Cooksonia caledonica*, a remnant of the primitive rhyniophytoid stock that more typically occurs in the Upper Silurian, and which is thought to represent the earliest type of upright land plant.

LLANOVER QUARRY

Highlights

Llanover Quarry has yielded one of the most diverse examples of a *Psilophyton* Zone (Siegenian) flora from Britain. It is the type locality for *Zosterophyllum llanoveranum* Croft and Lang, the only *Zosterophyllum* for which three-dimensional internal anatomy is known. This site has also yielded important information on the form and structure of *Uskiella*, *Drepanophycus*, *Gosslingia* and *Debeubarthia*.

Introduction

This small Old Red Sandstone exposure lies about 5 km south of Abergavenny, Gwent, Wales (SO 298079). Plant fossils were first discovered by Wickham King, who then showed the site to the palaeobotanist William Croft. Croft's collection was the basis of the classic study on the so-called Senni Beds flora (Croft and Lang, 1942). Further collecting has proved difficult, due to the small outcrop and awkwardly positioned tree roots, but some subsequent work on the assemblage has been done (Edwards, 1969a, b, 1970a, 1981; Edwards *et al.*, 1989; Shute and Edwards, 1989).

Description

Stratigraphy

The exposed sequence consists of about two metres of red sandstones and mudstones of the Brownstone Group (*sensu* Heard and Davies, 1924), which are correlatives of the Senni Beds of the Brecon Beacons. They were deposited on an alluvial plain crossed by fast, low sinuosity streams (Kelling *in* Owen *et al.*, 1965; Allen, 1979). No animal fossils have been reported, but the plant and microfossils suggest a Siegenian age (Croft and Lang, 1942; Mortimer, 1967; Richardson and Lister, 1969). The plant fossils occur in or near sediments of the fluvial channel (Allen, 1979), and probably originated from a variety of habitats (Edwards, 1979b).

Palaeobotany

The plant fossils are mostly preserved as compressions and iron oxide stained impressions, with no cuticles preserved, but some limonite petrifactions also occur. The following assemblage has been described to date:

Phaeophycophyta(?):
Prototaxites cf. *caledonianus* (Lang) Kräusel and Weyland
Nematothallus sp.

Chlorophycophyta(?):
Pachytheca sp.

Rhyniophytoids:
Sporogonites exuberans Halle
Taeniocrada sp.

Rhyniopsida:
Uskiella spargens Shute and Edwards

Zosterophyllopsida:
Zosterophyllum llanoveranum Croft and Lang
Z. cf. *australianum* Lang and Cookson
Z. cf. *fertile* Leclercq
Gosslingia breconensis Heard
Debeubarthia splendens Edwards, Kenrick and Carluccio

Lycopsida:
Drepanophycus spinaeformis Göppert

Trimerophytopsida:
Dawsonites arcuatus Halle

Uncertain affinities:
Sciadophyton cf. *steinmannii* Kräusel and Weyland
Sennicaulis hippocrepiformis Edwards
'spherical or circular bodies *incertae sedis*'

Interpretation

Coalified spheres of *Pachytheca* are common at Llanover. They are generally poorly preserved, but the cortical and medullary regions can sometimes be distinguished (Croft and Lang, 1942, pl. 11, fig. 78). Croft and Lang also reported some *Pachytheca*-like specimens with tuberculate surfaces, referring to them as 'spherical bodies *incertae sedis*'.

A feature of the Llanover assemblage noted by Croft and Lang is the presence of elongate, slender specimens of *Prototaxites*. The dimensions of the tubes and the presence of 'medullary spots' invite a comparison with *P. caledonianus* and with *Prototaxites* described from the Silurian of the Welsh Borderland (Lang, 1937) and the Devonian of Germany (Kräusel and Weyland, 1934).

The Rhyniaceae is represented here by *Uskiella spargens* Shute and Edwards (1989). It was first identified as *Cooksonia* sp. (Croft and Lang, 1942), but has quite a different shape and structure of the sporangia. Shute and Edwards interpreted it as a small plant of determinate growth-pattern, with naked, dichotomous axes forking at a wide angle (60–90°) and bearing ellipsoidal, terminal sporangia. Petrifactions from Llanover were particularly instructive in showing details of the sporangia, including the presence of a zone of differentiated cells around the major circumference, which may have been linked with dehiscence. This type of bivalved sporangial structure evidently had an adaptive advantage, perhaps because it maximized the area of spores exposed to the atmosphere after dehiscence, since it seems to have evolved independently in several other groups of plants, as well as the Rhyniaceae (reviewed by Shute and Edwards, 1989).

Several specimens of *Sporogonites* sporangia were described by Croft and Lang, from which they were able to prepare spores. One example was also found to have stomata preserved on the stem just below the sporangia. Their affinities are still unknown, and are currently being re-investigated by Shute and Edwards.

Croft and Lang's record of the rhyniophytoid genus *Taeniocrada* sp. is based on slender, flattened stems from a lenticular band of mudstone at Llanover. In the absence of fertile structures, it has been impossible to place them in a particular species, and even their generic assignment cannot be regarded as proven (Edwards, 1981).

This is the type locality for *Zosterophyllum llanoveranum* (Figure 4.14). It is the only species of *Zosterophyllum* for which the anatomy is known, following studies by Edwards (1969a) on petrifactions from here and Craig-y-Fro Quarry. Of particular significance was the determination of the form of the vascular strand, which is oval in cross-section and exarch, in contrast to the terete, centrarch strands of the Rhyniopsida and Trimerophytopsida. It was also possible to determine the form of the prominent sporangial dehiscence structure. A few specimens from Llanover have also been identified as *Z.* cf. *australianum* and *Z.* cf. *fertile* (Croft and Lang, 1942; Edwards, 1969b), although they may just be morphological variants of *Z. llanoveranum*.

Another member of the Zosterophyllopsida in the Llanover assemblage is *Gosslingia*. Rather better material of this form-genus has been found at Craig-y-Fro Quarry, and from these details of the anatomy have been described (Heard, 1927; Edwards, 1970a; Kenrick and Edwards, 1988a). However, the Llanover specimens have provided some important information on the gross morphology of the plant, in particular the arrangement of the sporangia.

The specimens described by Croft and Lang as cf. *Psilophyton princeps* have laterally attached sporangia similar to those of *Sawdonia ornata* (Dawson) Hueber described from the Gaspé Peninsula (Hueber and Banks, 1967; Hueber, 1968, 1971). Unlike *Sawdonia*, however, they have small bulges or curved branches just below each dichotomy, and lack the characteristic dark tip to the spines. For this reason, they have been assigned to a new genus and species, *Deheubarthia splendens* Edwards, Kenrick and Carluccio (1989).

Croft and Lang described the only fertile axes of *Drepanophycus spinaeformis* known from outside of Germany. Based on the German material, Kräusel and Weyland (1930) originally described

Figure 4.14 *Zosterophyllum llanoveranum* Croft and Lang. A group of fertile spikes probably originating from a single plant; Natural History Museum, London, specimen V.26516a. Brownstone Group (Siegenian), Llanover Quarry. × 1.5. (Photo: Photographic Studio, Natural History Museum, London.)

the sporangia as being attached adaxially to the leaves. Later, however, Kräusel and Weyland (1935) found sporangia attached to leaf apices, which seems to be confirmed by the Llanover specimens. It is currently believed that the position of attachment of the sporangia is variable (e.g. Meyen, 1987). *Drepanophycus* is regarded by Hueber (1992) as one of the earliest and most primitive lycopsids (order Drepanophycales), being only pre-dated by the Silurian *Baragwanathia* from Gondwana (see Chapter 3).

Isolated trusses of pendant, fusiform sporangia were identified by Croft and Lang as *Dawsonites arcuatus* (Figure 4.15). They are probably the fertile parts of a trimerophyte plant, but in the absence of attached vegetative structures it is impossible to place them in one of the more natural taxa based on whole-plant morphology. They are associated with spiny axes, suggesting possible affinities with *Psilophyton princeps*. However, at least some of these axes were found by Croft and Lang to have laterally attached sporangia, which means that they belong to the zosterophyllalean genus *Deheubarthia* (see above). Until the nature of the vegetative axes which bore these sporangial trusses at Llanover

Figure 4.15 *Dawsonites arcuatus* Halle. Terminal part of fertile truss; Natural History Museum, London, specimen V.26492. Brownstone Group (Siegenian), Llanover Quarry. × 2. (Photo: Photographic Studio, Natural History Museum, London.)

has been determined, they have to be retained within the generalized form-species *D. arcuatus* Halle. The fossils here and at Craig-y-Fro (see below) are the oldest known remains of trimerophytes from anywhere in the world.

A number of specimens were described by Croft and Lang as *Sciadophyton steinmannii*. Such structures are now believed to be gametophytes (Remy, Remy *et al.*, 1980; Remy, Schultka *et al.*, 1980), and have been compared with petrified specimens from Rhynie identified as *Lyonophyton* (Remy and Remy, 1980a, b). Schweitzer (1983a, b) has reported *Zosterophyllum*-like axes attached to German specimens of *Sciadophyton*, suggesting that the latter was a zosterophyll gametophyte. Croft and Lang noted that the Llanover specimens differ slightly from the type specimens of *S. steinmannii* Kräusel and Weyland, 1930 in the sizes of the discs and of the circular scars that they show. Contrary to Croft and Lang, therefore, they are referred to in the above species list as *S.* cf. *steinmannii*.

Sennicaulis hippocrepiformis Edwards, 1981 was described from specimens from both here and from Craig-y-Fro Quarry. Most of the anatomical details of this species were determined from the pyrite petrifactions from Craig-y-Fro, but the Llanover specimens showed certain details of the xylem structure particularly well. The affinities of these isolated axes remain uncertain, but probably lie either with the Rhyniopsida or Trimerophytopsida.

Llanover Quarry has yielded the most diverse *Psilophyton* Zone flora (*sensu* Banks, 1980) in Britain. Croft and Lang (1942) record comparable assemblages from the Deri Quarries near Abergavenny, along Kemeys Graig near Newport, from below the dam of Talybont Reservoir near Brecon and from a cliff near Llanthony Abbey in the Black Mountains; but none of these sites has yielded such diverse assemblages as Llanover Quarry and Craig-y-Fro.

These Welsh assemblages belong to the European phytogeographic subunit of the equatorial and low-latitude floras (as defined by Raymond *et al.*, 1985), which characterizes the southern and eastern parts of Laurussia. The closest comparison is with assemblages from Podolia in the Ukraine and the Dniester River in Moldavia (Ishchenko, 1965, 1974), particularly in the presence of *Gosslingia*, *Sciadophyton* and *Zosterophyllum*. Some comparison is also possible with floras from Belgium (Stockmans, 1940; Gerrienne, 1988, 1990a, b, 1991), although the latter have yielded fewer species.

Other *Psilophyton* Zone assemblages have been found in Britain in a borehole in Oxfordshire (Chaloner *et al.*, 1978) and in the Strathmore Group of Scotland, such as at Auchensail Quarry and Ballanucater (pp. 75–80). Raymond *et al.* (1985) assigned these to the American phytogeographic subunit and they differ markedly from the Llanover assemblage, being much less rich in species and dominated by *Pachytheca*, *Sawdonia*, *Dawsonites* and (in the Strathmore Group) *Drepanophycus*. However, this may be a function of the Llanover assemblage being marginally older than the Oxfordshire and Scottish fossils. The Llanover fossils provide a clearer reflection of the general diversity of the Siegenian vegetation of Laurussia, and are thus of considerable significance for studying the early phases of the diversification of vascular plants.

Conclusion

Llanover Quarry has yielded one of the most diverse flora in Britain from the Siegenian Stage, and is about 400 million years old. It is particularly important for our understanding of the group of plants known as the zosterophylls, which were the ancestors of the club-mosses that dominated much of the land vegetation later in the Palaeozoic, particularly the Late Carboniferous equatorial coal swamps (see Chapter 6). Not only is this one of the most diverse assemblages of zosterophylls (*Gosslingia*, *Deheubarthia*, and three species of *Zosterophyllum*), but much important information has been discovered from here about their anatomy, which has been vital for understanding the evolutionary significance of the group. The club-mosses themselves are represented by *Drepanophycus* stems bearing reproductive organs, which are the second oldest fertile club-mosses known from anywhere in the world. Also present is one of the world's earliest examples of a trimerophyte (*Dawsonites*), which is the group thought to be ancestral to the seed plants (and thus also of flowering plants). The fossils are very similar to those found at Craig-y-Fro (see below), but are not preserved differently and thus show different aspects of the anatomy. Similar assemblages have been reported from Belgium, Moldavia and Ukraine but, except for the first of these, they have not been studied in such detail, and do not yield such well-preserved anatomical detail.

CRAIG-Y-FRO QUARRY

Highlights

Craig-y-Fro Quarry has yielded one of the best preserved Devonian plant fossil assemblages from Britain, second only to the Rhynie Chert assemblage. It is the type locality for *Gosslingia breconensis* Heard and *Sennicaulis hippocrepiformis* Edwards, and the only locality to yield *Tarella trowenii* Edwards and Kenrick, *Hostinella heardii* Edwards and *Krithodeophyton croftii* Edwards. The latter is of particular interest as being the only record of a member of the Barinophytales from Britain.

Introduction

This disused quarry, cut in Old Red Sandstone clastic sediments, is in the Brecon Beacons, between the towns of Brecon and Merthyr Tydfil (SN 971208). At different times it has been called Brecon Beacons Quarry, Storey Arms Quarry and Craig-y-Fro Quarry, the latter name being adopted here because it is geographically more precise. Plant fossils from here were first described by Heard (1926, 1927, 1939), who noted that some of the specimens were petrifactions. His method of preparing these petrifactions led to their destruction, however, and the only permanent record of them was a series of photographs, most of which are now believed to be lost (Edwards, 1970a, p. 226). Plant fossils from Craig-y-Fro were also recorded by Crookall (*in* Robertson, 1932) and Cox and Heard (1937). In their classic study on the Senni Beds flora, Croft and Lang (1942) recorded material from this locality and figured a small piece of *Nematothallus*, but most of their material came from Llanover Quarry (p. 67). They made little effort to study the Craig-y-Fro petrifactions, and were mainly interested in the coalified compressions. This aspect of the assemblage has only been studied in detail in recent years, following the development of improved sectioning techniques compared with those used by Heard (Edwards, 1968, 1969a, b, 1970a, 1980a, 1981; Edwards and Kenrick 1986; Kenrick and Edwards, 1988a; see also Edwards and Banks, 1965; Shute and Edwards, 1989).

Description

Stratigraphy

The geology has been described by Edwards and Richardson (*in* Friend and Williams, 1978). A thickness of about 14 metres of fluviatile sandstones and siltstones belonging to the Senni Beds is exposed, and includes four horizons yielding plant fossils (Figure 4.16). The biostratigraphy has been discussed by Edwards and Kenrick (1986), who suggest that it is lower Siegenian, based on palynological evidence.

Palaeobotany

The plant fossils are preserved mainly as impressions or heavily carbonized compressions. However, some pyritized petrifactions also occur. The following assemblage has been described to date:

Phaeophycophyta(?):
  Prototaxites sp.
  Nematothallus sp.

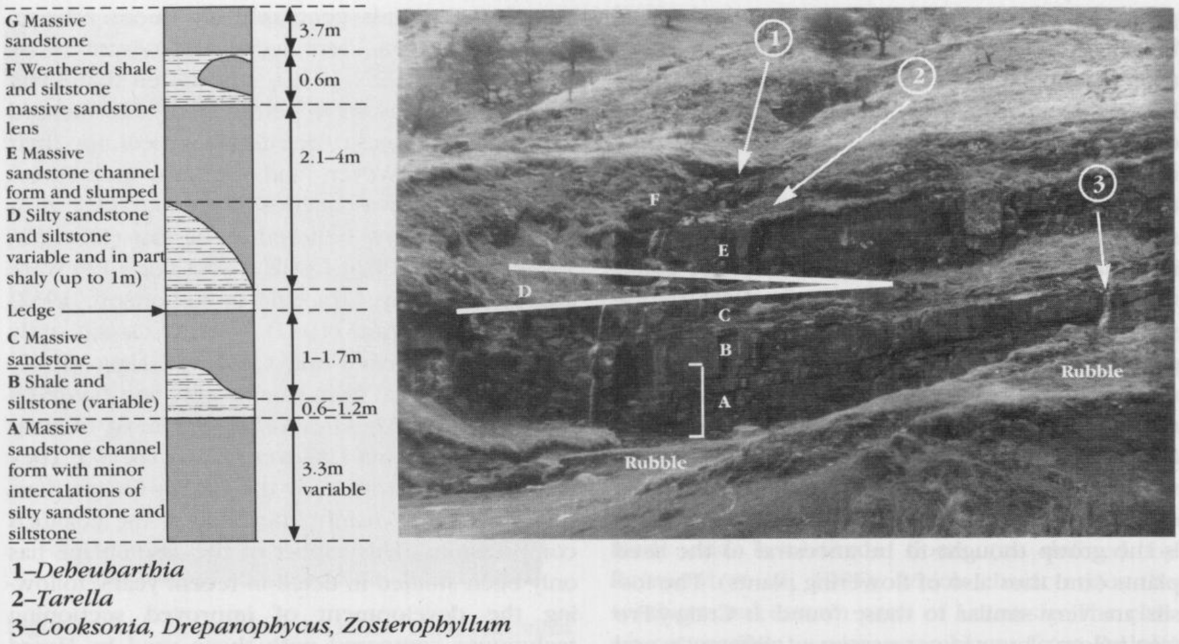

Figure 4.16 Craig-y-Fro Quarry. Sedimentological log through the exposed part of the Senni Beds, and a view of the quarry face showing the main beds. Also shown are three of the main plant-bearing horizons. Partly based on Friend and Williams (1978, figure 40). (Photo: D. Edwards.)

Chlorophycophyta(?):
Pachytheca sp.

Rhyniopsida:
Uskiella spargens Shute and Edwards

Zosterophyllopsida:
Zosterophyllum llanoveranum Croft and Lang
Z. cf. *fertile* Leclercq
Gosslingia breconensis Heard
Debeubarthia splendens Edwards, Kenrick and Carluccio

Lycopsida:
Drepanophycus spinaeformis Göppert

Trimerophytopsida:
Dawsonites arcuatus Halle

Barinophytales (*incertae sedis*):
Krithodeophyton croftii Edwards

Uncertain affinities:
Tarella trowenii Edwards and Kenrick
Sennicaulis hippocrepiformis Edwards
Hostinella heardii Edwards
cf.*Taitia* sp.
'spherical or circular bodies *incertae sedis*'

Interpretation

Pachytheca was recorded by Croft and Lang (1942). Heard (1927) had earlier described similar fossils, but with a tuberculate surface. Their internal structure is not well preserved and so they were not named by Heard, and Croft and Lang simply referred to them as 'spherical or circular bodies *incertae sedis*'.

Heard (1939) identified a pyritized specimen as cf. *Prototaxites (Nematophyton)* sp. The central part of the specimen had a pseudoparenchymatous anatomy typical of *Prototaxites*. This was surrounded by an amorphous layer referred to by Heard as a cortex, but which may be a product of the breakdown of organic tissue in the outer part of the specimen.

Heard (1939) also identified *Taitia* from here, and was supported in this by Crookall (1930), the original author of the form-genus. However, the figured specimen is poorly preserved and the record has been included in the above species list as doubtful.

The Rhyniaceae is represented by adpressions of *Uskiella spargens* Shute and Edwards (1989). Much of the key information about this species was determined from the petrifactions from Llanover. However, the Craig-y-Fro specimens have demonstrated details of the stem branching pattern and the attachment of the sporangia (Figure 4.17).

Much of the anatomical detail of *Zosterophyllum llanoveranum* described by Edwards (1969a) was based on the limonite petrifactions from Llanover Quarry, but the same features could also be seen in the Craig-y-Fro pyrite petrifactions. She noted, however, that petrified sporangia are more abundant at Craig-y-Fro, and that they yielded better preserved spores. She also found evidence of a possible tapetal structure surrounding the spores, not seen in the Llanover Quarry specimens.

Craig-y-Fro is the type locality for *Gosslingia breconensis* (Figure 4.18). The original descriptions (Heard, 1926, 1927) were brief, but covered the main features of the plant, and his conclusions have been mostly supported by subsequent studies (Croft and Lang, 1942; Edwards and Banks, 1965; Edwards, 1970a). The only significant exception is his interpretation of the small protuberances found below the branches of the axes, which he believed to be the remains of specialized 'sporangiferous branches'. The specimens described by Croft and Lang (1942) showed that the sporangia were in fact attached laterally to the axes, and were not aggregated into terminal spikes as in *Zosterophyllum*.

Figure 4.17 *Uskiella spargens* Shute and D. Edwards. Branched axes bearing terminal sporangia; Natural History Museum, London, specimen V.26461a. Senni Beds (Siegenian), Craig-y-Fro Quarry. x 1. (Photo: Photographic Studio, Natural History Museum, London.)

The most comprehensive description of *Gosslingia* is by Edwards (1970a), whose study was based mainly on specimens from Craig-y-Fro. Taxonomically significant features discussed by Edwards include the exarch xylem strand with an oval cross-section, and the laterally borne sporangia with a well developed distal dehiscence structure. Both features support its inclusion within the Zosterophyllopsida, as do details of the structure of the tracheids (Kenrick and Edwards, 1988a). Edwards discussed the nature of the axillary 'tubercle' found below each dichotomous branching point on the main axis, concluding that it was probably the remains of a third branch originally attached to the axis below the dichotomy, but which became detached either before or during preservation. The discovery by Banks and Davis (1969) of a sub-axillary branch in *Crenaticaulis*, another member of the Zosterophyllopsida, lends support to this interpretation.

Another probable member of the Zosterophyllopsida has been described from Craig-y-Fro by Edwards and Kenrick (1986) as *Tarella trowenii*. *Tarella* shares many features with *Gosslingia*, particularly the organization, orientation and general distribution of the sporangia, but it differs in having sporangia distributed in two vertical rows on opposite sides of the axes, in having isotomous branching of the main axial system, and in showing no evidence of axillary tubercles. *Tarella* also has prominent protuberances on the surface of the axes, not seen in *Gosslingia*, although the exact nature of these structures is uncertain. So far, no undoubted petrified axes of *Tarella* have been reported. Consequently, the form of the xylem strand is unknown, a feature essential before the form-genus can be unequivocally placed in the Zosterophyllopsida (Edwards and Edwards, 1986).

A species unique to Craig-y-Fro is *Krithodeophyton croftii* Edwards, 1968. It has naked, dichotomous axes bearing terminal, fertile spikes. The latter comprise of two vertical rows of alternating sporangia, and sterile bracts. It

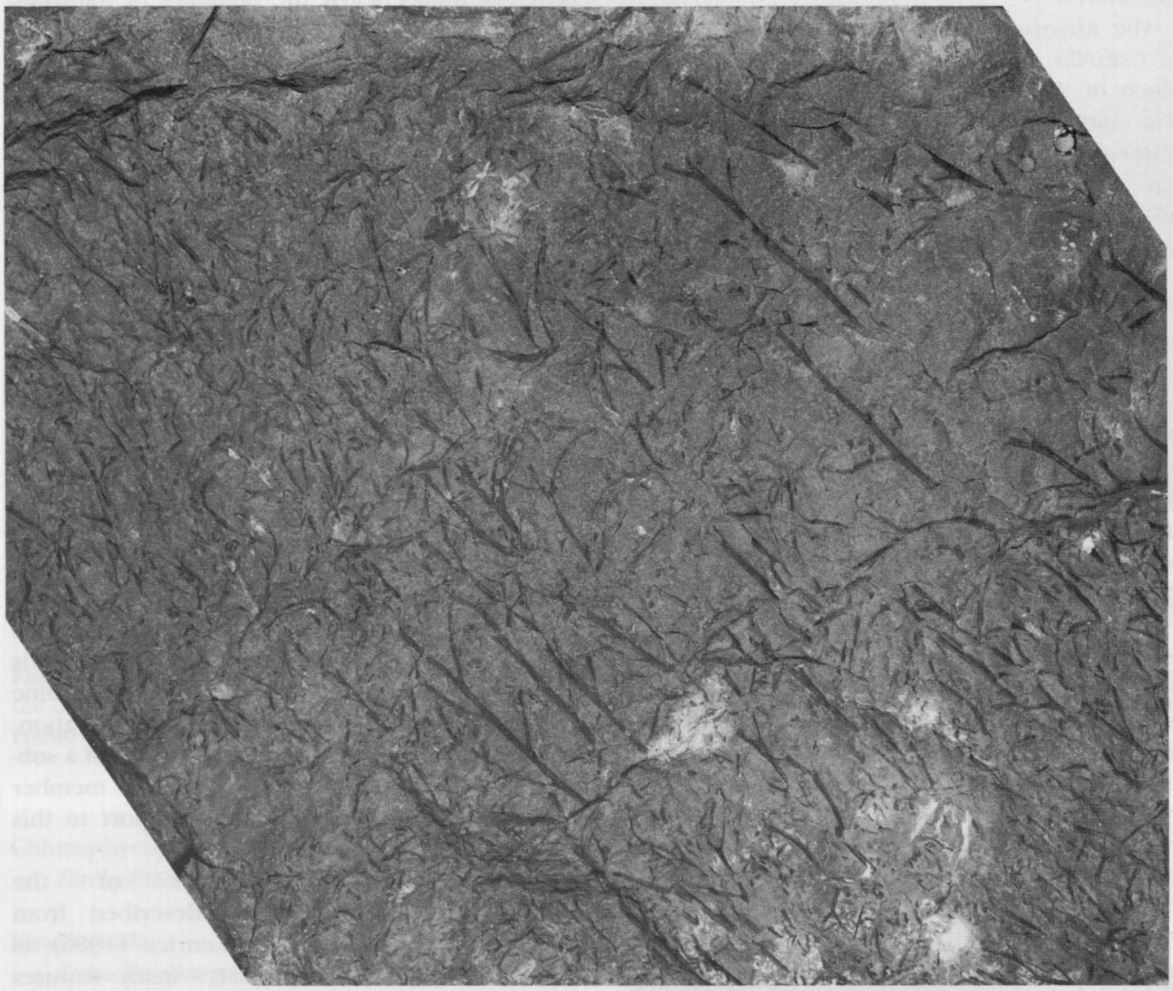

Figure 4.18 *Gosslingia breconensis* Heard. Branched axes with some lateral sporangia; Natural History Museum, London, specimen V.26575. Senni Beds (Siegenian), Craig-y-Fro Quarry. x 0.5. (Photo: Photographic Studio, Natural History Museum, London.)

compares closely with *Protobarinophyton* described from the Lower Devonian of Siberia (Ananiev, 1957), and is generally placed in the order Barinophytales. If this assignment is correct, it is the only member of the Barinophytales to have been described from Britain, and the oldest member of the order reported from anywhere in the world.

A number of petrified axes were included in *K. croftii* by Edwards (1968), but were later transferred by Edwards (1980a) to a separate species, *Hostinella beardii*. They are of only passing botanical interest, consisting merely of naked, dichotomous axes with a terete, centrarch xylem strand. However, Edwards (1980a) used them to explain how the tracheids became petrified. This seemed to have occurred in two phases: firstly, the filling of the tracheid lumen with pyrite; and then the replacement of the cell wall by pyrite. Little or no organic material seems to have remained (see also Kenrick and Edwards, 1988a).

A second type of petrified axis has been described as *Sennicaulis hippocrepiformis* Edwards (1981). It is represented by just a few specimens of smooth surfaced axes with a terete centrarch xylem strand, consisting of tracheids with distinctive helical and annular secondary thickenings. It probably belongs to either the Rhyniopsida or Trimerophytopsida.

The 'pyritized fructification' described by Heard

(1939) is a small capsule containing 250 µm diameter spherical objects. The latter were interpreted by Heard as spores, but they are far too large for this (they are more the size of megaspores) and show no evidence of a trilete mark. It is impossible to be certain at present exactly what this structure was.

The Craig-y-Fro assemblage is part of what is known as the Senni Beds group of floras, as described by Croft and Lang (1942). It belongs to the *Psilophyton* Zone of Banks (1980), and to the European phytogeographic subunit of Raymond *et al.* (1985) (comparable assemblages are dealt with in the discussion on Llanover Quarry, earlier in this chapter). It is second in diversity only to that found at Llanover Quarry, and includes some taxa not found there (*Tarella trowenii*, *Krithodeophyton croftii*, *Hostinella heardii*). It also yields pyrite petrifactions, which show the internal anatomy of the plants in finer detail than the limonite petrifactions of Llanover. Other than the Rhynie Chert assemblage, they represent the most completely known Devonian fossil plants from Britain.

Conclusion

Craig-y-Fro Quarry has yielded some of the best preserved Devonian plant fossils in Britain, second only in quality to those found in the Rhynie Chert (see below). They are about 400 million years old, and represent a flora typical of the southern and eastern margins of Laurussia. It is the best locality for two important types of early land plants, *Gosslingia* and *Tarella*. The first, and possibly the second of these are zosterophylls, which represent the ancestors of the club-mosses that dominated much of the land vegetation later in the Palaeozoic, including the Late Carboniferous equatorial coal swamps (see Chapter 7). It also has the earliest known example of a barinophyte (*Krithodeophyton*), which is one of the early groups of plants that adapted to the land environment during the Devonian, but which soon after disappeared, leaving no evolutionary successors. The fossils here are very similar to those from Llanover Quarry (see earlier in this chapter), but are more robustly preserved, which often makes them easier to study anatomically. Similar assemblages have also been reported from Belgium and Ukraine, but they have not been studied in such detail, and do not yield such well-preserved anatomical details.

BALLANUCATER FARM

R.J. Rayner

Highlights

Ballanucater Farm has yielded the best British assemblage of Emsian plant fossils with cuticles. They include the earliest known examples of spines with glandular tips.

Introduction

This small stream section near Callander, Central Region (Scotland – NN 630019) exposes plant-bearing clastic sediments of the Old Red Sandstone. Although plant fossils have been reported from localities in this area since the mid-nineteenth century (history summarized by Henderson, 1932 and Lang, 1932), the earliest records of specimens from Ballanucater Farm appear to be those by Henderson (1932) and Lang (1932). Since then some of the flora has been investigated by Edwards *et al.* (1982) and Rayner (1982, 1983, 1984), particularly with reference to the finely preserved cuticles.

Description

Stratigraphy

The sequence belongs to the Strathmore Group, as defined by Armstrong and Paterson (1970). It includes grey coarse flaggy sandstones and blue-green mudstones. Palynological evidence suggests that they are Emsian in age (Ford, 1974; Richardson *in* Rayner, 1983).

Palaeobotany

Plant fossils have been found in both the sandstones and the mudstones, the former yielding partially pyritized compressions and the latter carbonized compressions with cuticles. The following species have been described to date:

Chlorophycophyta(?):
    Pachytheca sp.

Zosterophyllopsida:
    Sawdonia ornata (Dawson) Hueber
    ?Margophyton goldschmidtii (Halle) Zacharova

Lycopsida:
Drepanophycus spinaeformis Göppert

Trimerophytopsida:
Dawsonites sp.

Discussion

Henderson (1932), Lang (1932), Edwards *et al.* (1982) and Rayner (1984) have all described specimens of *Drepanophycus spinaeformis* from here (Figure 4.19). Although there are older known examples of this form-genus, such as the Siegenian specimens from Craig-y-Fro (p. 71), these are the oldest yet found with cuticles preserved. The plant is lycopsid-like, with broad, leafy axes up to 30 mm wide, but with a comparatively narrow vascular strand, generally no more than 3 mm wide. No sporangia have been found at Ballanucater Farm but some excellent cuticle preparations show the arrangement of epidermal cells around the stomatal pore (Lang, 1932; Edwards *et al.*, 1982; Rayner, 1984). The twin guard cells are completely enclosed by two reniform subsidiary cells. These are the oldest compression fossils of land plants from which paired guard cells and paracytic subsidiary cells have been described. Comparable cuticles of *Drepanophycus* have been described from the Eifelian of North America (Stubblefield and Banks, 1978).

Figure 4.19 *Drepanophycus spinaeformis* Göppert. Leafy shoot; Natural History Museum, London, specimen V.58185. Strathmore Group (Emsian), Ballanucater Farm. x 1. (Photo: Photographic Studio, Natural History Museum, London.)

The most common constituent of the assemblage is *Sawdonia ornata* (syn. *Psilophyton princeps* var. *ornatum* Dawson), a spiny zosterophyll (*sensu* Banks, 1968). It was briefly described from here as part of the form-genus *Psilophyton* by Henderson (1932) and Lang (1932), but a fuller account is provided by Rayner (1983). The axes are up to 6.5 mm wide and divide pseudomonopodially. They are covered with black-tipped, multicellular spines (or trichomes), up to 3 mm long, which are believed to have been secretory. Cuticle preparations from here (Edwards *et al.*, 1982; Rayner, 1983) indicate the papillate nature of the epidermis, details of the 'hair bases' (*sensu* Edwards, 1924), and the structure of the stomata. The 'hair bases' consist of elongate, papillate epidermal cells around a central, isodiametric cell with a thin or incomplete cuticle cover. They have been termed 'rosettes' by Rayner (1983), but their function remains unknown. The stomata are round to elongate, and consist of a pore enclosed by a guard cell area. There is no evidence of the intercellular flanges in this area, which would have suggested that a pair of guard cells was present, and compare with the stomata of *Zosterophyllum myretonianum* Penhallow (Lele and Walton, 1962a; Edwards *et al.*, 1982). Nevertheless, Rayner (1983) interpreted the *Sawdonia* stomata as originally having had a pair of guard cells, and that the intercellular flanges were just not present in life. The guard cells lay at the bottom of a shallow stomatal pit, formed by cuticular thickenings between the subsidiary and guard cells (see also Zdebska, 1972; Chaloner *et al.*, 1978).

An interesting feature of this locality is the presence of small bodies (diameter 90 μm or less) inside many of the macerated *Sawdonia* spines. Lang (1932) described them as fungal vesicles, under the name *Palaeomyces* sp., whereas Rayner (1983) interpreted them as possibly the spore resting stage of a fungus.

Within the sandstones, there are many spiny axes that appear to conform to Halle's (1916) description of *Psilophyton goldschmidtii* Halle, and were identified as such by Lang (1932). Halle erected the species to describe sterile, spiny axes with a distinctive branching pattern, found in Norway. The specimens from Ballanucater Farm are also sterile and look very similar to those illustrated by Halle. The main axes are up to 5 mm wide and divide pseudomonopodially, in contrast to the much narrower lateral branches which fork dichotomously. There is a continuous line on the axes running parallel to the edges. There are also oval regions filled with matrix at the point of divergence of the lateral branches, which may correspond to axillary tubercles. This species has since been transferred to the genus *Margophyton* by Zakharova (1981), who regarded it as a zosterophyll (see also Edwards *et al.*, 1989). However, in the absence of fertile organs, it is impossible to be certain whether or not the Ballanucater specimens also belong here.

Clusters of fusiform sporangia are found both as fossils on the rock surfaces, and in maceration residues. They are best assigned to the form-genus *Dawsonites* as, although they are sometimes connected to quite extensive dichotomously branching axes, they lack any distinguishing features which would allow identification with any species of *Psilophyton*. The fusiform sporangia are elongate, 4–6 mm long, pendulous, and borne terminally on dichotomizing axes. They occur in pairs, the individuals of which are often twisted around one another. They dehisce longitudinally, and contain trilete spores averaging 60 μm in diameter. The spores are almost completely enclosed by a finely sculptured outer exine, which shows a tendency to break away from mature individuals.

The presence of *Dawsonites* in the Ballanucater assemblage indicates that it belongs to the *Psilophyton* Zone (Banks, 1980; Edwards and Berry *in* Cleal, 1991). Similar assemblages have been reported from a series of localities in the Callander area (Jack and Etheridge, 1877; Henderson, 1932; Lang, 1932), but Ballanucater Farm has yielded easily the best preserved and most abundant specimens. A similar assemblage has also been reported from Auchensail Quarry near Cardross (p. 78), but no evidence of cuticles has been found there.

Raymond *et al.* (1985) place this assemblage in their American phytogeographic subunit of the equatorial and low latitude floras. The only other British *Psilophyton* Zone assemblage belonging to this subunit was found in Emsian beds in a borehole in Oxfordshire (Chaloner *et al.*, 1978). Those from the Siegenian Senni Beds of south-east Wales, such as from Craig-y-Fro and Llanover (pp. 67–75), belong to the European subunit of Raymond *et al.* (1985) and differ from the Strathmore Group assemblages in their more diverse composition. From outside of Britain, assemblages with a more comparable, restricted composition have been reported from Rörangen, Norway (Halle, 1916), Matringhem, France (Danzé-Corsin, 1955) and James Bay, Canada (Hueber, 1964). However, none of these places has yielded such well-preserved cuticles as found at Ballanucater. This gives Ballanucater a unique significance in Lower Devonian palaeobotany, especially for work on early epidermal structures (e.g. stomata, trichomes), whose evolution was a key factor in allowing plants to overcome the problems of desiccation inherent in living in a terrestrial environment.

Conclusion

Ballanucater Farm has yielded an important assemblage of fossils representing plants of 390 Ma. The fossils are particularly important as they still preserve the outer, protective skin of the plant (known as the cuticle), in which details of the microscopic breathing pores (stomata) and hairs can be seen. They are some of the oldest known examples of modern-looking stomata, in which the pore is surrounded by two specialized cells (guard cells) that control the size of the opening. This was an important development for helping plants adapt to the land environment, allowing greater control over water-loss and gas-exchange with the atmosphere. A similar assemblage of fossils occurs at Auchensail Quarry (p. 78), as well as at localities in Norway, Belgium and Canada, but none has yielded such well-preserved cuticles as found at Ballanucater.

AUCHENSAIL QUARRY

R.J. Rayner

Highlights

Auchensail Quarry has yielded some of the best preserved plant fossils from the Emsian of Britain (Figure 4.20). These include exceptionally well-preserved examples of *Sawdonia*, and the youngest examples of *Prototaxites* known from Britain.

Introduction

Recent quarrying near Cardross, Strathclyde Region, has exposed Lower Devonian sandstones containing abundant plant fossils (NS 345795). They were first reported by Scott *et al.* (1976) and Morton (1976). Some of the species have since been studied in detail by Rayner (1982, 1983, 1984), and revealed considerable anatomical detail.

Description

Stratigraphy

The geology is described by Scott *et al.* (1976). The sequence consists of units of shallow-water, red siltstones and mudstones, up to 2 metres thick, alternating with well indurated, grey, upward-fining sandstones (Figure 4.21). They belong to the Strathmore Group (*sensu* Armstrong and Paterson, 1970), and were interpreted by Scott *et al.* as fluviatile in origin. An Emsian age has been suggested by Richardson (*in* Rayner, 1983).

Palaeobotany

The plant fossils occur abundantly in the sandstones. Mats of coalified compressions occur mainly within the upper part of the sandstone units, while discrete pyrite petrifactions occur throughout the beds.

Figure 4.20 Auchensail Quarry. Emsian sandstones and shales of the Strathmore Group. Note the igneous dyke just to the left of centre of the quarry face as shown. (Photo: C.J. Cleal.)

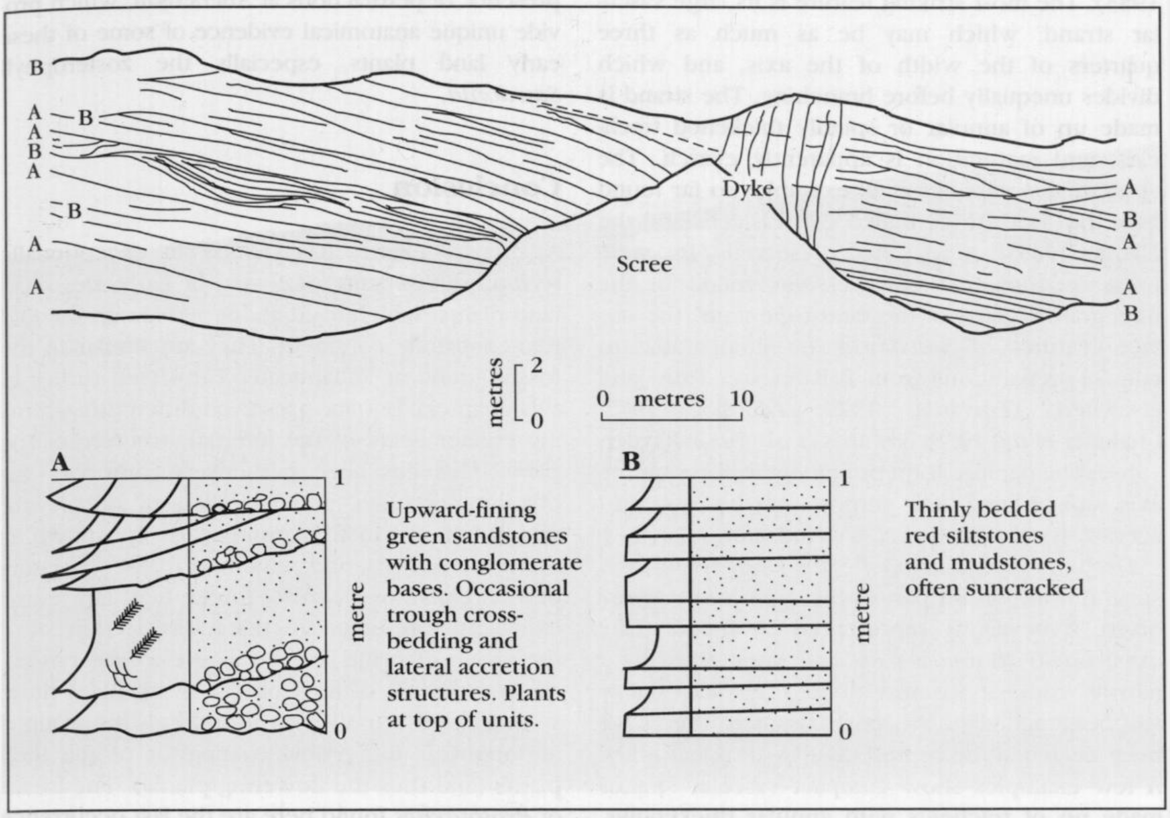

Figure 4.21 Sedimentology of the Strathmore Group (Emsian) at Auchensail Quarry. Based on Scott *et al.* (1976).

Phaeophycophyta(?):
  Prototaxites sp.

Rhyniophytoid:
  ?*Sporogonites* sp.

Zosterophyllopsida:
  Zosterophyllum sp.
  Sawdonia ornata (Dawson) Hueber

Lycopsida:
  Drepanophycus spinaeformis Göppert

Trimerophytopsida:
  Dawsonites sp.

Interpretation

Prototaxites is represented here by axes 5–50 mm wide. They have not been described in detail in the published literature, but are of interest as the youngest British specimens of this form-genus (younger specimens have been described from North America by Arnold, 1952).

Occurring within the mats of coalified compressions are many examples of narrow axes (<10 mm wide) that branch pseudomonopodially, have circinate vernation, a papillate epidermis and are covered with swollen-tipped spines. Despite the lack of well-preserved cuticles, these specimens have been identified as *Sawdonia ornata* (Rayner, 1983). The form of two fertile specimens, the first of such to be reported from Europe, indicate that the plant was a true zosterophyll (*sensu* Banks, 1968) with lateral sporangia apparently arranged in a terminal spike. The sporangia are sessile, oval in shape and up to 4 mm across. Several have a 'V'-shaped incision on the axial surface, which might be a dehiscence scar. Spores have been isolated from several sporangia and are small (35–40 μm), subtriangular, with an indistinct trilete mark.

The internal anatomy of the *Sawdonia* axes from here has been investigated using plastic embedding and sectioning techniques (Rayner, 1983). The most striking feature is its large vascular strand, which may be as much as three quarters of the width of the axis, and which divides unequally before branching. The strand is made up of annular or spirally thickened tracheids, and maturation is apparently exarch. The epidermis is missing on all examples so far found here, but both thick-walled cortical cells and the characteristic spines are preserved. In well-preserved coalified compressions found in the finer-grained parts of the sandstone units, the surface features of *Sawdonia* are comparable to cuticle preparations from Ballanucater Farm and elsewhere (Edwards, 1924; Zdebska, 1972; Chaloner *et al.*, 1978; Edwards *et al.*, 1982; Rayner, 1983). The papillae form prominent features on the axis surfaces, and their purpose may have been to act as a shield against excessive radiation.

Drepanophycus spinaeformis Göppert forms a small but important part of the Auchensail assemblage. It is mainly represented by broad, leafy axes, up to 25 mm across, and often showing a narrow zone of vascular tissue. The leaves may still be attached to the axis or, where they have been detached, be represented by oval leaf scars. A few examples show compact vascular strands made up of tracheids with annular thickenings. Petrifactions from another Strathmore Group exposure at Keltie Water (Rayner, 1984) have shown that the xylem had a deeply lobed cross-section, but this has yet to be observed in specimens from Auchensail.

Pairs of *Dawsonites*-type sporangia have been found here at the ends of dichotomizing branches. Several have yielded spores similar to those from Ballanucater Farm. The axes, which are up to 5 mm wide, are naked but have a series of longitudinal striations preserved on the upper surfaces. There is no evidence, however, of axillary structures.

Other terminal sporangia found here are similar to *Sporogonites* Halle. These sporangia have been compressed to form an oval capsule at the end of a simple striated stalk. The specimens have failed to yield spores, and they may only be compared with Halle's (1916) description on gross morphology.

This site has yielded plant fossils typical of the Strathmore Group of Scotland, and similar to those found at Ballanucater Farm (a discussion on similar plant fossil assemblages, from both Britain and abroad, is given in the section dealing with Ballanucater Farm). However, it differs from the latter site in having *Prototaxites* and *Sporogonites*, but lacking *Psilophyton*. More significant is the presence of petrifactions at Auchensail, which provide unique anatomical evidence of some of these early land plants, especially the zosterophyll *Sawdonia*.

Conclusion

Auchensail Quarry has yielded an exceptionally well-preserved suite of fossils of Early Devonian land plants, which lived about 390 Ma on the Old Red Sandstone continent. They are similar to the fossils found at Ballanucater Farm (see earlier in this chapter), but are preserved differently, showing greater detail of the internal structure of the plant. This has been particularly important for obtaining a fuller understanding of *Sawdonia*, which belongs to the primitive group known as the zosterophylls, and which were the ancestors of the club-mosses. Also found here are some excellently preserved fructifications (sporangia) of the group of plants known as the trimerophytes, showing details of how on the living plant these sporangia split to release the spores. This group is important as the probable ancestor of the seed plants (and thus the flowering plants). The fossils of *Prototaxites* found here are the last occurrence of this large, enigmatic alga in Britain, although Late Devonian examples have been reported from North America. These algae were an important component of land vegetation in the Late Silurian and earliest Devonian, but became displaced by the better adapted vascular plants during the later part of the Early Devonian.

RHYNIE

Highlights

Rhynie is probably the most important palaeobotanical site in Britain, yielding the oldest known vascular plant fossils with well-preserved anatomical details (Figure 4.22). The 22 species of plant fossil (including fungi) are unique to this locality, and include the 'type-genus' of the Rhyniophytina (*Rhynia* – the best-known early land plant), the earliest well-documented lycopsid (*Asteroxylon*), and a variety of enigmatic species evidently representing early experiments in adaptation to a terrestrial environment. It is also the oldest known example of an *in situ* fossilized terrestrial ecosystem.

Rhynie

Figure 4.22 Rhynie. The field just outside of the village, under which lies the Siegenian fossiliferous chert. (Photo: C.J. Cleal.)

Introduction

This famous locality lies beneath a field near the village of Rhynie, 14 km south of Huntly, in the Grampian Region of Scotland (NJ 495264). Probably no other single site has had such an impact on the development of palaeobotany. Walton (1959) described it as 'the most dramatic and important palaeobotanical discovery of the century'. Prior to its discovery, the structure and taxonomic affinities of Lower Devonian plant fossils (until then almost exclusively known as adpressions) were still a matter of debate, and many scientists argued that they were either algal or indeterminable fragments of 'advanced' vascular plants. The petrifactions discovered at Rhynie confirmed that vascular plants did exist during the Early Devonian and that they were truly 'primitive'. This has had a major impact on evolutionary ideas and the classification of the Plant Kingdom.

The general background to the Rhynie Chert locality and its fossilized biota is summarized by Chaloner and Macdonald (1980). There is no natural outcrop of the chert, and it was first found as loose blocks in a field and in a dry-stone wall (Mackie, 1913) (Figure 4.23). Subsequently, however, the Geological Survey excavated a series of trenches through the field, revealing the rock *in situ* and allowing a large quantity of the material to be collected (Horne, 1917; Horne and Mackie, 1917, 1920a, b; Kidston, 1922, 1923e). The specimens were the subject of a series of now classic monographs by Kidston and Lang (1917b, 1920a, b, 1921a, b), in which anatomical details of the plants were described from thin sections of the chert. Pant (1962) argued that Kidston and Lang had been able to determine such fine cellular structure that details of the Rhynie plants were 'nearly as complete as they could be even if the plants were living today'. The method used by Kidston and Lang was, however, not so good at

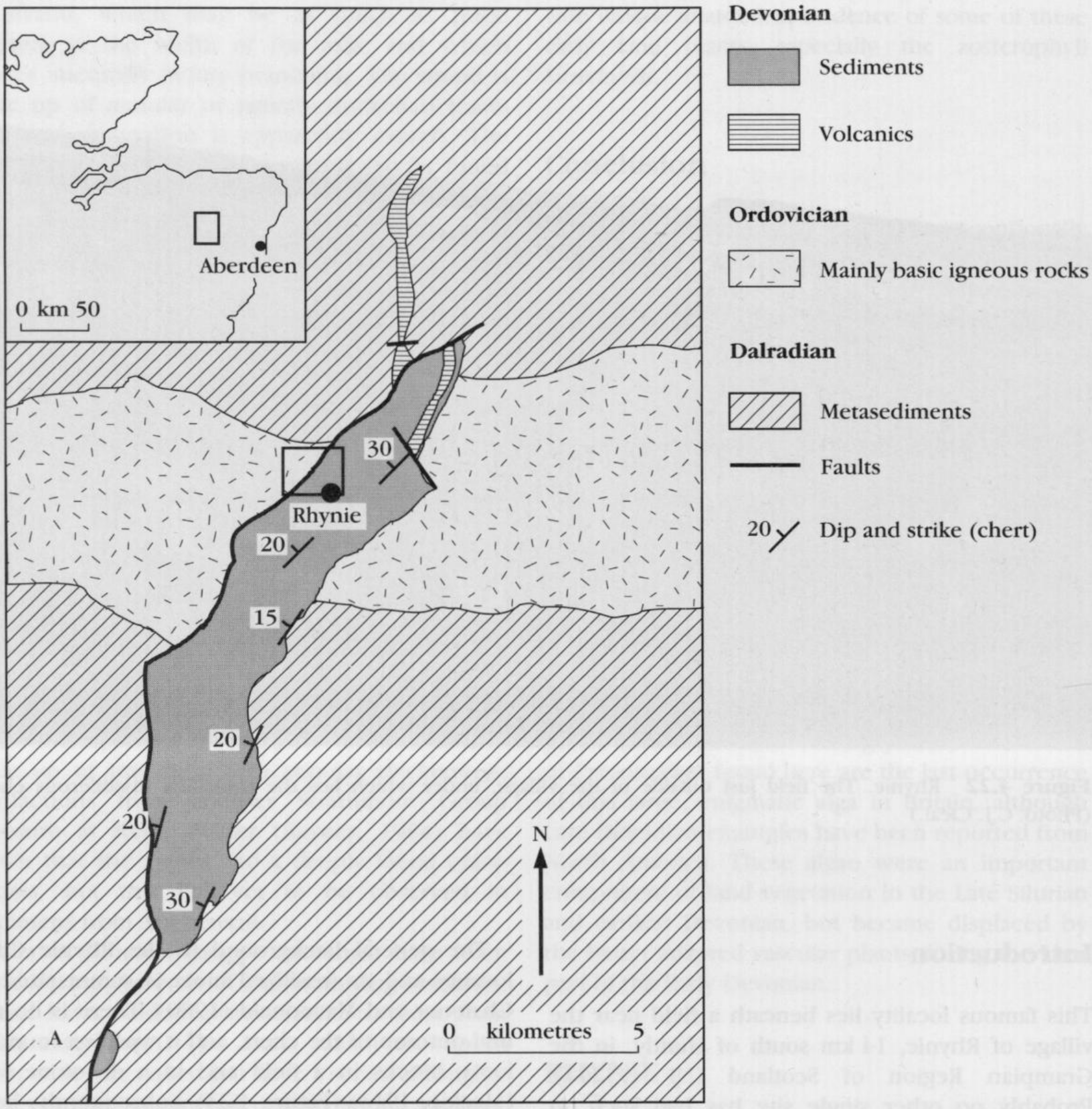

Figure 4.23 Geology of the Rhynie area. (A) Map showing the outline of the Rhynie outlier. (B, facing page) Map showing detail of that part of the outlier containing the fossiliferous chert (marked by a rectangle on A). Based on Trewin and Rice (1992, figure 1), who provide details of the boreholes marked on (B).

revealing the gross morphology of the plants; their reconstructions (Kidston and Lang, 1921a, pls 1–2) were rather oversimplified. More refined results were only possible when the peel method (Joy *et al.*, 1956) was used, allowing more closely-spaced serial sections to be made. Examples of the use of such techniques are given by Bhutta (1972), Eggert (1974), El-Saadawy and Lacey (1979a, b), Edwards (1980, 1986), Edwards and Lyon (1983), and Lyon and Edwards (1991). Despite being known for over 70 years, new discoveries are still being made at Rhynie (e.g. the vascularized gametophyte by Remy and Remy 1980a, Remy and Hass, 1991a, b, c and Remy, 1991) and there remains considerable potential for further work here.

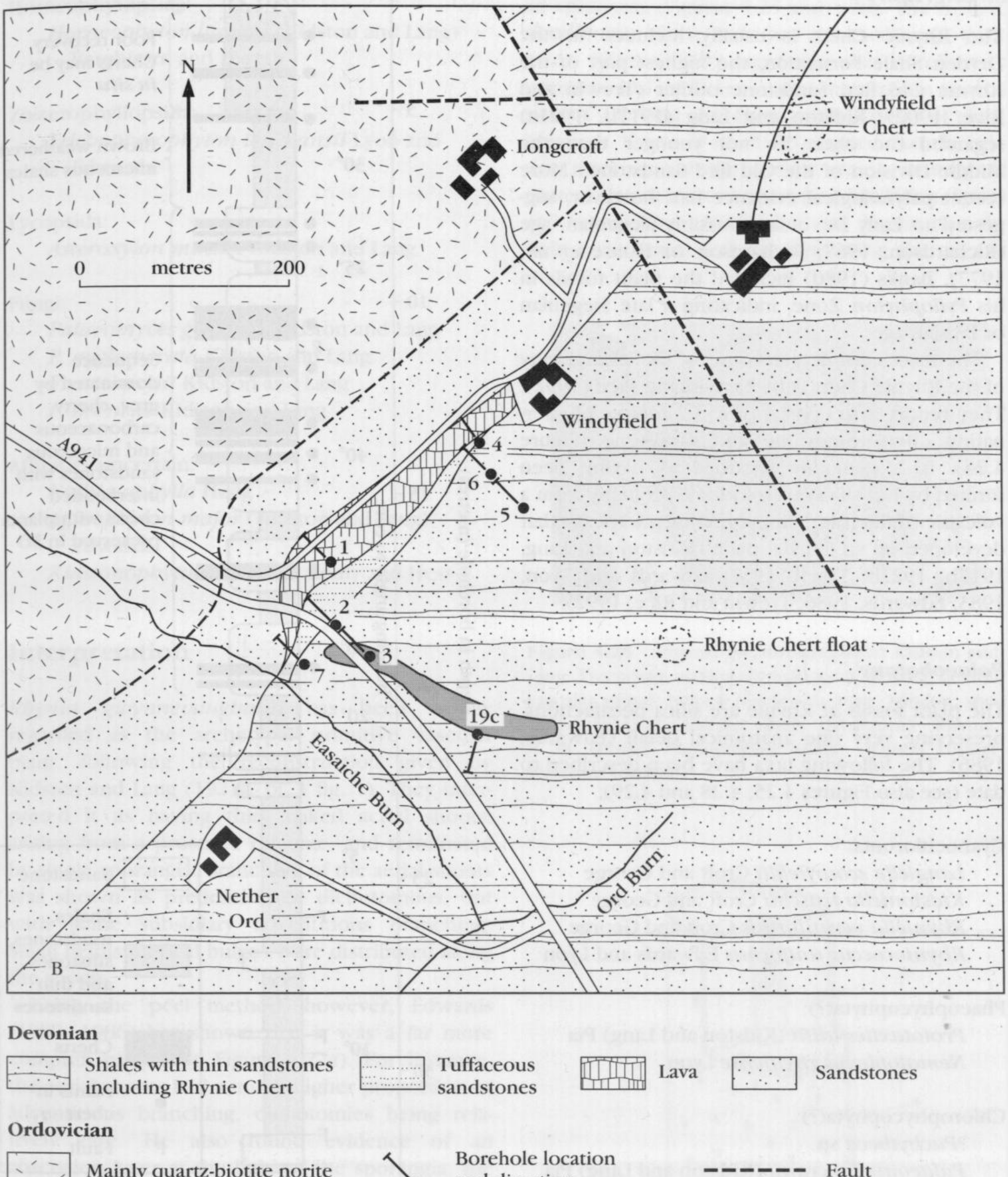

Figure 4.23 *contd*

Description

Stratigraphy

The Rhynie Chert is usually included in the Dryden Shale Formation, the highest part of the Rhynie Old Red Sandstone outlier (Trewin and Rice, 1992). Kidston and Lang (1917b, 1921a) regarded the chert as 'not younger than the Middle Division of the Old Red Sandstone'. More recent palynological evidence has, however, suggested an Early Devonian, possibly Siegenian, age (Richardson, 1967; Richardson *in* House *et al.*, 1977). Banks (1980) included the plant fossils in his *Psilophyton* Zone, indicating a late Siegenian or Emsian age.

The most complete account of the stratigraphy of the Rhynie Chert is by Trewin and Rice (1992). They report it to consist of *c.* 3.2 metres of alternating chert, mudstone and sandstone (Figure 4.24). It is generally regarded as having been formed by hot siliceous solutions, probably from a volcanic fumerole, impregnating a peat that developed on an alluvial plain (Kidston and Lang, 1917b, 1921b; Tasch, 1957; Edwards and Lyon, 1983; Edwards, 1986; Trewin and Rice, 1992):

Palaeobotany

The plant fossils at Rhynie are silica petrifactions, preserving very fine anatomical detail (Edwards, 1986). The following taxa have been described to date (see also Figures 4.25, 4.28 and 4.29):

Cyanochloronta:
  Langiella scourfieldii Croft and George
  Kidstoniella fritschii Croft and George
  Rhyniella vermiformis Croft and George
  Rhyniococcus uniformis Edwards and Lyon

Phaeophycophyta(?):
  Prototaxites taitii (Kidston and Lang) Pia
  Nematoplexus rhyniense Lyon

Chlorophycophyta(?):
  ?*Pachytheca* sp.
  Palaeonitella cranii (Kidston and Lang) Pia
  Archaeothrix oscillatoriformis Kidston and Lang
  A. contexta Kidston and Lang
  Mackiella rotundata Edwards and Lyon
  Rhynchertia punctata Edwards and Lyon

Rhyniopsida:
  Rhynia gwynnevaughanii Kidston and Lang

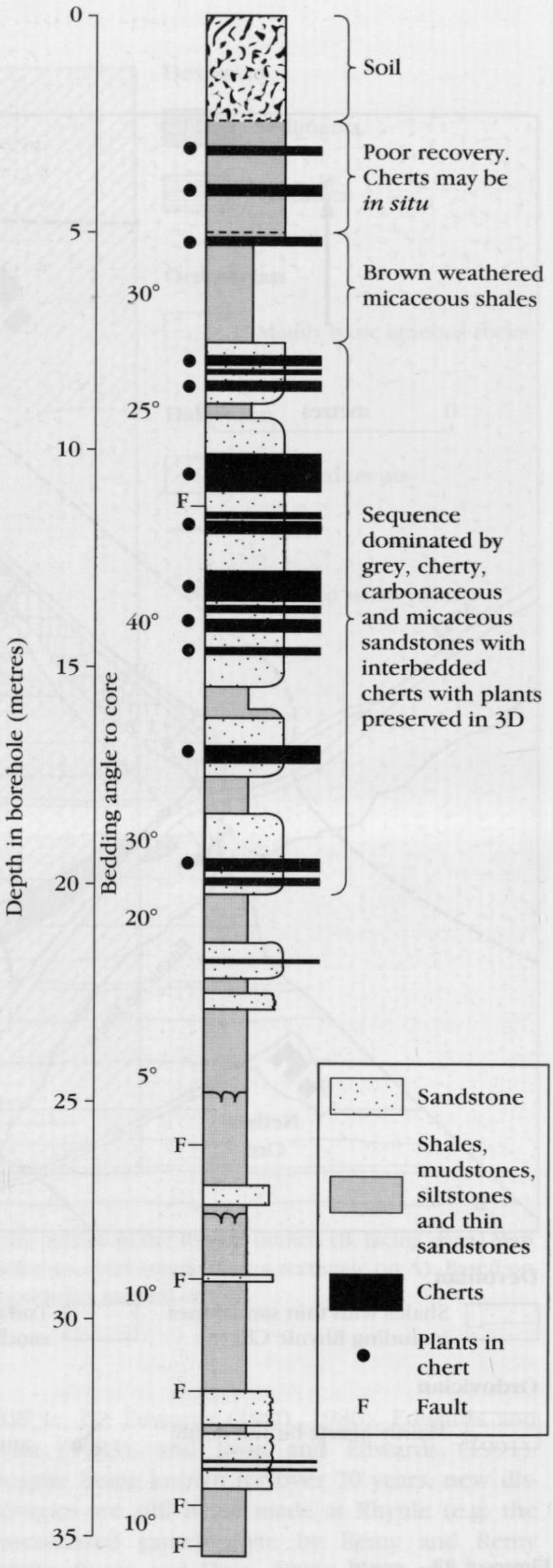

Figure 4.24 Composite log through Rhynie Chert showing distribution of plant-bearing horizons. Based on Trewin (1989, p. 11).

Lyonophyton rhyniensis Remy and Remy
Langiophyton mackei Remy and Hess

Horneophytopsida:
Horneophyton lignieri (Kidston and Lang) Barghoorn and Darrah

Zosterophyllopsida:
Trichopherophyton teuchansii Lyon and Edwards

Lycopsida:
Asteroxylon mackei Kidston and Lang

Fungi:
Palaeomyces gordonii Kidston and Lang
P. agglomerata Kidston and Lang
P. asteroxylii Kidston and Lang
P. horneae Kidston and Lang

Affinities uncertain:
Nothia aphylla Høeg
Aglaophyton major (Kidston and Lang) Edwards
Kidstonophyton discoides Remy and Hess

Interpretation

Rhynia gwynnevaughanii has been widely regarded as the archetypal primitive vascular plant, following the reconstruction given by Kidston and Lang (1921a, pl. 1 fig. 1). They interpreted it as having thin, naked aerial shoots, arising from a prostrate rhizome, and terminated by single sporangia. Branching of the aerial shoots was shown as predominantly dichotomous, but with some subsidiary adventitious branching. Small hemispherical bulges were distributed along the shoots.

Using the peel method, however, Edwards (1980, 1986) has shown that it was a far more complex plant (see Figure 4.27a). For instance, the aerial shoots had a much higher proportion of adventitious branching, dichotomies being relatively rare. He also found evidence of an abscission layer at the base of the sporangia, the latter being shed after the release of their spores. An adventitious branch occurs immediately below the site of many of the sporangia.

Although perceptions about the *R. gwynnevaughanii* gross morphology have changed over the years, Kidston and Lang's (1917a, b) interpretation of the anatomy of the aerial shoots is still generally accepted. The aerial shoots consist of a very slender, terete, centrarch stele, surrounded by a cylinder of phloem, a two-layered cortex and an epidermis (Figures 4.25 and 4.26). The relative slenderness of the stele has attracted some comment, Filzer (1948) suggesting that it reflects a primitive and inefficient water metabolism control system. Looking at it from another point of view, however, Kevan *et al.* (1975) argued that the relative thickness of the cortex was a strategy to protect the stele from arthropod predation. Speck and Vogellehner (1988a, b) have shown that the stele contributed little to supporting the axes in

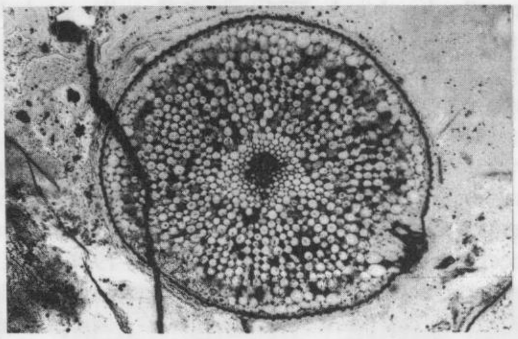

Figure 4.25 *Rhynia gwynnevaughanii* Kidston and Lang. Transverse section through stem showing central vascular strand; Natural History Museum, London, specimen SC.3132. Rhynie Chert (Siegenian), Rhynie. × 25. (Photo: Photographic Studio, Natural History Museum, London.)

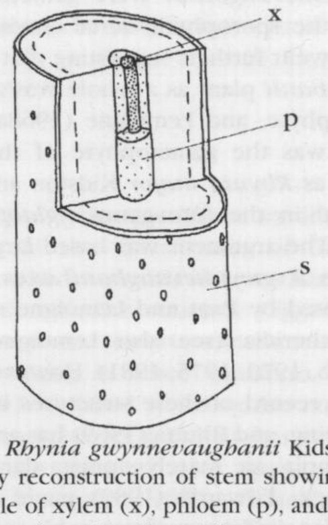

Figure 4.26 *Rhynia gwynnevaughanii* Kidston and Lang. Cut-away reconstruction of stem showing cylindrical protostele of xylem (x), phloem (p), and stomata on the stem surface (s). From Thomas and Spicer (1987, figure 3.2D; after Chaloner and Macdonald).

such early land plants, which was mainly controlled by turgor in the cortex.

Satterthwaite and Schopf (1972) described what they regarded as sieve-like structures in the cylinder of phloem (Satterthwaite and Schopf identified their specimens as *'Rhynia' major* Kidston and Lang, but Lemoigne and Zdebska (1980) have argued that they almost certainly belong to *R. gwynnevaughanii*). If correctly interpreted, this remains the oldest unequivocal evidence of phloem tissue in the fossil record.

R. gwynnevaughanii sporangia have traditionally been interpreted as lacking a dehiscence structure, a view which was supported by Edwards (1980). However, Remy (1978) has described a band of thin-walled cells, probably lying longitudinally along the sporangium, which may have functioned as a line of weakness to facilitate rupturing (a stomium). No evidence of an annulus was reported, but opposite the stomium was a flexible, so-called joint region, which again may have helped in the dehiscence process. Remy's interpretation has not received universal acceptance (Edwards and Edwards, 1986) but, if proved correct, it will require a significant modification to our view of *Rhynia* as a simple land plant.

Another contentious issue surrounding *R. gwynnevaughanii* is its possible status as a vascularized gametophyte. Considering the fine preservation in the chert, the apparent absence of readily identifiable gametophytes of the Rhynie plants had puzzled palaeobotanists (e.g. Chaloner, 1960; Pant, 1962). Merker (1958, 1959, 1961) argued that perhaps some of the prostrate axes of *R. gwynnevaughanii* were gametophytes, from which the sporophytic aerial shoots arose. Pant (1962) went further, suggesting that the *R. gwynnevaughanii* plant as a whole was a vascularized gametophyte, and Lemoigne (1968a) has argued that it was the gametophyte of the plant then known as *Rhynia major* Kidston and Lang (now included in the form-genus *Aglaophyton* – see p. 89). The argument was based largely on structures on *R. gwynnevaughanii* axes, which were interpreted by Pant and Lemoigne as archegonia and antheridia (see also Lemoigne, 1968b, c, 1969a, b, 1970, 1975, 1981). However, the photographic record of these structures is not entirely convincing, and Bhutta (1969) has argued that the 'archegonia' are merely stomata damaged by fungal attack. Edwards (1980) made an extensive search for similar structures in his specimens of *R. gwynnevaughanii*, without success, and furthermore found unequivocal evidence that at least the aerial shoots of the plant were sporophytic. Edwards (1979b) argued that the gametophytes of the primitive vascular plants were fast growing and quick to mature, and thus had a very low preservational potential. Alternatively, Edwards (1986) suggested that gametophytes of these plants only developed under relatively rare and favourable conditions, and that they normally spread by the development of extensive growth of the sporophytic generation. Whatever the true explanation, the nature of the *R. gwynnevaughanii* gametophytes is unknown.

Based mainly on Kidston and Lang's observations, *Rhynia* has been used as the effective type of the most primitive class of vascular plants – the Rhyniopsida (Banks, 1975b). In this role, it has tended to be central to any discussion on the early evolution of vascular plants. However, the new evidence provided by Edwards (1980) has required the concept of the Rhyniopsida to be modified and enlarged (Edwards and Edwards, 1986). It still probably represents the most primitive class of vascular plants, but now includes forms such as *Renalia* showing a wider diversity of morphologies, particularly in the branching of the axes.

R. gwynnevaughanii has also played a key role in understanding the early evolution of the stele and leaves. It had been argued that the stele first evolved in leaves, and only later developed in stems by the coalescence of the leaf traces (for example see comments by Arber, 1921). The evidence from *Rhynia* clearly indicates that the primitive condition is a simple protostele in the stem (Scott, 1924a). Zimmermann's (1926) discovery that the stomata are associated mainly with the hemispherical bulges on the aerial shoots suggests that these bulges may represent the early phases in the development of non-vascularized, leaf-like emergences, similar to those of *Asteroxylon* (see below). Further aspects of the epidermal structure of *Rhynia* are discussed by Edwards *et al.* (1982).

Another primitive vascular plant found at Rhynie was described as *Hornea lignieri* Kidston and Lang (later re-named *Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah, 1938). It has been reconstructed, with thin, dichotomous axes arising from a corm-like rhizome (Kidston and Lang, 1921a; Eggert, 1974) (Figures 4.27B, C and 4.28). The axes have a very irregular surface, which Eggert (1974) argued to be a taphonomic effect, but which El-Saadawy and Lacey (1979b)

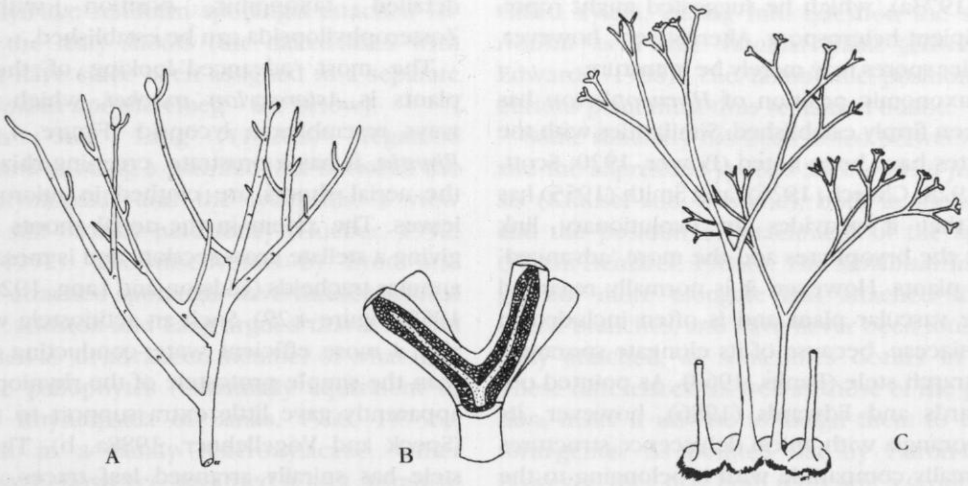

Figure 4.27 (A) *Rhynia gwynnevaughanii* Kidston and Lang; reconstruction of aerial parts of plant including terminal sporangia. (B-C) *Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah; (B) cut-away reconstruction of dichotomizing sporangia showing the central columella; (C) reconstruction of whole plant. From Thomas and Spicer (1987, figure 3.2C, E, and F; after Eggert and D.S. Edwards).

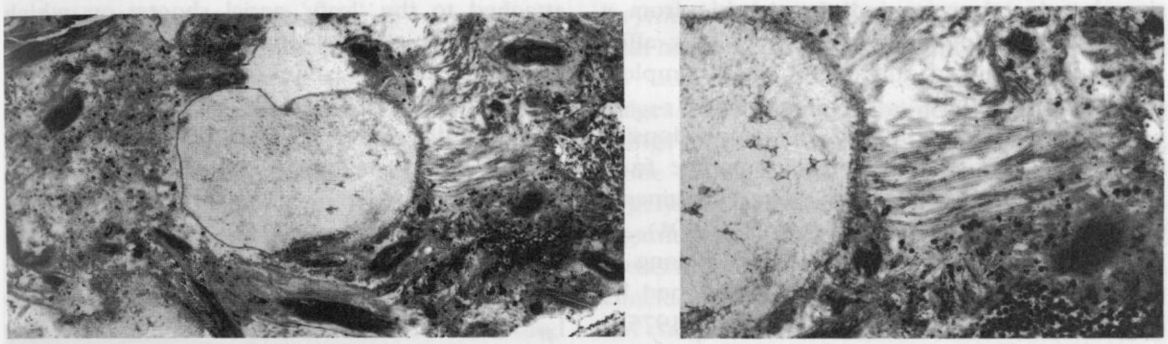

Figure 4.28 *Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah. Longitudinal sections through corm-like rhizome; Natural History Museum, London, specimen V.15648. Rhynie Chert (Siegenian), Rhynie. (left) × 8, (right) × 5. (Photos: Photographic Studio, Natural History Museum, London.)

interpreted as being due to small emergences, as in *Nothia* (p. 89). The anatomy of the aerial shoots is essentially similar to that of *Rhynia*, except that the terete, centrarch stele is rather thicker. The nature of the transverse breaks in the protostele observed by Kidston and Lang (1920a) has never been properly established, but might be a preservational feature. The limited available evidence of the cuticles of *Horneophyton* is discussed by Edwards *et al.* (1982).

In addition to its corm-like rhizome, *Horneophyton* is distinctive because of the structure of its apical sporangia. These are little more than cavities in the apical parts of the aerial shoots, into which extends the vascular tissue, forming a columella-like structure (Eggert, 1974, fig. 28). These fertile shoot-terminations are often branched, resulting in lobed sporangia. Kidston and Lang (1920a) failed to recognize any dehiscence structures, but an apical slit has since been reported in the apex of each sporangial lobe (Bhutta, 1972; Eggert, 1974; El-Saadawy and Lacey, 1979b). Considerable variation in the size and ornamentation of the spores was found by

Bhutta (1973a), which he suggested might represent incipient heterospory. Alternatively, however, the smaller spores may merely be immature.

The taxonomic position of *Horneophyton* has never been firmly established. Similarities with the bryophytes have been noted (Bower, 1920; Scott, 1924a, 1928; Church, 1926), and Smith (1955) has argued that it provides an evolutionary link between the bryophytes and the more 'advanced' vascular plants. However, it is normally regarded as a true vascular plant and is often included in the Rhyniaceae, because of its elongate sporangia and centrarch stele (Banks, 1968). As pointed out by Edwards and Edwards (1986), however, its lobed sporangia with apical dehiscence structures are not really compatible with it belonging to the Rhyniopsida. Eames (1936) placed it in its own family, the Horneaceae, whereas Meyen (1978, 1987) included it in a monotypic class, the Horneophytopsida. The latter view has been followed here.

Lemoigne (1966) has described a possible spore-producing capsule of a bryophyte from Rhynie. It contains spores of only about half the size, but is otherwise indistinguishable from a *Horneophyton* sporangium. Its bryophytic affinities must remain in doubt until more complete specimens are found.

For many years, the zosterophyllopsids appeared to be notable by their absence from Rhynie. Recently, however, some fragments described by Lyon and Edwards (1991) as *Trichopherophyton teuchansii,* clearly belong to that class (they had earlier been mentioned by Lyon *in* Lindley (1968) and Gensel *et al*. (1975)). Particularly distinctive features are their spiny axes with a terete, exarch stele, circinately-tipped shoots, and marginally dehiscent sporangia. The main difficulty with interpreting the fossils was that many features of the gross-morphology could not be determined, in particular the configuration of the sporangia on the axes; most other zosterophyllopsids are identified on such features of gross morphology. However, that the spines on the axes are unicellular structures seems to be unique in the class; the emergences found in the other genera such as *Sawdonia* and *Crenaticaulis* are multicellular. The more or less terete stele also contrasts with that present in most other members of the class, in which it tends to be oval in cross-section. These factors alone are enough to justify placing this Rhynie species in a separate form-genus. However, much more information on its gross morphology will be needed before its detailed taxonomic position within the Zosterophyllopsida can be established.

The most 'advanced'-looking of the Rhynie plants is *Asteroxylon mackei*, which in many ways resembles a lycopsid (Figure 4.4a). Like *Rhynia*, it has a prostrate, creeping rhizome, but the aerial shoots are clothed in microphyll-like leaves. The xylem in the aerial shoots is fluted, giving a stellate cross-section, and is mesarch with annular tracheids (Kidston and Lang, 1920b; Lang, 1952; Figure 4.29). Such an actinostele was probably a more efficient water-conducting structure than the simple protostele of the rhyniopsids, but apparently gave little extra support to the plant (Speck and Vogellehner, 1988a, b). The actinostele has spirally arranged leaf traces, but they only enter the very base of the leaves, which are thus not the same as true lycopsid microphylls. Two types of leaves were recognized by Edwards *et al.* (1982), those with a smooth surface, and those with an undulate surface caused by epidermal cells with a strongly convex outer wall.

Kidston and Lang (1921a) reconstructed *Asteroxylon* with naked, dichotomous axes attached to the 'leafy' aerial shoots, on which were borne terminal sporangia. This was based on the frequent association of such naked shoots with the more typical *Asteroxylon* axes. Subsequently, however, Lyon (1964) and Bhutta (1969) found examples of *Asteroxylon* with

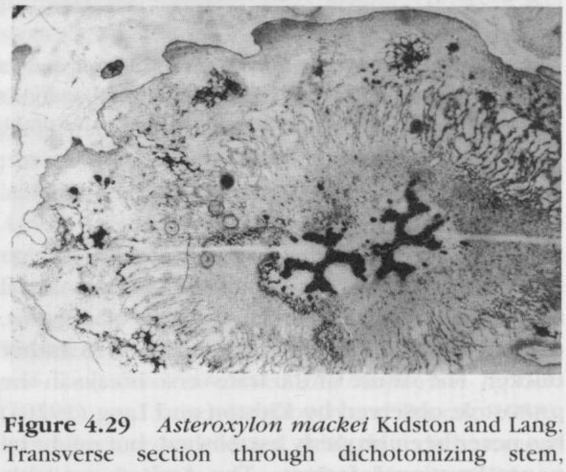

Figure 4.29 *Asteroxylon mackei* Kidston and Lang. Transverse section through dichotomizing stem, showing two vascular traces with the characteristic stellar cross-section; Natural History Museum, London, specimen V.15643. Rhynie Chert (Siegenian), Rhynie. × 6.66. (Photo: Photographic Studio, Natural History Museum, London.)

zosterophyll-like reniform sporangia attached laterally to the leafy shoots (the naked axes with sporangia have since been assigned to a separate species *Nothia aphylla* Høeg – see below).

Kidston and Lang (1920b) regarded *Asteroxylon* as being a possible link between the simple rhyniopsids and the lycopsids, a view which is still broadly held today (Hueber, 1992; Gensel, 1992). The discoveries by Lyon and Bhutta of attached sporangia have further refined this view. Kidston and Lang argued that it should be regarded as an advanced member of what they called the psilophytes (essentially equivalent to the class Rhyniopsida of Banks, 1968, 1975b), placing it in a family Asteroxylaceae. Other authors have, however, regarded it as a primitive lycopsid, including it in the Protolepidodendrales (e.g. Taylor, 1981). A third solution has been to assign it to a separate taxon, intermediate between the zosterophylls and lycopsids, such as the class Drepanophycopsida of Rayner (1984). Whatever solution is found to the problem of classifying this plant, it holds a key position in helping us to understand the origins and early evolution of the lycopsids.

As stated above, the fertile axes originally assigned to *Asteroxylon* by Kidston and Lang, are now recognized to belong to a quite separate plant. Lyon (1964) introduced the name *Nothia aphylla* for it, but this remained a *nomen nudum* until Høeg (*in* Boureau *et al.*, 1967) provided the first validly published diagnosis. Only the terminal parts of the plant are known; these consist of slender, dichotomous axes, covered with small, tuberous emergences. Stomata are usually situated on these emergences but, unlike those of *Rhynia* and *Horneophyton*, have distinctive broad guard cells (Edwards *et al.*, 1982). Lyon (1964) originally regarded it as rhyniophytoid. Subsequent work by El-Saadawy and Lacey (1979a) has shown, however, that it has what appear to be a combination of rhyniopsid characters (thin dichotomous axes and a centrarch 'stele') and zosterophyll characters (rhizomes with 'H'-type branching, aerial shoots with circinately curved tips, oval crosssection to the 'stele', and reniform sporangia with a dehiscence slit). There are also certain characters which place it outside either of these taxa, such as the mixture of both terminally and laterally borne sporangia, and the absence of thickening of the sporangial wall near the dehiscence slit. Perhaps most significantly, however, El-Saadawy and Lacey failed to find any evidence of thickenings or pitting on the cells in the so-called xylem, calling into question the status of *Nothia* as a true vascular plant (Edwards and Edwards, 1986). The taxonomic position of this curious plant must thus remain in doubt.

Some similarity has been noted between *Nothia* and the adpression species *Sartilmania jabachensis* (Kräusel and Weyland), both in the structure and the position of attachment of the sporangia (Fairon-Demaret, 1986b). The *Sartilmania* sporangia are more elongate and attached to longer lateral branches, and have never been found terminally attached, as sometimes occurs in *Nothia*. These differences, as well as those of the preservation, make it unwise to assign them to the same form-genus. As pointed out by Fairon-Demaret, however, they may both represent a group of Early Devonian plants in the process of diversifying to form the major taxonomic groups more clearly recognizable in later floras.

Another Rhynie species whose status as a vascular plant has recently been questioned is *Aglaophyton major*. Kidston and Lang (1920a) regarded it as a second species of *Rhynia*, and they reconstructed it as looking similar to *R. gwynnevaughanii* except that it was larger (more than half a metre high), and had aerial shoots with no adventitious branching or hemispherical bulges. They noted the absence of any clear thickenings on the cells in the central conducting tissue of the aerial shoots, but put this down largely to taphonomy. However, Edwards (1986) regarded this as unlikely, considering the fine preservation of other tissues in this plant, and concluded that the central conducting tissue was not composed of tracheids, but of tissue similar to the hydroids of certain bryophytes. As pointed out by Speck and Vogellehner (1988a, b), the central conducting strand in the early land plants provided little strength to the axes, and so the development of thickenings on the 'tracheids' would give them little immediate advantage. Edwards also reconstructed the plant rather differently, giving it an essentially decumbent habit, with vertical shoots attaining a height of no more than 0.18 metres (less than one third of the height suggested by Kidston and Lang) and with a much wider angle of branching (Figure 4.30). Germinating spores of *Aglaophyton* showing immature gametophytes have been described by Lyon (1957) and Bhutta (1973b).

It is difficult at present to classify non-vascular rhyniophytoids such as *Aglaophyton* and *Nothia*, there being no established high-ranked taxa to receive them. Edwards suggested that

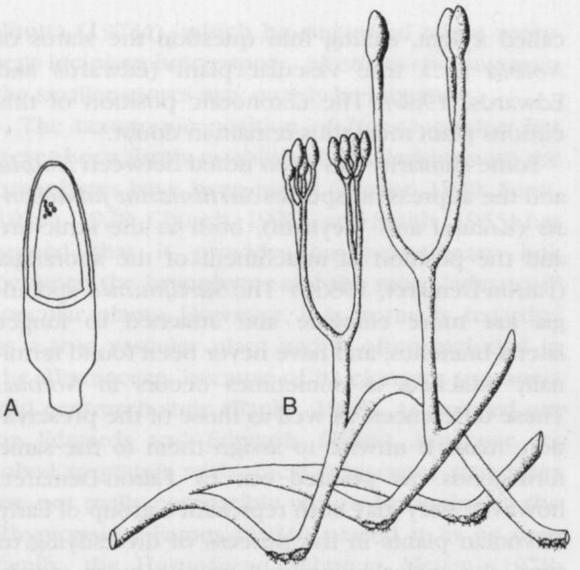

Figure 4.30 *Aglaophyton major* (Kidston and Lang) D.S. Edwards. (A) cut-away reconstruction of sporangium. (B) reconstruction of whole plant. From Thomas and Spicer (1987, figure 3.2A-B; after D.S. Edwards).

Aglaophyton might represent a group of primitive land plants, ancestral to both bryophytes and vascular plants, but he was reluctant to propose a formal taxon (which would have to be at the rank of division at least) in the absence of any other definite members of the group (he did not regard *Nothia* as part of it). Whatever formal classification is eventually adopted, however, these taxa will play an important role in helping unravel the early evolutionary history of land plants, and perhaps the relationship between the vascular plants and the bryophytes (the earliest unequivocal bryophyte fossil is from the Middle Devonian of Podolia – Ishchenko and Shlyakov, 1979).

Some of the more remarkable discoveries in recent years at Rhynie have been vascularized gametophytes, which were named *Lyonophyton rhyniensis, Langiophyton mackei* and *Kidstonophyton discoides* (Remy and Remy, 1980a, b; Remy, 1991; Remy and Hass, 1991a, b, c). The former was thought to be probably the gametophyte of either *Horneophyton* or *Aglaophyton*, with which it was found closely associated (Figure 4.31A). Germinating spores of *Horneophyton* showing immature gametophytes had been earlier described by Bhutta (1973a), but the specimens described by Remy and Remy are clearly in a mature condition. They have dichotomous aerial shoots (similar to *Horneophyton*) but with a non-vascular conducting strand (similar to *Aglaophyton*), and terminated by discoidal gametangiophores with archegonia and antheridia. The fact that in its vegetative form it is probably isomorphous with the sporophytic generation gives this oldest unequivocal gametophyte particular significance. It provides a possible stem-condition from which both the bryophytic and more typical pteridophytic heteromorphic generations could be derived (Remy, 1980a). It has also given added impetus to the search for the missing *Rhynia* gametophyte, discussed above.

Other non-vascular plants represented at Rhynie include the so-called nematophytes. The best documented to date is *Prototaxites taitii* (Kidston and Lang, 1921b). The species was originally based on two fragments, one of which shows the typical pseudoparenchymatous tissue with smooth-walled thick tubes normally associated

Figure 4.31 Putative Devonian gametophytes. (A) *Lyonophyton rhyniensis* Remy and Remy, based on Rhynie fossils. (B) *Sciadophyton steinmannii* Kräusel and Weyland, based on Lower Devonian fossils from Germany. From Thomas and Spicer (1987, figure 3.9; after W. Remy and R. Remy).

with the form-genus, but the second has thick tubes with spiral thickenings (further material has been described by Lyon, 1962). Burgess and Edwards (1988) have suggested that if Kidston and Lang's two specimens represent the same species, they might not be true *Prototaxites*, but belong to their new form-genus *Nematasketum*. Another type of nematophyte from Rhynie was described as *Nematoplexus* by Lyon (1962). This also has tubes with spiral or occasionally annular thickenings, but which are characterized by localized areas of branching known as 'branch knots'. An unpublished thesis by D.S. Edwards (1973) provides the most extensive account of this group from Rhynie, and this makes it evident that other species occur here. He also demonstrated possible evidence of the anatomy of the outer parts of these prototaxitoid axes (also mentioned by Kidston and Lang, 1921b) and of appendages (?rhizomorphs) to a holdfast. It is clear that Rhynie may hold the key to establishing the true nature of these enigmatic plants, although considerably more work is required.

D.S. Edwards (1973) described from Rhynie a poorly preserved spherical object, with a structure reminiscent of *Pachytheca*. Lang (1945) also recorded *Pachytheca* from the Rhynie outlier, but did not state if it came from the chert.

Examples of fine, septate filaments with distinctive nodal structures have been described by Kidston and Lang (1921b) and Edwards and Lyon (1983) as *Palaeonitella cranii* (Kidston and Lang). They have been interpreted as probably the vegetative parts of a charophyte, but no reproductive organs have yet been found.

A variety of other green and blue-green algae have been described from here (Kidston and Lang, 1921b; Croft and George, 1959; Edwards and Lyon, 1983), including filamentous, palmelloid and unicellular forms. It is by far the most diverse, non-marine algal assemblage to be described to date from the Devonian, but there remains little information on their reproductive structures and thus their taxonomic positions.

Also abundant in the Rhynie Chert are mycelia, vesicles and resting spores of fungi (Kidston and Lang, 1921b; Harvey *et al.*, 1969; Boullard and Lemoigne, 1971; Taylor *et al.*, 1992a, b). In the absence of detailed information on their reproductive organs, they have been assigned to the generalized form-genus *Palaeomyces*. *P. gordonii* and *P. agglomerata* were found throughout the chert and were undoubtedly saprophytic. Others, however, occur only in the rhizomes of particular vascular plants, such as *P. asteroxylii* in *Asteroxylon* and *P. horneae* in *Horneophyton*. Boullard and Lemoigne argued that these were mycorrhizal and, if this is correct, they represent the oldest known examples of such a symbiosis. It has been suggested that symbiosis between vascular plants and mycorrhizal fungi was essential to the early colonization of the land, allowing the vascular plants to obtain sufficient nutrients from a relatively impoverished environment (Pirozynski and Malloch, 1975; Pirozynski, 1981). Most recently, Taylor *et al.* (1992a, b) have argued that, at least in some cases (e.g. the putative charaphyte *Palaeonitella*), the fungi were parasitic, resulting in a reaction by the host plant.

None of the vascular plant fossil species from Rhynie has been found anywhere else in the world. Even at the rank of form-genus, the plants are unique. Two other species were included for a time in *Asteroxylon*: *A. elberfeldense* Kräusel and Weyland, 1926, from the Middle Devonian of Germany (see also Scott, 1926); and *A. setchellii* Read and Campbell, 1939, from the Mississippian of the USA. However, the former has been transferred to *Thursophyton* because of its medullated stele and scalariform tracheids (Lyon, 1964; Høeg *in* Boureau *et al.*, 1967); and the latter is now included in the ?pteridosperm form-genus *Stenokoleos* (Hoskins and Cross, 1951, 1952). A possible correlation between *Lyonophyton* and the adpression form-genus *Sciadophyton* (Figure 4.31B) has been suggested (Remy *et al.*, 1980a), but the limited anatomical detail preserved in the latter makes it difficult to confirm this. A possible correlation between *Rhynia* and *Salopella* has also been suggested (e.g. Edwards and Richardson, 1974; Taylor, 1981) but again the preservation of the latter is a problem.

In addition to the significance of its individual plant fossil taxa, the Rhynie Chert is important as a preserved *in situ* ecosystem (Edwards, 1986), the oldest of its kind discovered to date (Figure 4.32). The palaeoecology of the chert has been discussed by Kidston and Lang (1917b, 1921b), Tasch (1957), Kevan *et al.* (1975) and Trewin and Rice (1992). Of particular interest is the evidence that it provides of the triangular interaction between the 'vascular' plants, the fungi and an arthropod fauna. The relationship between the 'vascular' plants and the fungi has already been mentioned, but it is also worth noting that the arthropods may have been a significant dispersal vector for the fungi (Kevan *et al.*, 1975). There is considerable evidence, particularly in the aerial

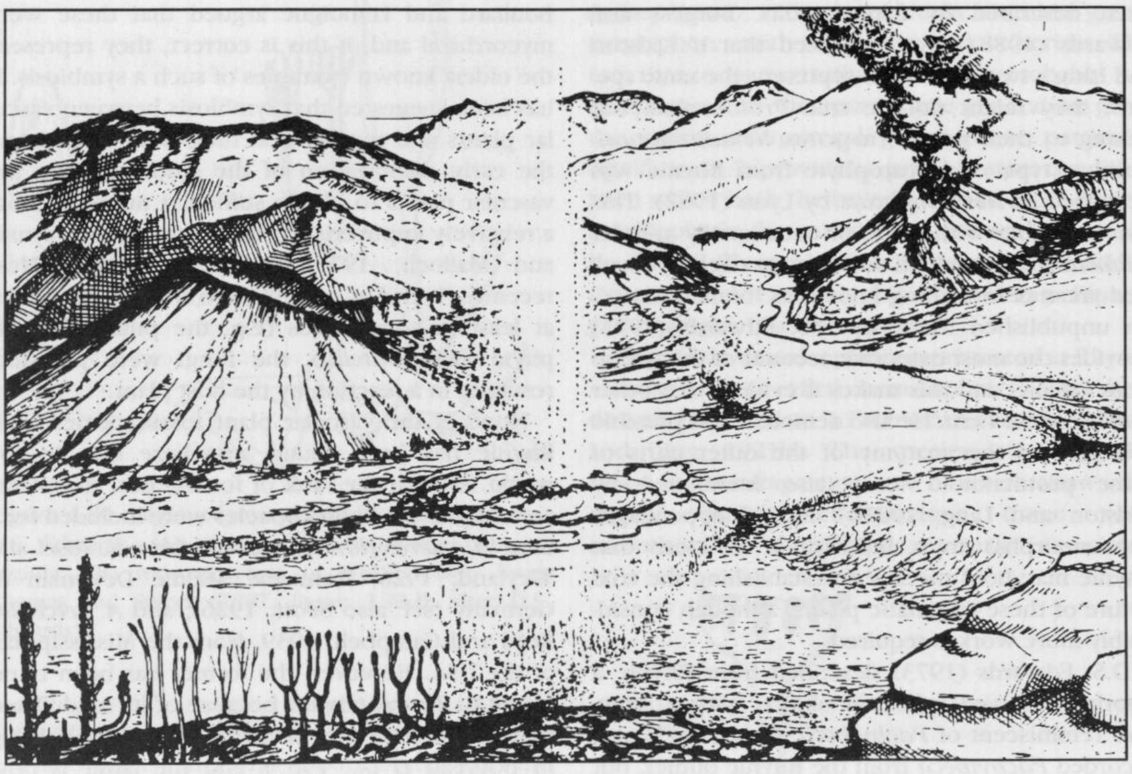

Figure 4.32 Reconstruction of the Early Devonian vegetation at Rhynie. Based on Trewin (1989, p. 12).

shoots of *Rhynia*, of lesions possibly produced by sap-sucking animals. There is also some evidence that the smaller arachnids occupied empty sporangia and cavities in the aerial shoots of *Rhynia*, which may have represented a more equable micro-environment than conditions outside. There is considerable potential for further elucidating the structure of this early terrestrial ecosystem, particularly if observations on the *in situ* chert become possible.

Conclusion

Rhynie is the most important single Devonian palaeobotanical site, and one of the most important of any age in the world. It yields the oldest examples of land plants, *c.* 390 million years old, in which anatomical details are still largely preserved intact. It provided the first indisputable evidence that Devonian plants were truly primitive, and not just badly preserved remains of more advanced groups seen in younger rocks. Its discovery just before the First World War catalysed the search for other Devonian (and subsequently Silurian) plant fossils throughout the world, and has resulted in the model for the early evolution of land plants that is accepted today (summarized in Chapter 3). Practically all that is known about the early evolution of land plants is a direct consequence of the discoveries at Rhynie, and this in turn provided a focus for the rest of palaeobotanical research. The 22 species of plant fossil (including fungi) are unique to this locality, and include what is widely regarded as the archetypal early land plant (*Rhynia*), the earliest club-moss for which a detailed anatomy has been described (*Asteroxylon*), and a variety of enigmatic species evidently representing early experiments in adapting to a terrestrial environment. Rhynie is also important as the oldest known example of an entire terrestrial ecosystem preserved in place, showing how plants and animals interacted with each other and with the abiotic environment at this early stage in the development of life on land.

BAY OF SKAILL

Highlights

The Bay of Skaill has yielded the most diverse *Hyenia* Zone plant fossil assemblage in Britain. It is the type locality for ***Protopteridium thomsonii*** (Dawson), the oldest and most primitive known progymnosperm (Figure 4.33).

Introduction

This exposure of the Sandwick Fish Bed, on the west coast of Mainland Island, Orkney (HY 233196) has yielded some of the best examples of Middle Devonian plant fossils from Britain. Although heavily out-numbered by the fish fossils, plant remains have been recorded from this horizon in Orkney for nearly 150 years (Clouston, 1845; Miller, 1849; Carruthers, 1873; Dawson, 1870; 1871, 1878; Lang, 1925, 1926, 1927a, b; Lang *in* Wilson *et al.*, 1935).

Description

Stratigraphy

The geology has been briefly described by Wilson *et al.* (1935). The fish bed is *c.* 3 metres thick here and consists of thinly laminated, 'varved' sandstones and siltstones. It is believed that it is part of an extensive lacustrine deposit originally extending over large areas of north-eastern Scotland, including Cromarty (the Cromarty Fish Bed), Caithness (the Achanarras Fish Bed) and Shetland (Melby Fish Bed). The 'varved' structure of the bed probably reflects an annual cyclicity, of either algal blooms (Rayner, 1963) or climatically induced variations in sediment input (Trewin, 1985). The chronostratigraphical position of the

Figure 4.33 Bay of Skaill. Beds associated with the Sandwick Fish Bed, at the Eifelian–Givetian boundary. (Photo: C.J. Cleal.)

bed appears to be near the Eifelian–Givetian boundary based on fish and spores (Westoll, 1951; Westoll in House *et al.*, 1977; Richardson, 1964).

Palaeobotany

The plant fossils are preserved mainly as compressions. To date, the following species have been reported:

Lycopsida:
  Thursophyton milleri (Salter) Nathorst

Progymnospermopsida:
  Protopteridium thomsonii (Dawson) Kräusel and Weyland

Uncertain affinities:
  Barrandeina pectinata Høeg
  'Fern' *sensu* Miller (1849)

Interpretation

The most significant element in the assemblage is *Protopteridium thomsonii*, for which Bay of Skaill is the type locality (Dawson, 1878). The nomenclature of this species has undergone a number of changes but, according to Matten and Schweitzer (1982), *P. thomsonii* is the correct combination. It has been most extensively investigated by Leclercq and Bonamo (1971), who have shown that it has a combination of trimerophyte-like sporangial trusses and gymnosperm-like secondary wood (Figure 4.34). Details of the vegetative parts of the plant are not well shown in the specimens found to date from Bay of Skaill, but material from elsewhere suggests that they consist of helically arranged, dichotomous branches. The ultimate sterile appendages may be bi- or trifurcate and often show an incipient, narrow lamina. The combination of trimerophyte- and gymnosperm-like features has resulted in *Protopteridium* being assigned to the progymnosperms, usually to the order Aneurophytales. It is the oldest and most primitive known progymnosperm, and provides valuable evidence as to how they evolved from the trimerophytes, probably in the Middle Devonian.

According to Leclercq and Bonamo (1971), *Milleria pinnata* (Lang) from the Cromarty Fish Bed (Lang, 1925, 1926) should be included in *Protopteridium thomsonii*. It has also been suggested by Kidston (1903a and *in* Hinxman and Grant Wilson, 1902) that *Caulopteris? peachii* Salter, described by Salter (*in* Murchison, 1859) from the Achanarras Fish Bed, was the trunk of this plant. Consequently, *P. thomsonii* has often been reconstructed as a semi-arborescent plant (e.g. Seward, 1931, fig. 45). As pointed out by Leclercq and Bonamo (1971), however, the connection has never been proved.

Thursophyton milleri refers to branching axes with microphyllous leaves or spines, but without leaf cushions (Salter, 1858; Lang, 1925). Specimens figured by Penhallow (1892) and Reid and Macnair (1896, 1899) show what appear to be sporangia borne in the axils of the leaves, but Nathorst (1915) and Lang (1925) regarded the evidence as doubtful. Little is known of the anatomy of the axes, other than that they contained annular tracheids (Lang, 1925). The general aspect of the plant suggests affinities with the lycopsids, but further evidence of its anatomy and fertile structures is needed to confirm its taxonomic position.

Lang (*in* Wilson *et al.*, 1935) reported *Barrandeina pectinata* from Bay of Skaill, but the Lang specimens have never been figured. This species belongs to an enigmatic group of Devonian plants with apparently fan-shaped leaves (also including *Enigmophyton* Høeg, 1942 from the Middle Devonian of Spitsbergen), which Høeg (*in* Boureau *et al.*, 1967) has referred to the order Palaeophyllales. The taxonomic position of these Devonian megaphyllous plants is not known.

The 'fern?' figured by Miller (1849) and re-figured by Lang (1925, pl. 4, fig. 66) is an extremely faint impression of what appears to be a small, pinna-like structure. Kidston (*in* Lang, 1925) reported markings on its surface suggesting the presence of spores, and thus it may be some sort of fructification. However, nothing more is known about it.

In addition to the above taxa, *Hostinella racemosa* Lang, *H. globosa* Lang, *Protolepidodendron karlsteinii* Potonié and Bernard, and *Pseudosporochnus krejcii* Potonié and Bernard have been described from other localities in north-east Scotland at this horizon (Lang, 1925, 1926, 1927a). Although not yet reported from Bay of Skaill, further work there may well reveal them.

Although of rather restricted composition, the Bay of Skaill assemblage appears to belong to the *Hyenia* Zone of Banks (1980). Similar assemblages have been reported from other exposures of this fish bed and its correlatives in north-east Scotland,

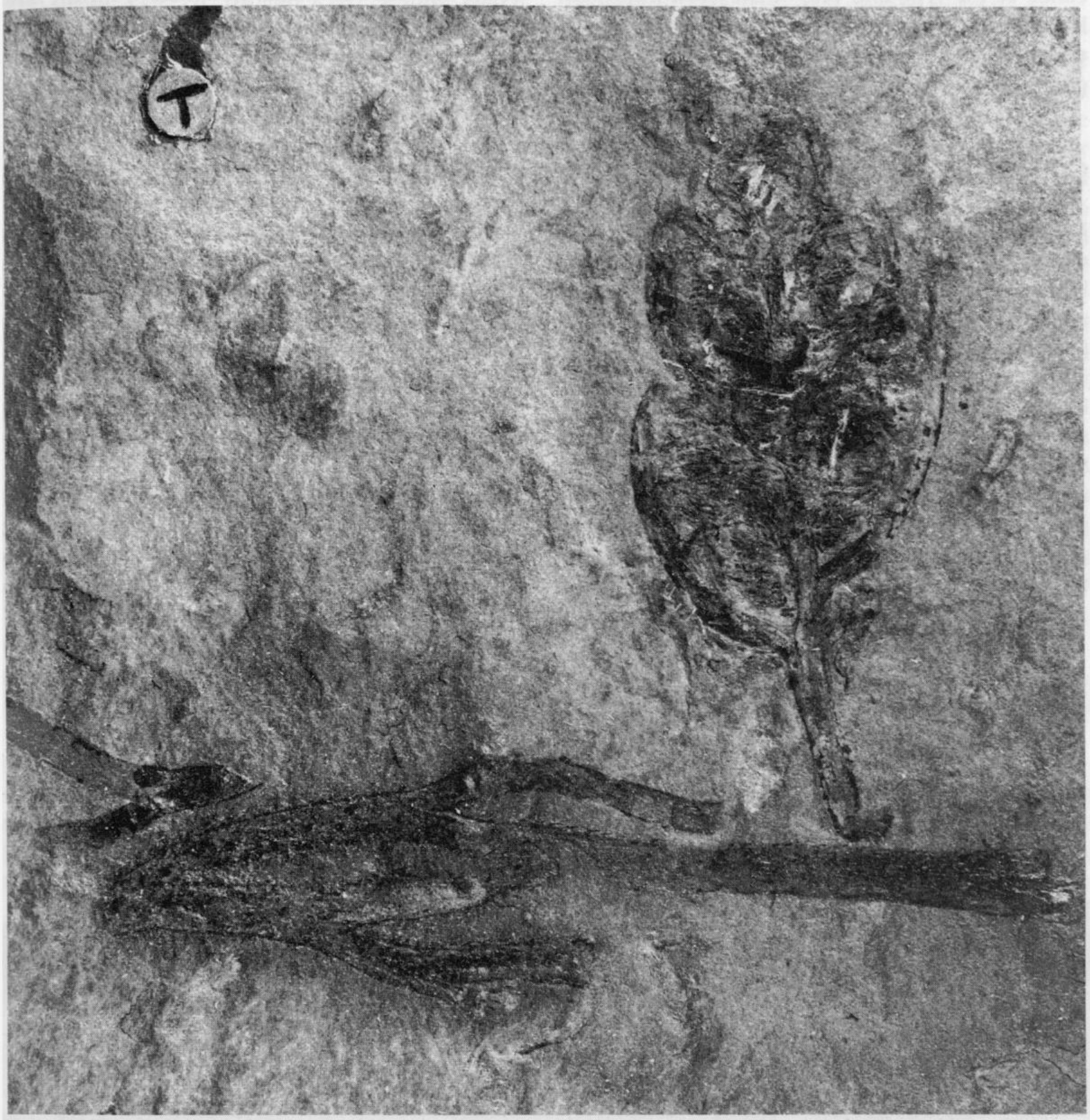

Figure 4.34 *Protopteridium thomsonii* (Dawson) Kräusel and Weyland. Fertile spike of the oldest known progymnosperm; Natural History Museum, London, specimen V.9425. Sandwick Fish Bed (Eifelian–Givetian boundary), Bay of Skaill. × 2. (Photo: Photographic Studio, Natural History Museum, London.)

including Lyking Quarry in Orkney, Achanarras Quarry in Caithness, and further south at Coal Heugh and Navity in the Cromarty Black Isle (Peach, 1877; Kidston and Lang, 1923a; Lang, 1925, 1926, 1927a). However, many of these localities have been filled-in and, of those remaining, Bay of Skaill yields the most diverse plant fossils of this age.

Coeval assemblages are also known from Germany (Kräusel and Weyland, 1929, 1932, 1938), the former Czechoslovakia (Obrhel, 1968) and Spitsbergen (Høeg, 1942). These are mostly more diverse than the Scottish assemblages, and include a number of taxa not yet reported from Scotland, such as *Aneurophyton*, *Hyenia*, *Pectinophyton* and *Duisbergia*. Bay of Skaill is nevertheless of considerable international significance as the type and one of the most important localities for *Protopteridium*, the earliest progymnosperm, and thus probably the remote ancestor of all seed plants, including the angiosperms.

Conclusion

Bay of Skaill has yielded an important assemblage of Middle Devonian plant fossils, about 380 million years old. It cannot compare in diversity with similar aged floras abroad, especially Germany, the former Czechoslovakia and Spitsbergen, but it is the best that is known in Britain. It is particularly important as the best locality for the oldest and most primitive known progymnosperm (*Protopteridium*), which is one of a group of plants thought to be the immediate ancestors of the seed plants (and thus the flowering plants). It is thus of great significance for charting the development of the seed as a reproductive organ, which was probably the single most important evolutionary event that allowed plants to spread from the lowland, coastal areas into drier, inland habitats.

SLOAGAR

Highlights

Sloagar provides the best example of a *Svalbardia* Zone flora in Britain. It is also the type locality for *Svalbardia scotica* Chaloner, the only known species of this form-genus known from Britain (Figure 4.35).

Introduction

Plant fossils are abundant throughout the Old Red Sandstone of Shetland but have been studied little by palaeobotanists. Stems known as 'corduroy plant' occur extensively and have been noted by

Figure 4.35 Sloagar. Steeply-dipping Givetian lacustrine beds of the North Gavel Formation. Plant fossils occur in the shales in the middle of the picture. (Photo: C.J. Cleal.)

Hooker (*in* Tufnell, 1853), Miller (1857), Murchison (1859), Gibson (1877) and Peach (1877), and *Thursophyton* and *Hostinella* axes have been recorded by Mykura (1972) and Mykura and Pheimister (1976). In none of these cases, however, were the specimens described. During the early twentieth century, W.H. Lang made an extensive collection of Shetland plant fossils (now stored in the Natural History Museum) but the results of his work were never published. The only sites to have been subject to any detailed work are those yielding *Svalbardia* (Chaloner, 1972; Allen and Marshall, 1986), the most prolific of which is this one high in the Middle Devonian on the coast of Fair Isle, Shetland Islands (HZ 228726; see Figure 4.36).

Description

Stratigraphy

The sequence at Sloagar has been described by Mykura (1972), Marshall and Allen (1982) and Allen and Marshall (1986). It consists of alternating lacustrine shales and sandstones of the North Gavel Formation (Figure 4.37). Palynological evidence indicates a late Givetian age (Marshall and Allen, 1982), which is also supported by the plant fossils, which belong to the *Svalbardia* Zone of Banks (1980).

Palaeobotany

The shales here have yielded heavily carbonized compressions of just one species, *Svalbardia scotica* Chaloner. The sandstones contain casts and adpressions of wide axes known as 'corduroy plant', which may have been the stems of the *Svalbardia* plant.

Interpretation

Other than this locality, *Svalbardia scotica* has only otherwise been recorded from Voe of Cullingsburgh and Leebotten on Shetland (Allen and Marshall, 1986). It consists of 20 mm wide, ribbed axes with ?spirally attached, subsidiary axes. Mostly wedge-shaped, digitate leaves are attached probably spirally to both orders of axes. Associated with the vegetative shoots are fertile axes bearing sporophylls, again probably in a spiral arrangement. The sporophylls bear 8–12 fusiform sporangia on their adaxial surface.

These fructifications associated with *Svalbardia* are very similar to those of the Upper Devonian *Archaeopteris*, and the two form-genera were traditionally distinguished only by the more deeply digitate leaves of the former. Scheckler (1978) argued that *Svalbardia* was merely a developmental stage of *Archaeopteris*, but Matten (1981) has maintained that it is a morphological and evolutionary precursor of the latter. Marshall and Allen (1986) concluded that the evidence for separating the form-genera was doubtful, although they provisionally retained the name *Svalbardia* for the Shetland material until a more thorough analysis had been made of all the species. Whatever the taxonomic results of such an analysis, the *Svalbardia*-type species will hold an important evolutionary position between the more primitive progymnosperms which did not have dorsiventral, laminate leaves (e.g. *Protopteridium* from Bay of Skaill) and the more typical *Archaeopteris* species with flattened, fully laminate leaves.

As to the specimens recorded from Sloagar by Mykura (1972), ?aff. *Zosterophyllum* and *Hostinella* sp. are probably conspecific with *S. scotica* Chaloner.

The early records of *Calamites* from Shetland have subsequently been referred to as 'corduroy plant' (Finlay, 1926). They are axes up to 150 mm wide, which occasionally show monopodial branching (Allen and Marshall, 1986). They are characterized by uninterrupted longitudinal ribs (hence, their original assignment to *Calamites*), similar to those found on the *S. scotica* axes, with which they are often associated. Allen and Marshall (1986) concluded that the 'corduroy plant' may well represent the main stem that bore *Svalbardia*, although evidence of attachment has yet to be found. If correct, this would call into question Scheckler's (1978) view that *Svalbardia* was a developmental form of *Archaeopteris*.

Mykura (1972) recorded cf. *Prototaxites* sp. from Sloagar. This would be of considerable interest as the youngest record of this group of enigmatic, non-vascular plants from Britain. However, it is possible that they refer simply to axes of 'corduroy plant'.

Although yielding only one species, Sloagar is of considerable palaeobotanical importance. It has yielded the best specimens for showing the overall morphology of the *Svalbardia* plant, as well as some well-preserved fructifications and foliage. It

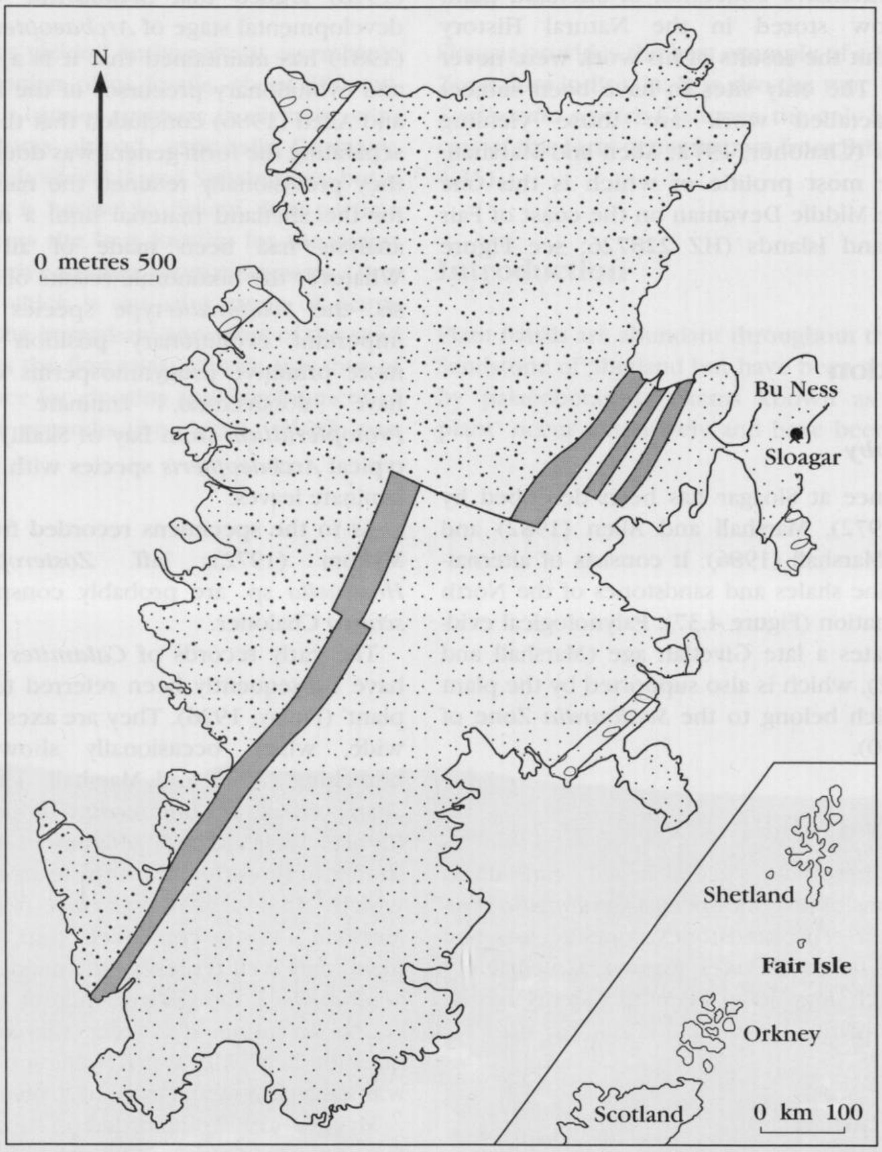

Figure 4.36 Geological map of Fair Isle, showing position of Givetian palaeobotanical site at Sloagar. Based on Marshall and Allen (1982, text-figure 1).

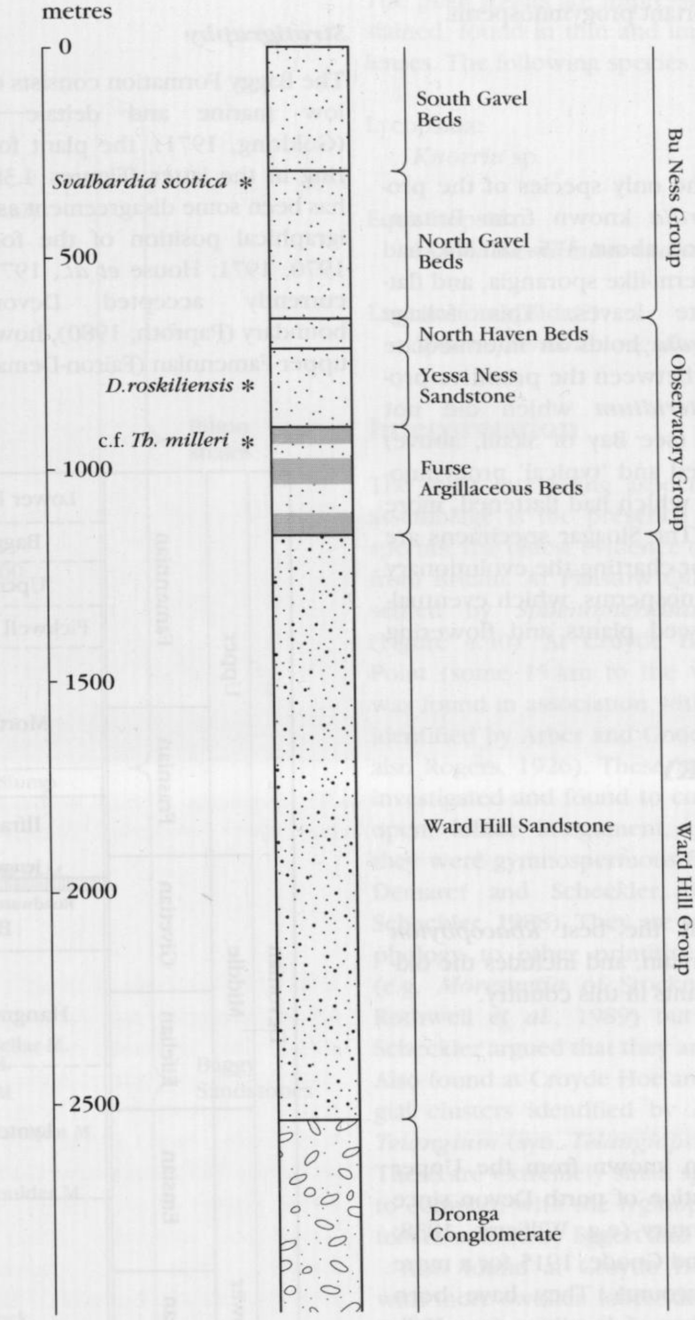

Figure 4.37 Stratigraphical section of the Middle Devonian of Fair Isle, showing the main plant fossil-bearing horizons. Based on Marshall and Allen (1982, text-figure 2).

is second only to Spitsbergen and New York State for understanding the detailed structures of this phylogenetically important progymnosperm.

Conclusion

Sloagar has yielded the only species of the progymnosperm *Svalbardia* known from Britain. This plant, which lived about 375–380 Ma, had typically progymnosperm-like sporangia, and flattened, deeply-digitate leaves. This foliage suggests that *Svalbardia* holds an intermediate evolutionary position between the primitive progymnosperm *Protopteridium* which did not have flattened leaves (see Bay of Skaill, above) and the more advanced and 'typical' progymnosperm *Archaeopteris*, which had flattened, more fully laminate leaves. The Sloagar specimens are of great importance for charting the evolutionary history of the progymnosperms, which eventually gave rise to the seed plants and flowering plants.

PLAISTOW QUARRY

Highlights

Plaistow Quarry yields the best *Rhacophyton* Zone plant fossils in Britain, and includes the oldest evidence of seed plants in this country.

Introduction

Plant fossils have been known from the Upper Devonian Baggy Formation of north Devon since the mid-nineteenth century (e.g. Williams, 1838; Hall, 1867; see Arber and Goode, 1915 for a more complete historical account). They have been recorded from a number of localities (see Hall, 1867 for the most complete list) but the most abundant are found at Plaistow Quarry (also known as Sloley Quarry), 4 km north of Barnstaple, Devon (SS 568373). The only detailed account of the assemblage is that given by Arber and Goode (1915), although Fairon-Demaret and Scheckler (1987) have recently commented on one of the species.

Description

Stratigraphy

The Baggy Formation consists of a mixture of shallow marine and deltaic non-marine strata (Goldring, 1971), the plant fossils usually occurring in the latter (Figures 4.38 and 4.39). There has been some disagreement as to the chronostratigraphical position of the formation (Goldring, 1970, 1971; House *et al.*, 1977). In terms of the currently accepted Devonian–Carboniferous boundary (Paproth, 1980), however, it is probably upper Famennian (Fairon-Demaret, 1986a).

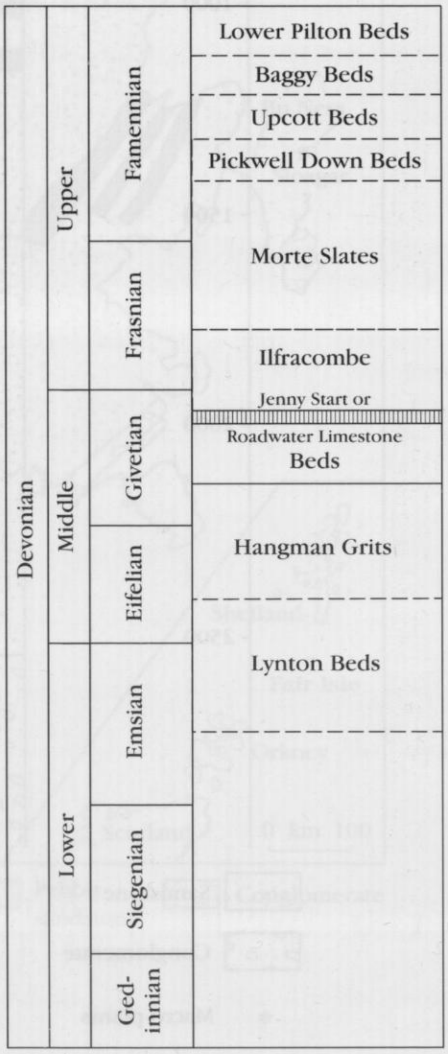

Figure 4.38 Devonian stratigraphy of North Devon, showing position of the Baggy Beds.

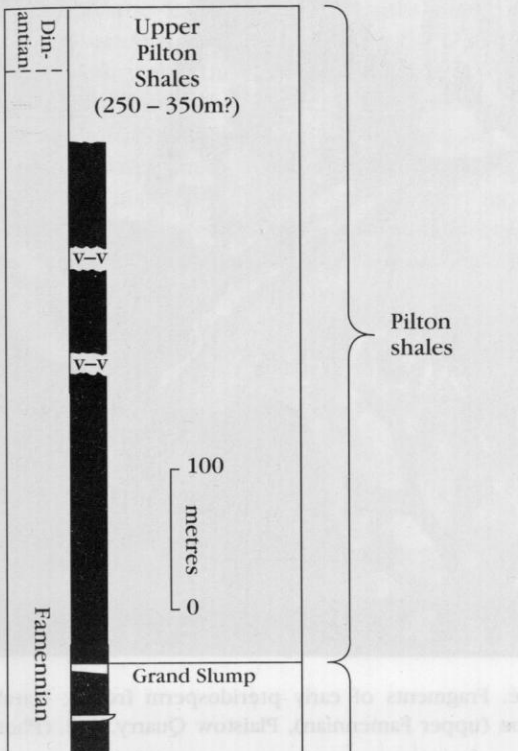

Figure 4.39 Details of the stratigraphy of the Baggy and Pilton formations in North Devon. Based on Scrutton (1978, figure 6).

Palaeobotany

The plant fossils are impressions, sometimes iron stained, found in thin and impersistent mudstone lenses. The following species are known:

Lycopsida:
Knorria sp.

Equisetopsida:
?Archaeocalamites radiatus (Brongniart) Stur

Lagenostomopsida(?):
Sphenopteridium rigidum (Ludwig) Potonié

Interpretation

The most interesting aspect of the Baggy Beds assemblage is the presence of probable gymnosperms, the oldest evidence of such plants known from Britain. At Plaistow Quarry, they are represented by *Sphenopteridium* frond fragments (Figure 4.40). At Croyde Hoe Quarry at Baggy Point (some 15 km to the west), similar foliage was found in association with cupulate structures identified by Arber and Goode as *Xenotheca* (see also Rogers, 1926). These have recently been re-investigated and found to contain ovules with an open, lobate integument, thus confirming that they were gymnospermous fructifications (Fairon-Demaret and Scheckler, 1987; Rothwell and Scheckler, 1988). They are similar in general morphology to other primitive cupulate structures (e.g. *Moresnetia* of Stockmans, 1948; *Elkinsia* Rothwell *et al.*, 1989) but Fairon-Demaret and Scheckler argued that they are generically distinct. Also found at Croyde Hoe are fragmentary sporangial clusters identified by Arber and Goode as *Telangium* (syn. *Telangiopsis* Eggert and Taylor). These are extremely small specimens, but appear to compare with the lyginopterid sporangial clusters described by Eggert and Taylor (1971).

Also found at Croyde Hoe is pinnate foliage with more swollen lobes, described by Arber and Goode (1915) as *Sphenopteris* sp. There is a comparison with certain species of *Triphyllopteris* (Read and Mamay, 1964) and *Eusphenopteris foliolata* (Stur) (van Amerom, 1975), although neither of these usually range below the Tournaisian. Since Arber and Goode's material is very fragmentary, their original identification as *Sphenopteris* sp. should probably be retained.

Hall (1867) and Etheridge (1867) record *Adiantites hibernicus* Forbes (syn. *Archaeopteris*

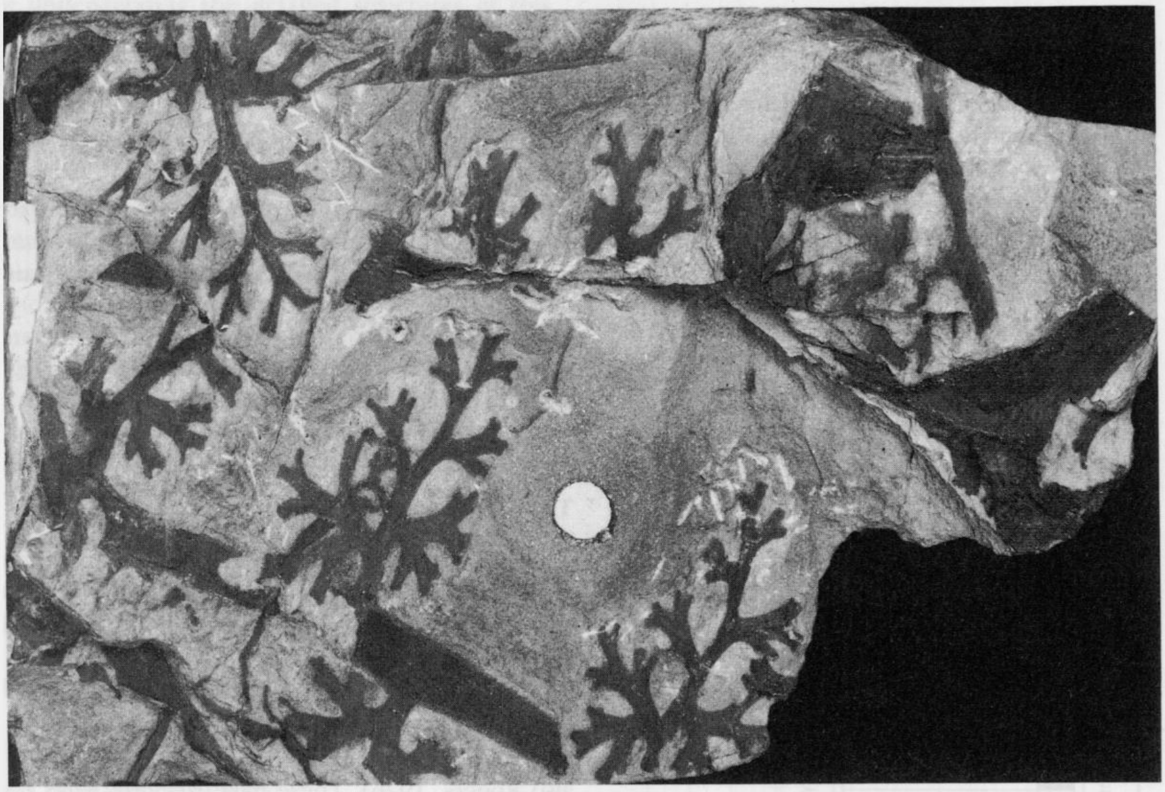

Figure 4.40 *Sphenopteridium rigidum* (Ludwig) Potonié. Fragments of early pteridosperm fronds; Natural History Museum, London, specimen V.3562. Baggy Formation (upper Famennian), Plaistow Quarry. x 2. (Photo: Photographic Studio, Natural History Museum, London.)

hibernica) from Plaistow Quarry. Arber and Goode (1915) attempted to verify the records, but could find neither the original specimens, nor any new ones from the locality. It may be significant that small fragments of Arber and Goode's *Sphenopteris* sp. bear a passing resemblance to *Archaeopteris*.

Specimens from Plaistow Quarry, identified by Arber and Goode (1915) as *Knorria*, were regarded by them as decorticated axes of arborescent lycopsids. Alternatively, they may be examples of more primitive lycopsids without leaf-scars. The specimens clearly need reappraisal.

Arber and Goode (1915) mention ribbed axes from here. These possibly represent internodes of *Archaeocalamites radiatus*. No evidence of nodes was found to confirm the identification, however, and Arber and Goode suggested that they might be poorly preserved lycopsid axes.

The presence of *Sphenopteridium* and *Xenotheca* in the Baggy Formation indicates the *Rhacophyton* Zone of Banks (1980), and supports a late Famennian age. Although of limited composition, this formation nevertheless has the most diverse *Rhacophyton* Zone assemblage known from the British Isles. The nearest comparison is with fossils found in the Lower Limestone Shale along the Taff Gorge near Cardiff (Evans and Cox, 1956; Gayer *et al.*, 1973), which includes cf. *Xenotheca devonica* Arber and Goode and another type of cupulate fructification, *Telangiopsis* sp., but which has no recorded specimens of megaphyllous foliage. The best documented assemblages of this age are from Kiltorcan in Ireland (Chaloner, 1968) and the lost site of Prestonhaugh in southern Scotland (Miller, 1857; Crookall, 1939; Long, 1973), but these are restricted mainly to *Archaeopteris* and *Cyclostigma*. From outside of the British Isles, the best known assemblages are from Belgium (Stockmans, 1948) and Bear Island near Spitsbergen (Schweitzer, 1967, 1969), which are significantly more diverse. Typically, such assemblages include (in addition to the form-genera mentioned above) *Protolepidodendropsis*, *Sublepidodendron*, *Pseudobornia*, *Sphenophyllum* and *Aneurophyton*.

Amongst the Baggy Formation sites that have been reported to yield plant fossils, Plaistow Quarry now yields the best material. The Croyde Hoe Quarry, from where Arber and Goode (1915) obtained much of their material, including the fertile pteridospermous organs, is no longer available. This site may thus be regarded as of national significance for understanding the vegetation in this country towards the end of the Devonian Period, as it evolves into the more advanced floras found in the Carboniferous.

Conclusion

Plaistow Quarry is the best site in Britain for Upper Devonian plant fossils, some 360 million years old, which are otherwise very poorly represented in this country. The site is particularly important in providing at least some reflection of the vegetation growing in the tropical belt towards the end of the Devonian. It is transitional between the more primitive Devonian vegetation, dominated by zosterophylls, trimerophytes and progymnosperms, and the more modern-looking Carboniferous vegetation, which is dominated by ferns, club-mosses, horsetails and seed plants. This particular site has yielded the earliest horsetail and seed plant remains known from this country.