Chapter 2 History of research on British plant fossils

Silurian

British sites, particularly in Wales and the Welsh Borders, have played a key role in developing ideas about the evolution of land plants during the Silurian (440–410 Ma). This may be due, at least in part, to it being the type area for much of the Silurian and having been subject to more intensive investigation than other outcrops of this age (Bassett, 1984; Holland and Bassett, 1989). It has meant that there is a long history of records of plant fragments from these strata, dating back to the mid-nineteenth century (e.g. Phillips, 1848; Brodie, 1869, 1871; see Lang, 1937 for a more complete account of the early records). However, no serious attempt was made to investigate the form and structure of these difficult fossils until Lang's (1937) classic monograph. For many years, Lang's paper was regarded as the definitive statement on Silurian vegetation, and not until the 1970s was any attempt made to re-evaluate his observations, principally by Dianne Edwards (e.g. Edwards, 1979a, 1982; Edwards and Davies, 1976; Edwards and Rogerson, 1979; Edwards *et al.,* 1979, 1986; Fanning *et al.,* 1988, 1990, 1991). Edwards and her co-workers are continuing to investigate the fossil evidence for Silurian terrestrial vegetation.

Devonian

Plant fossils from the Devonian (410–355 Ma) have been investigated in Britain for over 150 years, but this long history can be broken down into three main phases. The first effectively started with the work of Hugh Miller (Rosie, 1981), who collected from a number of Scottish localities. Although there had been earlier records (Fleming, 1811, 1831; Williams, 1838; De la Beche, 1839; Murchison, 1839), Miller was the first to describe and discuss such fossils in detail (Miller, 1841, 1849, 1855, 1857). His contributions to palaeobotany have been largely overshadowed by his work on vertebrate palaeozoology. However, he was probably the first palaeontologist in the world to treat Devonian plant fossils seriously, and he laid the foundations for the studies of later nineteenth century workers (e.g. Dawson, 1888).

Considering the poor preservation of most Devonian plant fossils, it is not surprising that many of the nineteenth century palaeobotanists had difficulty interpreting them. For a time, it became widely believed that the 'fossil plants of the Devonian rocks in Europe resemble generically, with very few exceptions, those of the coal-measures' (Lyell, 1865, p. 542). The discovery of 'conifer' wood (now known in fact to be from a progymnosperm) in the Middle Devonian of Scotland tended to reinforce this misconception (Miller, 1841; M'Nab, 1871). Some geologists such as Dawson (1859, 1870, 1871) argued that at least some of the Devonian fossils represented truly simple and primitive plants, but others just regarded them as poorly preserved fragments of more advanced plants. Despite this confusion, the nineteenth and early twentieth centuries saw a gradual accumulation of a pool of information on the Devonian plant fossils, which is admirably summarized by Arber (1921).

The second phase of research on British Devonian plant fossils commenced with the description of the Rhynie Chert assemblage by Kidston and Lang (1917b, 1920a, b, 1921a, b). This was the first unequivocal evidence that Devonian plants really were simple and primitive, and provided a significant impetus to the further investigation of the less well-preserved adpression assemblages from elsewhere. In Britain, the field was dominated at this time by Lang. Following the work at Rhynie, he continued to collaborate with Kidston on the Scottish assemblages (Kidston and Lang, 1923a, b, 1924). After Kidston's death in 1924, Lang continued to work on the Scottish sites, but later moved on to material from Wales and the Welsh Borders. During this second phase, Devonian palaeobotany became an established discipline and many of our presently held views on early land plant evolution were developed.

From about 1945, there was a lull in the investigation of British Devonian plant fossils. During the mid-1960s, however, the third and most recent phase in their investigation began, mainly as a result of the work of Dianne Edwards. She has instigated new work on many of the classic Devonian plant adpression localities, collecting fresh material and applying new and improved techniques to its study. She has also searched out new localities, such as Auchensail Quarry (see also Edwards and Richardson, 1974; Edwards and Rose, 1984; Edwards *et al.,* 1986). This has all provided significant new information on the morphological variation and anatomy of many of these plants. Recent attempts at

biostratigraphical (Banks, 1980), palaeoecological (Edwards, 1980b) and palaeogeographical analyses (Raymond *et al.,* 1985; Edwards, 1990) have leaned heavily on this new data. There has also been significant recent progress on the Rhynie fossils, mainly through the work of Lyon (1957, 1962, 1964), Bhutta (1972, 1973a, b), El-Saadawy and Lacey (1979a, b), Remy (1978, 1980a, b, 1991), Remy and Remy (1980a, b), Remy *et al.* (1980b), D.S. Edwards (1980, 1986), Edwards and Lyon (1983), Lyon and Edwards (1991) and Remy and Hass (1991a, b). This was mainly as a result of using new techniques, particularly serial sectioning using acetate peels, which allowed far more refined reconstructions of the plants to be achieved.

Despite the recent resurgence of interest, there are many aspects of British Devonian palaeobotany that remain neglected. For instance, other than papers by Chaloner (1972), Edwards (1976) and Allen and Marshall (1986), there has been no recent work on the Middle Devonian plant fossils from northern Scotland. This is despite there being numerous sites available for further collecting. The British Upper Devonian assemblages have been even more neglected, the only recent references to them being by Long (1973) and Fairon-Demaret and Scheckler (1987). There is evidently considerable potential for further work in this country.

Lower Carboniferous

Plant adpressions were reported from the Lower Carboniferous (355–320 Ma) of Britain in the early to mid-nineteenth century, in particular from the Burdiehouse Limestone near Edinburgh (e.g. Lindley and Hutton, 1831–1837; Miller, 1857). However, intensive work on fossils from these strata did not start until the late nineteenth century, principally by Kidston (Edwards, 1984). Kidston's immense contribution to the subject culminated in his classic monographs published between 1923 and 1925, which remain the definitive publications on the Lower Carboniferous adpression palaeobotany of Britain (those parts of this monograph not published before his death were subsequently updated and published by Crookall, 1955–1975). Probably the most significant aspect of Kidston's work, other than the fact that he placed on record so many fossils of this age, was his analysis of the frond architecture of the early pteridosperms and his consequent refinement of their classification.

The next major phase of work on the British fossils of this age was by Walton (1926, 1931, 1941), Benson (1904, 1933, 1935a, b) and later Lacey (1962). They mainly concentrated on sites in Wales and south-west England, although Walton also reported on adpressions from the Clyde Plateau Volcanic Formation near Glasgow (Walton *et al.,* 1938). Walton's work was particularly important for helping establish reconstructions of the plants, especially for determining the connection between foliage and fructifications. Lacey's work is also of considerable significance, if only because it is one of the few attempts to prepare cuticles from plant fossils of this age.

Most recently, the only significant contribution to British Lower Carboniferous adpression palaeobotany has been Rowe's (1988a, b, c) work on material from the Drybrook Sandstone in the Forest of Dean. Although previously studied by Lele and Walton (1962b), Rowe has applied new techniques to provide a fresh insight into the fossils.

The first records of British Lower Carboniferous petrifactions were in the early nineteenth century, by Witham (1831, 1833), who described material from a number of sites in the Cementstone Group of southern Scotland. Witham's work is mainly significant in having developed the method of thin sectioning rocks, which was not only important for the future development of palaeobotany, but was perhaps more significant for petrology and mineralogy. The first major advance in this field for palaeobotany, however, was the discovery in the 1870s of the petrifactions from the Pettycur Limestone. The work of Williamson and Scott at this site established it as of international significance (Williamson, 1872, 1873, 1874a, b, 1877, 1880, 1883, 1895; Williamson and Scott, 1894, 1895; Scott, 1897, 1901); until the discoveries 40 years later at Rhynie (see Chapter 4), it provided some of the oldest evidence of cell structure in plants and was central to ideas about early plant evolution.

Various other petrifaction sites were discovered in Scotland during the late nineteenth and early twentieth centuries, but these were mainly found by chance. The first concerted effort to search for new sites was by Gordon (1935a, b, 1938, 1941), who discovered petrifactions at various localities in the volcanogenic deposits exposed along the south-east coast of Scotland. Gordon described a variety of new taxa from both these new and some of the old localities, his work on the ferns being particularly important. Other major contributions to Lower Carboniferous petrifaction palaeobotany during the

mid-twentieth century were by Calder (1934, 1935, 1938), Walton (1935, 1949a, b, c, 1957, 1969), Beck (1958), Chaphekar (1963) and Chaphekar and Alvin (1972).

In more recent years, by far the most important work on Lower Carboniferous petrifactions has been by Long (1959–1987) on the Cementstone Group sites. By utilizing the peel method, Long has revolutionized our view of the Early Carboniferous plants, particularly of the seed plants. His views on the evolution of these plants have not always met with universal acceptance, but the quality of his observations and the degree to which other palaeobotanists have had to use them in developing their ideas concerning seed plant evolution, in particular, are indisputable.

Another approach to the study of the British Lower Carboniferous petrifaction sites has been by Scott, who has integrated the analysis of species distribution and sedimentology to develop ideas about the plant ecology of the time (Scott *et al.,* 1984, 1985, 1986; Scott and Rex, 1987; Rex and Scott, 1987). Scott's work has produced particularly interesting results from exposures of the volcanogenic strata in southern Scotland, such as the Pettycur Limestone and the Oxroad Bay tuffs. He has also instigated the collection of additional new material from many of these sites, which have been worked on mainly by other palaeobotanists (Rothwell and Wight, 1989; Galtier and Scott, 1986a, b; Meyer-Berthaud, 1986; Meyer-Berthaud and Galtier, 1986a, b; Bateman, 1988; Bateman and Rothwell, 1990). The review paper by Scott *et al.* (1984) provides one of the best sources of information on the distribution of Lower Carboniferous petrifactions in Britain.

Upper Carboniferous

Upper Carboniferous (320–290 Ma) plant fossils have been known from Britain since at least the seventeenth century, the first published account usually being credited to Lhuyd (1699). A number of subsequent publications by British naturalists during the eighteenth and early nineteenth centuries, described Upper Carboniferous plant fossils, the most widely quoted being Artis (1825) and Lindley and Hutton (1831–1837) (for a fuller account of early British work on these fossils, see Kidston, 1923a and Andrews, 1980). Unlike continental Europe, however, Britain failed to produce any significant contributors to the subject until the mid-nineteenth century. The first major British palaeobotanist to deal with the adpression plant fossils was Kidston, whose impressive list of publications started in the 1880s (Crookall, 1938; Edwards, 1984) and culminated in his classic 1923–1925 monographs. During the first half of the twentieth century, notable contributions were also made by Arber (1904b, 1912, 1914, 1916).

Most of this work was of a floristic nature, documenting assemblages and species distributions; Kidston's work on fern fructifications and pteridosperm frond architectures being the most significant exceptions. More botanically orientated, morphological/anatomical study was instead concentrated on the Langsettian coal-balls from Yorkshire and Lancashire. Petrified plant fossils were first noted in coal-balls in the 1850s by Binney, but their true significance was established first by Williamson in a series of papers starting in the 1860s, and later by Scott. The results of this main phase of British coal-ball work is admirably summarized by Scott (1920–1923).

After this 'golden period' of British Upper Carboniferous palaeobotany, ending in the mid-1920s, interest in the subject suffered a decline. Crookall attempted to continue Kidston's work on the adpressions, although this amounted mainly to further documenting the distribution of species in Britain. His main achievement was the 1955–1975 monographs, which described those plant groups not covered in the Kidston volumes. However, they were published some time after Crookall's main phase of work, in the 1930s, and despite some attempts to update them, they have a rather archaic feel. It is also worth mentioning here the work of Dix (1933, 1934, 1935) on the biostratigraphy and Davies (1929) on the palaeoecology of the Upper Carboniferous plant fossils, although in both cases their publications are weakened by a failure to document fully the taxa they were recording.

The most significant recent contributions to Upper Carboniferous palaeobotany in Britain have been on the lycopsids, by Chaloner (much of whose work is summarized by Chaloner *in* Boureau *et al.,* 1967), Thomas (1967a, b, 1970, 1977, 1978a, b, 1981b) and Boulter (1968). There has also been some recent interest in the ferns and pteridosperms (Thomas and Crampton, 1971; Cleal and Laveine, 1988; Shute and Cleal, 1989; Cleal and Shute, 1991, 1992). Finally, there has also been interest in the use of plant fossils for Late Carboniferous palaeoecology (e.g. Scott, 1977, 1978, 1979) and biostratigraphy (Wagner and Spinner, 1972; Cleal, 1978, 1984b, 1986c, 1987b; Cleal and Thomas, 1988).

Coal-ball work also underwent somewhat of a decline after the 1930s. Contributions were made by Holden and Long (reviewed briefly by Andrews, 1980). The most significant work has, however, been that of Holmes on some of the herbaceous ferns found in the coal-balls (reviewed by Holmes, 1989).

Permian

Most work on the Permian (290–250 Ma) palaeobotany of Britain has been on the Marl Slate and its equivalents. The best historical account of studies on these fossils is by Stoneley (1958), who notes records dating back to the mid-nineteenth century (Sedgwick, 1829; Lindley and Hutton, 1937; King, 1850; Kirkby, 1862, 1864, 1867). Stoneley provides the only attempt at a monographic analysis of these fossils, although a useful review is also provided by Schweitzer (1986). Individual taxa have also been dealt with by Townrow (1960) and Poort and Kerp (1990).

References