

A REVIEW OF THE ECOLOGY OF UPPER CARBONIFEROUS PLANT ASSEMBLAGES, WITH NEW DATA FROM STRATHCLYDE

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ABSTRACT. Previous studies on Upper Carboniferous floral palaeoecology are reviewed and relationships between fossil plant assemblages, depositional environments, and contemporaneous plant communities are discussed. A point-quadrat sampling technique was applied to a quantitative study of plant horizons in a 'roof shale' of a thin coal below Skipsey's Marine Band (Westphalian B) at a locality near Annbank, Strathclyde. This study has shown that the number and percentage cover of 'drifted' and *in situ* species varies up the succession. Changes in the depositional environment from swampy flood plain to near channel alluvial discharge, interpreted from the lithofacies, are thought to account for these differences by affecting the quantity of plant material deposited and by incorporating a variety of 'Plant Communities' to yield different 'Fossil Plant Assemblages'. The latter consist of two main types, one of pteridosperms with some *Cordaites* and another of sphenopsids and pteridosperms with *Cordaites*. Only very few lycopod remains were found. This is in contrast to the coal-forming swamp 'community' (as seen in the spores contained in the coal) which was dominated by lycopods with some sphenopsids.

A NUMBER of plant communities existed during the Upper Palaeozoic, for example various authors have recognized 'upland' and 'swamp' floras (Cridland and Morris 1963; Havlena 1971; Leary 1974). The relationships, however, of fossil plant assemblages to contemporaneous plant communities and their sedimentary history has received less attention, although a few workers have tried to define more clearly the ecology of these 'floras' (Havlena 1971). Little attempt has been made to relate fossil plant assemblages to depositional environments, which is necessary in order to understand the nature of the assemblages. A number of sampling techniques have been developed by ecologists studying extant floras (Greig-Smith 1964), some of which may be adapted to the fossil situation. The interpretation of the results obtained in the two different examples are fundamentally different.

This paper sets out to review previous work on Upper Carboniferous floral palaeoecology and discusses the application of Recent ecological-sampling techniques to fossils. A 'roof shale flora' of Westphalian B age from Annbank, Strathclyde, Scotland, is taken to illustrate the use of a half-metre square-quadrat technique on cleared bedding planes. The study of the Annbank section is intended to illustrate how detailed analysis of the sediments and flora, together with palynological data from the underlying coal, can give a better understanding of the Coal Measure environment and the possible plant community structure.

PREVIOUS STUDIES ON UPPER CARBONIFEROUS FLORAL PALAEOECOLOGY

Most early work on Upper Carboniferous (mainly Coal Measures) plants has been concerned with general description: new taxa, their botanical affinities, lists of floras,

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and considerations of their stratigraphic age (Scott 1906; Arber 1906). Most discussions concerning the nature and origin of coal concerned an *in situ* or drifted theory (Potonié 1899*a*; Grand'Eury 1900; Kendall 1922; Bennett 1963). Understandably, as little work had been done on the ecology of extant floras, few workers were concerned primarily with this aspect although occasional observations were noted in passing (Grand'Eury 1897; Wunsch 1865; Walton 1935; MacGreggor and Walton 1948; Jongmans 1955). Most of the reconstructions of Coal Measure swamp vegetation (Westphalian) included known plants together and showed plant reconstructions rather than ecological associations (Geinitz 1855; Potonié 1899*b*; Noé 1932; Dahlgren 1931); although sometimes the species associations were noted (drawings by Nathorst *in* Magdefrau 1968, by Bertrand *in* Bertrand and Corsin 1950).

Lycopods clearly played an important role in the peat accumulations contributing to formation of coal seams (seen both from the stigmarian seatearths of most Westphalian coals (Logan 1841), and in the abundance of those plants in coal balls (Binney 1868, 1871, 1872, 1875)) but the detailed ecology of Westphalian floras was generally not investigated. Advances in the study of coal petrology (Stopes and Wheeler 1918) gave an impetus to the ecological study of the peat- (coal-) forming floras. The recognition of the major coal constituents (Stopes 1919) and later coal macerals (Stopes 1935) enabled those studying compressions of plants to relate these to their material (Hickling and Marshall 1932, 1933) thus allowing the general type of peat composition of a coal to be identified.

Several attempts have been made to interpret the habitat of Upper Carboniferous plants by comparison of the internal structure with that of extant plants (Thomas 1911; Weiss 1925; Noé 1932; Cridland 1964; Wartmann 1969). It was concluded that lycopods and sphenopsids lived in wetter conditions than pteridosperms and some cordaites (interpreted from root, stem, and leaf structures). Cridland showed (1964) that one type of *Cordaites* had stilt roots which may be compared with those of mangroves. This does not necessarily mean, however, that it occupied the same ecological niche. It would appear that different species of the genus *Cordaites* could live in widely different habitats, from coastal plain (Cridland 1964) to dryer 'upland' (Cridland and Morris 1963; Wartmann 1969). The ecological interpretations of some of these botanical structures are difficult as Chaloner and Collinson (1975) have shown that comparing the structures of Recent and fossil plants is 'fraught with hazards'.

Care must also be taken when arguing detailed ecology between Recent and fossil peat-forming environments (Leclercq 1926; Griffiths 1927; R. Teichmüller 1955) as, although general principles of the environment may be correct, detailed vegetational comparison is not possible (at least with the Upper Carboniferous) (Spackman *et al.* 1966; Habib *et al.* 1966; Habib and Groth 1967; papers in Dapples and Hopkins 1969; Cohen and Spackman 1972; Cohen 1975). The evidence concerning the climatic conditions of the Euramerian coal swamps has been the cause of much debate (Schopf 1974). The interpretations differ widely from a tropical to a temperate climate (White 1931; Friedrichsen 1972; Schopf 1974) although the absence of growth rings in the wood from the Coal Measures (Westphalian) indicates a uniform climate (Chaloner and Creber 1974), perhaps tropical but at least semitropical and

moist (Noé 1932) straddling the equatorial belt (Friedricksen 1972; Chaloner and Lacey 1973).

The first attempt at a quantitative palaeoecological study of the Coal Measure (Westphalian) flora was the pioneering work of Davies (1908, 1920, 1921, 1929 and summarized by North 1935). Davies showed that data collected in both a quantitative and qualitative way was necessary in any serious attempt to unravel Upper Carboniferous shale floras. Davies also showed that the roof-shale floras associated with coal seams varied in terms of variety of species and total quantity of plant material. He noted the change through time of the floras from ones dominated by sphenopsids (in the lower part of the Coal Measure sequence) to ones dominated by pteridosperms (in the upper part). These changes Davies interpreted in terms of a wet flora giving way to a dry flora. These roof-shale floras do not necessarily indicate changes in coal-swamp floras, rather than changes in sedimentary environments, which Davies did not study in detail. North (1935) commenting on these results remarked 'it is necessary to remember that in collecting fossil plants we are not dealing with organisms *in situ*; the plant impressions in the Coal Measure shales are almost always derived from drifted fragments, and it does not necessarily follow that they represent plants identical with those that gave rise to the carbonaceous material of the next subjacent seam; they may have been transported for a considerable distance by the water that carried the mud in which they were ultimately buried and preserved'. Seward (1933) was one of the first to realize the importance of environments of deposition when he wrote, 'we cannot assume that the contemporary vegetation was exceptionally meagre or locally unrepresented merely because no fossils have been found; it may be because the conditions under which barren sediments were formed were not such as were favourable to the preservation of plant fragments'.

Davies (1929) determined a general pattern of change in the Upper Carboniferous floras of South Wales, a theme taken up by Dix (1934) who set up floral zones, using South Wales as her type area, which were later interpreted by R. Potonié (1951, 1952) as changing due to broad climatic shifts affecting the community structure. Subsequently floral zones were established in other areas, such as the United States (Read and Mamay 1964). Patton (1922) showed how, in Recent times, sedimentation, physiographic features, and plant distribution are all interrelated, a theme pursued in a speculative paper by Robertson (1952), who considered the role that plants played in controlling rhythmic sediments. Chaloner (1968) suggested that the two are intimately related; changes in one affecting the other and both being affected by other variables (such as climate).

Following the early work on coal petrology and using her work on the German Brown Coals, Teichmüller (1952; Teichmüller and Teichmüller 1968) proposed relationships between plant assemblages and coal lithotypes of the Carboniferous. This work led to a theory concerning the ecology of peat-forming communities (Smith 1962, 1963). These studies, together with those of Oswald (1937) and Karmasin (1952), led Haquebard and Donaldson (1969) to reach slightly different conclusions concerning relations between floral changes and coal petrographic variations. These authors adopted the terms used by Karmasin (1952) of different swamp environments and related forest-moor type peat to the formation of vitrite and

vitro-clarite with abundant pteridosperms, lepidophytes, and ferns; open moor with subaquatic cannell deposition (and spore-rich durite) and a transitional reed-moor for the deposition of spore-rich clarite formed mainly by sphenopsids. They also considered Oswald's (1937) relations of preservation of plant debris in relation to ground water and recognized 'a terrestrial zone (above the high water mark)' where dry fusite-clarite was formed, 'a telamitic zone (between high and low water marks)' where bright coals would form, and a 'limnic (subaqueous) zone' where dull coals were formed. Again rather different assemblages have been found by Habib (1966, 1968) in the Pennsylvanian of the United States, probably as the general sedimentary environment and ecology is not the same as in Canada or Great Britain. The presence of abundant fusain in coal has caused controversy (White and Thiessen 1913; Stüzer 1929; Crickmay 1935; Marshall 1954; Francis 1961; Komarek 1972). Some believe that fusain represents true charcoal, and is the result of forest fire, because of the similar three-dimensional preservation (unaltered by subsequent compaction and hence a rigidity acquired before or very early in peat formation); a similar temperature of formation as shown by electron spin resonance studies and specific heat determinations; a general resemblance to charcoal, often with fine detail preserved without any sign of fungal or bacterial attack, and finally the fragmentation of the material (Grebe 1953; Terres *et al.* 1956; Harris 1958; Francis 1961; Austen *et al.* 1966; Stach 1968; Alvin 1974; Scott 1974). Others, however, feel that the resemblance to charcoal is only superficial and object to this method of formation because of the abundance of fusain in Palaeozoic coals in relation to those of subsequent eras; the absence of conflagration and drought in tropical swamp areas today and the presence of unaltered resin bodies associated with the fusain, but no alternative satisfactory mechanisms have yet been found (White and Thiessen 1913; Stüzer 1929; Terres *et al.* 1956 for Gondwanan coals; see discussion in Austen *et al.* 1966; Schopf 1975). This controversy remains unresolved.

White (1907, 1908, 1909, 1931) showed that in the topmost Upper Carboniferous and Lower Permian rocks there were representatives of an 'upland' flora. This idea was expanded by Gothan and Gimm (1930) for the European Permian and again later by Gothan and Remy (1957) who recognized a lowland association of *Calamites* and *Pecopteris* and an upland association of *Callipteris* and *Walchia*. Subsequently such upland floras have been recognized extensively throughout the Carboniferous. Cridland and Morris (1963) in the Pennsylvanian of Kansas extended the work of Moore *et al.* (1936) and demonstrated the major differences between Upper Carboniferous upland and lowland floras, the former containing *Taeniopteris*, *Walchia*, and *Dichophyllum*. Daber (1955, 1957) recognized different plant associations in the Viséan and Westphalian of Germany and Havlena (1961, 1970, 1971), working on Carboniferous successions of Czechoslovakia, described both a coal-forming association of plants (Flöznah) and an association drifted into the coal-forming area (Flözfern). Obrhel (1960), studying the Stephanian successions in Bohemia, noted relationships between plant assemblages and facies and discussed allochthonous and autochthonous plant preservation.

Josten (1961), studying German Upper Carboniferous stratigraphy, noted the presence of definite and repeated cycles of fossil plant assemblages. Following this work Dräger (1964), in an extensive quantitative study of roof-shale floras from

a sequence of coals which could be traced some distance laterally, found a differentiation of plant associations which he believed to represent actual plant communities. He argued that where the associations have been transported they have the same composition as those which appear to have been preserved *in situ*. He recognized three associations or 'community types': (1) articulate (sphenopsid), (2) pteridosperm, and (3) lepidophyte-cordaites. It was found that above most coal seams the lycophyte-cordaites association was laterally replaced by the pteridosperm association which was itself replaced by the arthrophyte (sphenopsid) association and rarely was the first and last of these associations found in juxtaposition. It is difficult to know to what extent the assemblages were related to the coal-forming swamp itself or whether to other physiographic features of a flood plain or another environment. As well as providing a stimulating study this work contains an important reference source to the German literature. More recent work has not solved the problems raised by this work (Keller 1972), although Pfefferkorn *et al.* (1975) have recalculated the data and compared it with other sites in Europe and America.

Several Russian workers have interpreted the palaeoecology of Upper Carboniferous plant assemblages (Radchenko 1964; Fissunenکو 1965; Krassilov 1972). These studies have included both the Karaganda Basin (Oshurkova 1967, 1975) and the Donetz Basin (Stschegolev 1965, 1975; Fissunenکو 1967; Fissunenکو and Stschegolev 1975). However, this work has been mainly qualitative and only one quantitative study has been published (Oshurkova 1974). Nevertheless three types of plant community have been recognized (Oshurkova 1967): (1) foreshore-hydrous silvan vegetation (waterlogged marginal lake forests), accumulating on coastal plains consisting mainly of arthrophytes (sphenopsids); (2) 'Swampy Silvan' (swamp forest) vegetation in coal-forming areas characterized by lepidophytes (lycopods); and (3) 'woody shrub vegetation', in conditions of well-drained plains consisting mainly of pteridosperms. These broad community-types should be regarded as a hypothesis leading towards the recognition of real communities, rather than as real communities in themselves. This pioneering work will be strengthened as more becomes known of the depositional histories of the rock sequences.

Knight (1974) has shown that in the Sabero Coalfield of Spain there were two distinctive floras within the Stephanian A; firstly a flora associated with the coal-forming environment (Flöznah) where fern species dominated pteridosperm species and secondly a hillslope flora (of younger aspect) in the northern area associated with sandier rocks (Flözfern) where pteridosperm species dominated fern species. A recent discovery of abundant *Sporangiostrobus* together with an abundant associated flora preserved in volcanic ash within a coal seam from the Upper Stephanian of Puertollano, Spain (Wagner and Spinner 1976) gives us for the first time a detailed picture of this important coal-forming community. The spores of *Sporangiostrobus* (micro-, *Densosporites* and mega-, *Zonalesporites*) are known to occur abundantly at many levels in coals of Upper Carboniferous age (Grebe 1966), but until now only a few specimens of the parent plant were known. Associated with this plant in the same ash band, which presumably engulfed and preserved this community *in situ*, are abundant ferns (mainly pectopterids yielding *Torispora*), *Scolecopteris*, sphenopsids (*Asterophyllites* and *Macrostachya*), and cordaites (mainly *Cordaitanthus* with only a few leaves).

There has been renewed interest in various aspects of Upper Carboniferous floral palaeoecology in the United States (Phillips *et al.* 1973). Peppers and Pfefferkorn (1970) examined both macro- and micro-plant remains from a stratigraphic interval in the Carbondale formation, and distinguished qualitatively numerous plant 'associations', related to different physiographic features: 'Wet swampy' with lycopods, ferns, and rare cordaites; 'Dry swampy' with ferns, lycopods, and sphenopsids; 'Levées and flood plains' with pteridosperms, ferns, and sphenopsids; and 'Upland' with pteridosperms, cordaites, and rare Noeggerathiales. Their schematic interpretation of floral distribution in sedimentary facies has proved useful as a working model, although the basis for some of the ecological interpretation (such as a wet or dry swampy area) remains uncertain.

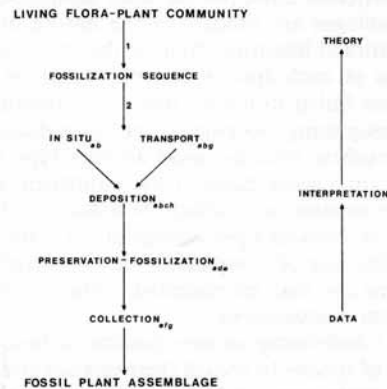
Phillips *et al.* 1974a and Phillips *et al.* 1974b described the quantitative analysis of coal-swamp vegetation in relation to coal, using the plants present in coal balls as a guide to the constitution of the coal. They have noted that in the Illinois Basin there is a major change in coal-ball floras from the Westphalian to the Stephanian from one dominated by lycopods to one dominated by tree ferns. This change has been interpreted as indicating a broad climatic shift at that time. Darrah (1941) noted that the coal-ball floras from Iowa are dominated by cordaites, pteridosperms, and ferns and so if these floras really represent those plants which formed the coal, as most workers argue, then it would appear that many groups of plants were capable of coal formation and it may have been environmental factors rather than specific communities which were responsible for coal formation, although some were more suited than others. This work is supported by recent advances in coal chemistry (Niklas and Phillips 1974).

The age of the Dunkard Series of the eastern United States (Clendening and Gillespie 1972) is a problem showing the importance of ecology in any palaeobotanical stratigraphical work—see also Oshurkova (1975). Pennsylvanian upland floras have been studied by Leary (1974, 1975; Blazey 1974) who showed a rather different floral composition from the normal swamp flora, which was rich in Pteridospermales and Noeggerathiales and deficient in ferns and lycopods. Although upland floras were recognized as macrofossils early in this century it was not until 1958 that Chaloner (reinterpreting data from Neves 1958) showed that such floras could be recognized in the palynological record. Schopf *et al.* (1944) had commented that some of their conifer pollen might have been produced by upland species (p. 28), but this aspect of their work was not followed up until the stratigraphical distribution of spores had been studied (Smith and Butterworth 1967; Chaloner and Muir 1968; Friedrichsen 1972).

Many workers across the Euramerian coal-forming belt have recognized, particularly in the Westphalian, three major lowland plant assemblages; one dominated by lycopods, one by sphenopsids, and one by pteridosperms as well as various upland floras. It is now important to relate these assemblages to depositional environments with the hope of unravelling the Upper Carboniferous plant community structure.

PROBLEMS IN RELATING FOSSIL PLANT ASSEMBLAGES TO
CONTEMPORANEOUS PLANT COMMUNITIES

Ecologists studying living plant associations have long argued over the definition of a plant community and how to characterize it statistically (Greig-Smith 1964), but the fossil plants a geologist finds generally represent the fragmented parts of individuals, often derived from plant communities only brought together by transport and sedimentary processes. Further the plants observed may have undergone changes of one sort or another during the fossilization process (Rolfe and Brett 1969). Problems in relating invertebrate fossil assemblages to their living communities have been discussed extensively over the last fifteen years (see references in Walker and Alberstadt 1975), and have included the study of processes that may affect an organism after death (Taphonomy). Little work concerning macrofloras has been published, although these problems have been recently discussed in some unpublished theses (Hill, Leeds, 1974; Spicer, London, 1975). Krassilov (1969, 1972, 1974) emphasized palaeofloristic successions and their causes, rather than relating fossil plant assemblages to contemporaneous plant communities. Once that data has been collected in a repeatable fashion, then hypotheses concerning possible plant communities will involve the intermediate steps of an interpretation of transport and depositional histories of the plants. These hypotheses may be constantly modified with the collection of new data and also with changes of interpretation of the



TEXT-FIG. 1. Problems in relating fossil plant assemblages to contemporaneous plant communities. 1, Initiators of the fossilization sequence (on some or all of the plants in a community): (i) Internal factors; organ abscission; organ shedding; disease; resistance of plant organ to decay. (ii) External factors; animal destruction; storms; floods; land subsidence; climatic change; erosion; other natural catastrophies, e.g. forest fire, proximity to site of transport. 2, Key to factors controlling fossil plant assemblages (on some or all the plants in the fossilization sequence): (i) Destructive mechanisms; (a) decay, (b) mechanical break-up, (c) immediate post-depositional reworking, (d) diagenesis, (e) weathering, (f) collecting bias. (ii) Interference, (g) sorting, (h) additions from other communities.

sedimentary environments. The major processes involved in the formation of a fossil assemblage are set out in text-fig. 1. Initiators of a sequence are listed under internal and external factors and 'noise' may be related to destruction of all or some of the plants at any stage, or interference by other factors during the major sequence. Text-fig. 1 shows in the left-hand column, those processes which have gone into forming a fossil plant assemblage and in the right-hand column those steps an investigator must take to retrace these paths. This sequence does not interpret the changes in assemblages up a succession but represents primary taphogenic assemblages (those connected with changes affecting plant remains in the course of their transportation and burial, Krassilov 1969).

SAMPLING TECHNIQUES

Numerous sampling techniques have been employed in ecological studies on fossil plants. The merits of different techniques have recently been discussed by Hill (unpublished thesis, Leeds, 1974) and Spicer (unpublished thesis, London, 1975) but those considered here have been used in Palaeozoic studies. Coal Measure palaeoecological studies were pioneered in South Wales by Davies (1908, 1920, 1921, 1929) and this work was continued by Dix (1934). Techniques employed by both authors suffer from subjectivity and so are not reproducible. Much of the quantitative data collected by Davies was obtained by counting the number of plant fragments found at a particular level. No standard sample size was used and genuine changes in floral assemblages are hidden by the nature of fragmentation of each species and their depositional histories. Neither the absolute numbers obtained nor the relative proportions of each species can be compared with those from other horizons. Dix (1934) also failed to use an objective sampling technique but used a subjective method of designating 'dominant' and 'subsidiary' species. Harris (1952), whilst studying the Yorkshire Jurassic, used another type of quantitative method, a measure of frequency (in a sense more or less equivalent to 'fidelity' of ecologists studying Recent plant communities), which he defined as the number of localities at which a species has occurred as a percentage of the total number of exposures of that horizon studied. This use of 'frequency' may be helpful in recording the persistence of species and its use may be extended to the study of Coal Measure plant beds rather than localities or exposures.

Dräger (1964) used a half-metre square quadrat technique, and used in essence the presence or absence of species to record their vertical and horizontal frequency in roof shales. A common technique for Recent ecologists is the quadrat, either by an analysis of cover or frequency determination (Greig-Smith 1964). The interpretation and problems of quadrat analyses on modern plant communities have been reviewed by Frenkel and Harrison (1974). Both the size of quadrat and the type of data obtained from the quadrat are important and are directly related to the type of palaeontological section to be examined, to the type of data required, and to the time available for study. The quadrat size may have to be smaller than ideal, due to the numerous problems in excavation and data collection. The basic counts which can be made from a fossil quadrat are (1) the number of fragments of each species (Hill, unpublished thesis, Leeds, 1974) and (2) the cover area of each species (this paper). The

first method has the problems that the results are greatly affected by the extent to which different species break up during transport and also by the process of sampling itself. However, the cover technique does not take into consideration the degree of fragmentation of the plants, and some plants may be under- or over-represented because of their morphology or because of their uneven scatter on the bedding plane. A cover technique has been used in the example described here, but some assessment of the fragmentation and density of each species was also made.

The sampling technique used at Annbank was as follows:

At each plant horizon a half-metre square quadrat of one or more closely spaced bedding planes was cleared and a grid with 100 random points was placed over the area. The presence and identity of plant remains was recorded underneath each point to give a numerical assessment of the percentage 'cover' of each species on the quadrat; the bare rock was also recorded. When a quadrat could not be conveniently cleared, blocks of one horizon were split and laid out in the quadrat area and then the count was made. Using this method counts of plant, bare rock, and space were made and so extra random points were recorded until the total of plants plus bare rock was 100. There are several factors influencing the results (text-fig. 1). Because of the small extent of exposure the quadrats could not be placed in a random fashion but only where the section allowed. Errors may also occur from the nature of the technique itself and also that only 100 points per quadrat were taken. It is felt that 100 points represents a justifiable compromise between the time taken and the reliability of the results. The way in which a rock splits along the bedding may also influence the results, and it is rarely possible to measure cover on a single bedding plane. This problem is accentuated by the presence of plants such as *Cordaites* whose typically large strap-like leaves increase the probability of the rock cleaving open wherever they occur. In a given volume of rock, therefore, containing some *Cordaites* but perhaps a greater quantity of smaller parts of other plants, the rock will cleave preferentially to expose the *Cordaites*, resulting in some bias favouring such large plant parts.

This use of 'cover' differs from that used by plant ecologists in a living community. There one is measuring the result of interactions between the plants, e.g. the extent to which a species is successfully using the light for photosynthesis. In the fossil (death) assemblages there is no interaction of assembled species and the percentage cover is merely a measure of area of plants (leaves and stems which were originally upright before transport) on the rock surface exposed by splitting. It is probably the easiest parameter to measure related to the mass of plant material contributed by any constituent of the community(ies) from which the assemblage was derived, as well as being related to the total photosynthetic surface of the plant in life—which is related to its status in the living plant community. The 'cover area' of each species, therefore, is related in part to its original biomass, in part to its preservability, and in part to its hydrodynamic qualities. Such a cover area is a measure of its 'thanatomass'. Some plants may have a high thanatomass but may have been small contributors to a community whilst others such as ferns may have had an important role in a plant community and perhaps a large biomass, but because of the relative ease with which they are broken up they may have only a small thanatomass in a fossil plant assemblage.

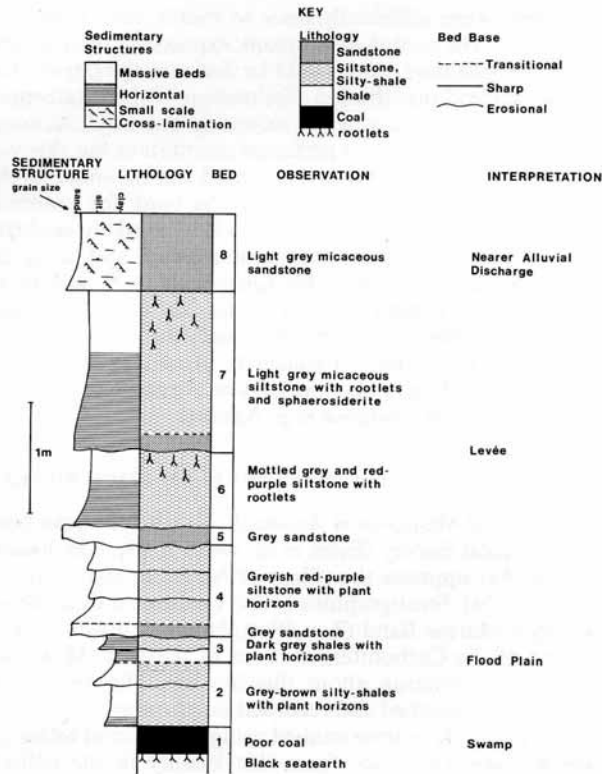
Few of the plant beds were sufficiently thick to enable more than one quadrat to be carried out through it. The section at Annbank exposed 10 m of sediment laterally in the banks and no quantitative work could be done on the lateral distribution of species as well as the vertical distribution. Estimation of the fragmentation of each species at each level was undertaken when recording quadrats. At some levels, i.e. Bed 2a, text-fig. 3, the plants showed a preferred orientation but this was not so for every horizon. Measurements could only be carried out on some levels because of the necessity of removing blocks of a bed from the bank for examination. Semi-quantitative cover abundance scales have been widely used by ecologists studying extant plant communities for quick estimation of quadrat, and hence cover, values. Two scales are in general use, the Braun-Blanquet Scale (1-5) and the Domin Scale (1-10). Both scales use a combination of statistics, i.e. both frequency and cover value. The cover values obtained during this study have been converted to the Domin Scale and are shown in Table 1. This has the advantage of showing up changes in members of the flora which may be numerous but because of their size and shape always record very low cover abundance (e.g. *Annularia*).

AN ECOLOGICAL STUDY OF A WESTPHALIAN ROOF-SHALE FLORA

Fossil plants from the Coal Measures of Annbank, Strathclyde have been previously recorded by the Geological Survey (Eyles *et al.* 1949, p. 93). The locality is 'on the left bank of the River Ayr opposite the village of Annbank just south of the piers of an old bridge' (NS 400 234). Stratigraphically it is considered to lie between the Top Ell Coal and Skipsey's Marine Band (Top Westphalian B, Eyles *et al.* 1949, p. 93). Subsequent mapping of the Carboniferous rocks of the area (Mykura 1967) failed to reveal any further information about this locality. The locality has been re-examined and the section described and recorded in lithographic log form, text-fig. 2 (Selley 1970) and the plants have been studied using the quadrat technique described above. Other species were examined from this locality in the collections of the Geological Survey of Edinburgh and the Hunterian Museum, Glasgow. A palynological investigation of the coal was also undertaken to compare with the compression (Walton 1936, p. 220) flora in the roof shales.

SECTION DESCRIPTION

Lithology. The strata exposed in the river bank consists of 5 m of sediments dipping 10° north at 120° (text-fig. 2). At the base of the section, 12 cm of coal (Bed 1), mainly shaley but bright in part is underlain by a dark grey to black micaceous seat earth with stigmarian rootlets. Resting on the coal are 75 cm of grey silty shales (Bed 2), consisting of eleven upward-fining units, each of which generally has abundant plant material at the top (text-fig. 3). The top unit grades into a fine black shale (Bed 3) with abundant plants and *Pinnularia* (small detached roots showing extensive branching) at one level. The base of the next bed (Bed 4a) is a slightly erosive red (iron-rich, haematitic) silty-sand which is followed by three upward-fining sequences of reddish-grey siltstones, laminated at the top with plants, and very iron-rich in parts. Above these rocks is a grey micaceous fine sandstone with an erosive base (Bed 5), followed by grey micaceous silty shales laminated at the base. These pass into mottled red and green micaceous silts which contain numerous rootlets (not *Stigmaria*) consisting of leached brown traces. This horizon is followed by a micaceous siltstone, finely laminated at the base and passes into light-grey micaceous siltstone with small rootlets and abundant, dispersed sphaerosiderite. There is then a sharp planar erosional

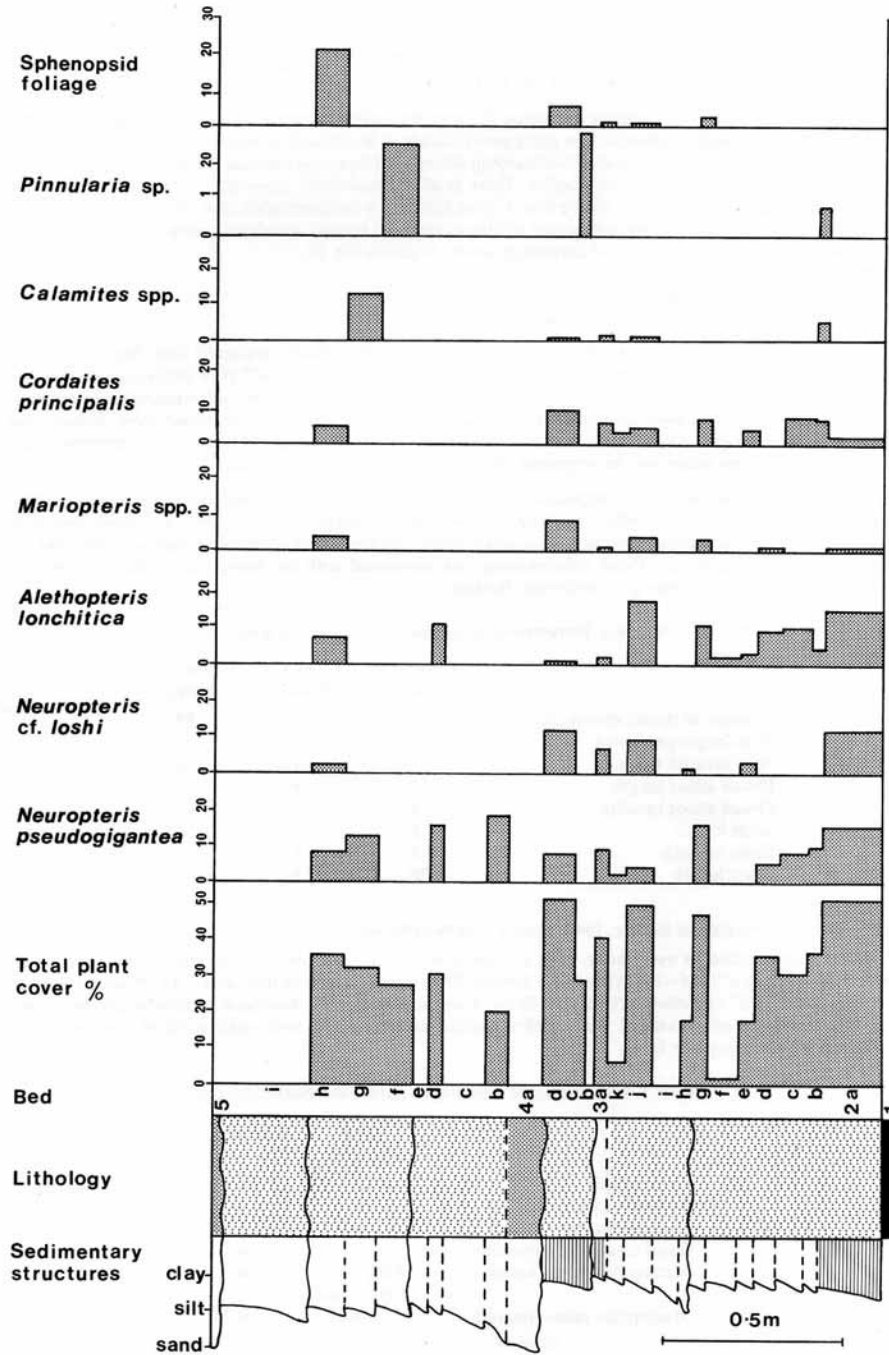


TEXT-FIG. 2. The Annbank Section, with possible interpretations.

base followed by a reddish-grey coarsely micaceous fine sandstone which exhibits small-scale cross-lamination. The Geological Society of America rock-colour chart (1970) was used for the rock-colour descriptions and the grain size was measured in thin section (using the Standard Wentworth Scale).

Plant horizons. The occurrence and distribution of the plants at Annbank is shown in Table 1. The cover variation of the major elements of the flora is shown in text-fig. 3. Owing to limited exposure little quantitative work on lateral variation in the plant horizons could be carried out. Although this did not seem considerable, the possibility of variation was considered when interpreting the significance of vertical changes. The plants occur mainly in the upper part of each upward-fining unit giving it an appearance of having a laminated top but this may be due to the abundance of flat-lying foliage which allows the rock to be easily split.

The basal horizon is a black micaceous seatearth which contains numerous rootlets of *Stigmara* (a lycopod). This seatearth grades into a shaley coal and then a bright coal; this sequence is then repeated, before being followed by medium-grey micaceous silty shales with plants. There is a general increase in the pteridosperm foliage (*Neuropteris*, *Alethopteris*, *Mariopteris*, etc.) with decreasing grain size of rock (Beds 2 and 3) which may be interpreted in terms of both the hydrodynamic properties of the fern-like foliage and the original composition of the assemblage (Ferguson 1971). Part of the assemblage will not



TEXT-FIG. 3. Percentage cover of major plant constituents in the lower part of the succession at Annbank.

be identifiable in the coarser lithology, because the finer details of the plants are not preserved or the plants consist of comminuted fragments. The sphenopsid foliage is first found in Bed 3 and becomes more conspicuous up the succession as do layers containing abundant *Pinnularia* (interpreted as roots of *Calamites*, Crookall 1969) and *Calamites* (pith casts). There is also, consistently throughout the succession, some *Cordaites*. No plants were found above Bed 4 other than a few unidentifiable rootlets (but not *Stigmara*) in Beds 6 and 7. There is, in the upper part of the succession, a small correlation between the presence of sphenopsid foliage and a large total percentage cover of plants (fig. 3).

Notes on the status of some plants

(i) *Cordaitanthus* sp. Plate 50, figs. 1-3 (Pb 4457, Pb 4458).

Two specimens referable to the genus *Cordaitanthus* Feistmantel were collected from Bed 2a. *Cordaitanthus* Feistmantel, 1876 takes priority over *Cordaitanthus* Grand 'Eury, 1877 (Fry 1955) even though the latter is a *nomen conservandum* over *Botryoconus* Goepfert (International Code of Botanical Nomenclature 1972). These two specimens are considerably larger than most previously described from Britain, the closest species being *C. nostellensis* (Barker) 1943 (in Barker and Whittle 1943) and may represent a new species, although no name will be proposed until more specimens are obtained.

Description. Inflorescence in a compound 'catkin', a long narrow axis. Dwarf shoots (Crookall 1970; Florin 1950 = flowers Florin 1950 = buds Barker 1943) are alternate and distichously arranged, diminishing in size towards the apex of the axis. The dwarf shoots are formed of rounded triangular scales and are subtended by a long bract. These inflorescences are associated with the leaves of *Cordaites principalis* Germar and the seeds *Samaropsis pyriformis* Barker.

TABLE 2. Dimensions of *Cordaitanthus* spp. (in mm).

	<i>C. sp. (1)</i> (Pb 4457)	<i>C. sp. (2)</i> (Pb 4458)	<i>C. nostellensis</i> (Barker)
Number of dwarf shoots (buds)	5	5	13
Axis length preserved	30	40	138
Axis breadth (max.)	3	3.5	1-5.5
Dwarf shoot length	15	14	19
Dwarf shoot breadth	8	8	15
Scale length	6	?	10
Scale breadth	4	?	3
Bract length	20	?	?

(ii) *Samaropsis pyriformis* Barker, 1944. Plate 51, fig. 14 (Pb 4469).

These seeds, found in association with *Cordaitanthus* sp. (cf. *nostellensis*) have only been previously recorded by Barker 1944—the types from Nostell Brickworks, low Westphalian C, which were found in association with *C. nostellensis* (Crookall 1976). The size range of the Annbank specimens are very comparable (Table 3) being winged seeds with a nucule, cordate-acute, with shallow basal concavity, and a long narrow micropylar tube.

TABLE 3. Dimensions of *Samaropsis pyriformis* Barker (in mm).

	Type specimen	Annbank (Pb 4469)
Total length	13.5	14
Total breadth	9	9
Basal concavity—length	6.5	7
Basal concavity—breadth	7	6
Micropylar tube—length	4 (up to 6 if restored)	6
Micropylar tube—breadth	0.65	0.75

(iii) *Cordaites principalis* Germar. Plate 50, figs. 4, 5 (Pb 4459).

These large strap-like leaves are frequent at Annbank, often reaching 5 cm in width and 50 cm in length. Very few apices are preserved and the leaves have tended to break up parallel (during transport) to their margin into ribbon-like strips (Crookall 1970). No cuticle was preserved.

(iv) *Mariopteris* cf. *sauveri* (Brongniart). Plate 51, fig. 7 (Pb 4444).

Numerous specimens of this species were collected, all fairly fragmented. It differs from *M. nervosa* (Brongniart) in that the venation, where seen, is delicate and relatively dense, the apices of pinnules rounded to obtuse and differs from *M. muricata* (Schlotheim) in its pinnule margins not having basiscopic incisions and there being a length/width pinnule ratio of 1.5:1.0 instead of 2.5:1.0 (see Boersma 1972). It may be pointed out that these specimens do resemble apical parts of secondary pinnae of *M. muricata*, and both this species (Pl. 51, fig. 11) and *M. nervosa* occur at Annbank. The possibility exists that all this foliage belongs to one species but it is felt that there are sufficient differences to justify specific separation.

(v) *Alethopteris lonchitica* auct. (non Schlotheim?). Plate 51, figs. 1-3, 11, 12 (Pb 4449, Pb 4462, Pb 4446).

A large number of specimens showing a wide range of morphology was found at Annbank. It is believed that these fragments represent different parts of fronds as seen in a more complete specimen figured by Crookall (1955, pl. X, fig. 1). A lot of confusion surrounds this species and the range of morphologies fit with those originally described as *A. urophylla* Brongniart. The name *A. lonchitica* will be retained until there is a revision of this species.

(vi) *Sphenophyllum cuneifolium* (Sternberg). Plate 51, fig. 6 (Pb 4443).

Included with *S. cuneifolium* is its variety *S. cuneifolium* var. *saxifragifolium* (Sternberg) which is considered to belong to the same plant (Crookall 1969).

(vii) *Neuropteris pseudogigantea* H. Potonié. Plate 51, fig. 13 (Pb 4440).

This species has recently been described from the French Westphalian as *Paripteris pseudogigantea* (Potonié) by Laveine (1967). It is a common British species, often confused with *N. gigantea* Sternberg, the latter having much more arcuate and tapering pinnules. The Annbank specimens (mainly isolated pinnules) may be compared with *N. (Paripteris) linguaefolia* P. Bertrand in having very straight-sided pinnules. The two species *N. pseudogigantea* and *N. linguaefolia* in France, have similar stratigraphic ranges—mid Westphalian B to Westphalian C (Laveine 1967).

Palynology. Another 'view' of the flora may be gained by examining the rocks, especially the coals where no macroplants can be identified, for spores and pollen of plants. Many of these spores are known from fructifications which have been examined *in situ* (Courvoisier and Phillips 1975) so it is possible to some extent to gain a compositional view of the flora from this study. However, the relative spore production of each type of plant presents a major difficulty as some, e.g. *Lepidodendron*, produced vast numbers of microspores whereas others such as pteridosperms seemed to have produced fewer but larger. The transport and sorting of these assemblages presents another problem although it is generally considered that the spore composition of a coal gives a good quantitative estimate and certainly a good qualitative view of the coal-forming flora (Smith 1963). The botanical affinities of many of these spores are known (see Potonié 1962 *et seq.*) but the spore genus or species does not necessarily correspond with a macrofossil genus or species, i.e. one cone may contain a variety of spore morphologies, which may be regarded as a number of different spore genera, or else one type of spore may be known from a variety of different plants.

Spore preparations of a channel sample of coal was undertaken. This was macerated using Schulz's solution followed by dilute ammonia (Smith and Butterworth 1967). The spores were mounted on five slides in glycerine jelly and 200 spores were counted on each in order to overcome sorting problems in slide preparation (Chaloner and Orbell 1971). Only genera were recorded in order to give a general view of the spore spectrum. There are many *Lycospora* as well as other spores known to have been produced by lycophytes (*Crassispora*, *Endosporites*). The next most abundant group of spores are those produced by

sphenopsids (Table 4). It is striking that the data obtained from the roof using macrofloras is so different from that obtained from the spores composing the coal. If the spores represent the *in situ* flora, as most people believe, then peat forming must have stopped before the inundation of detritus bringing with it the pteridosperm assemblage or else one would expect more macrofossil evidence of lycopods. If, however, the spores represented a more regional picture of the coal-forming flora then these spores would have been transported into this environment. The former explanation is preferred as there is little evidence of lycopods in the roof of the coal and yet it has a stigmarian seatearth.

TABLE 4. The spore composition of the Coal (Bed 1) and their natural affinities.

LYCOPODS. *Lycospora* 39%, *Crassispora* 6%, *Endosporites* 4%,
Cristatisporites present < 1%, *Densosporites* < 1%, TOTAL 49%.

ARTICULATES. *Laevigatosporites* 23%, *Calamospora* 13%, TOTAL 36%.

FERNS. *Raistrickia* 2%, *Leiotriletes* 1%, TOTAL 3%.

PTERIDOSPERMS. *Schopfipollenites* < 1%.

CORDAITES. *Florinites* 2%, TOTAL 2%.

CONIFERS. *Potonieisporites* < 1%.

UNKNOWN AFFINITY. *Dictyotriletes* < 1%, *Vestispora* < 1%, *Cingulizonates* < 1%, Unknown 10%.

The affinities of spores were taken from Potonié and Kremp (1954) and Potonié (1962, 1965).

Stratigraphical significance of the flora. Of the twenty-six species of plant recorded only four are considered overall to be abundant and six, common. The stratigraphical ranges in Western Europe of these plants are shown in Table 5. From this it may be said that the flora is considered to be of a Westphalian B age,

TABLE 5. The ranges of the most common Annbank plants through the North-west European Westphalian (from Stockmans 1962; Crookall 1939, 1955; Dix 1934; Josten 1971a, b; Boersma pers. comm.). The first four are abundant, the remainder common. r = rare.

	Westphalian			
	A	B	C	D
<i>Neuropteris loshi</i>	×	×	r	
<i>N. pseudogigantia</i>		r	×	×
<i>Alethopteris lonchitica</i>	×	×	r	r
<i>Cordaites principalis</i>	×	×	×	×
<i>Annularia radiata</i>	×	×	×	r
<i>Mariopteris saueri</i>		r	×	r
<i>M. muricata</i>	r	×	×	
<i>Calamites cisti</i>	×	×	×	×
<i>Asterophyllites equisetiformis</i>	r	×	×	×
<i>Sphenophyllum cuneifolium</i>	×	×	r	r

EXPLANATION OF PLATE 50

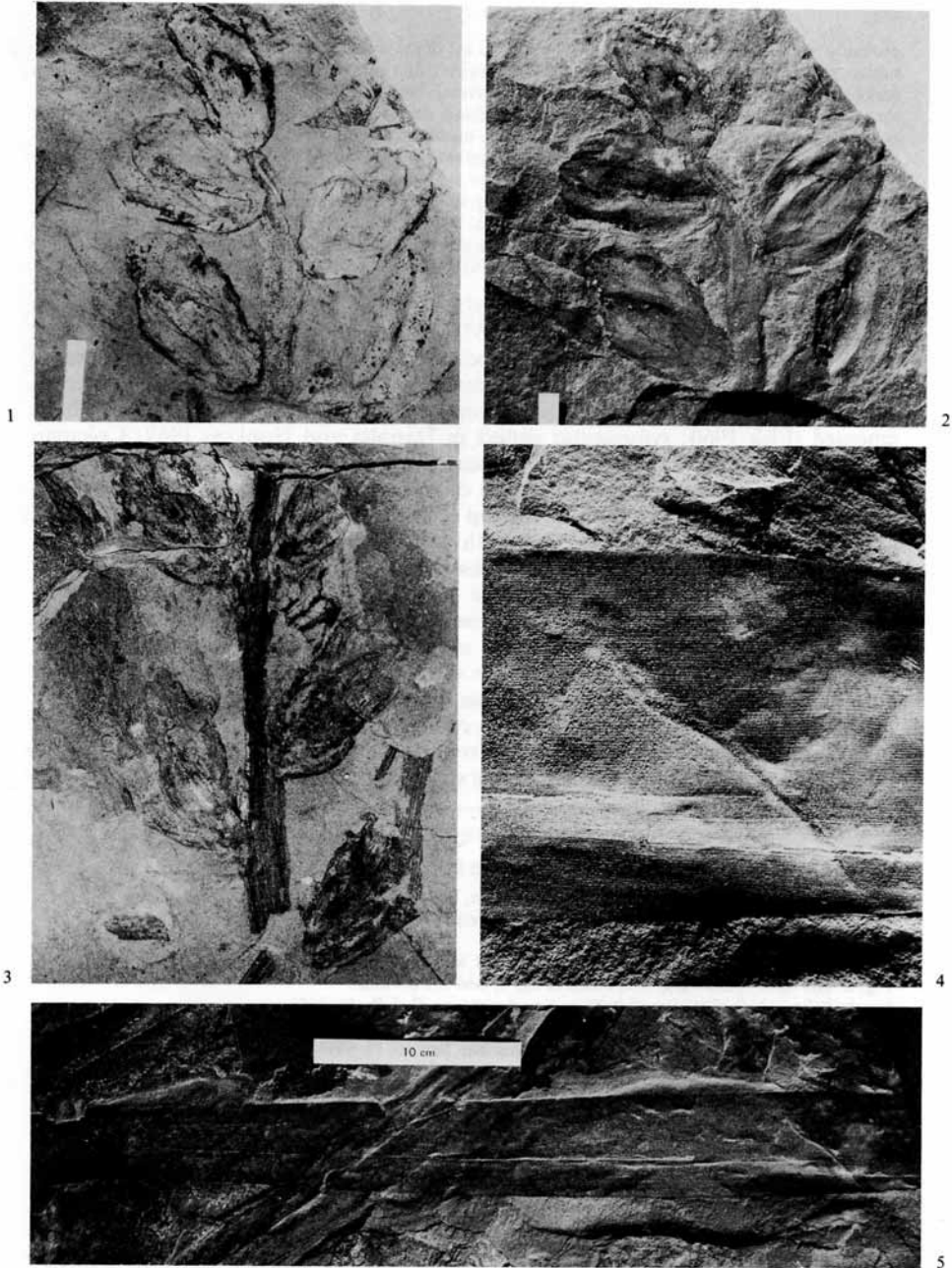
Fossil plants from the Coal Measures of Annbank, Strathclyde.

Figs. 1, 2. 1, *Cordaitanthus* sp., under xylene, $\times 1\frac{1}{2}$, Bed 2a, Pb 4457a. 2, same specimen, top illumination, $\times 1\frac{1}{2}$.

Fig. 3. *Cordaitanthus* sp., under xylene, $\times 1\frac{1}{2}$, Bed 2a, Pb 4458.

Figs. 4, 5. 4, *Cordaites principalis*, $\times 1\frac{1}{4}$, top illumination, Bed 2, Pb 4459. 5, same specimen, top illumination, $\times \frac{1}{3}$.

All the figured specimens are in the Hunterian Museum, Glasgow (Pb).



SCOTT, Coal Measure plants from Ayrshire

probably from high in the stage. The stratigraphical use of plants in the Upper Carboniferous has been the subject of many papers, notably by Dix (1934) and Crookall (1938, 1955). Other workers have also dated rocks by floras (Stockmans 1962; Josten 1971*a, b*; Novik 1969), and in America similar studies have been made leading to the recognition of Floral Zones (Read and Mamay 1964; Cridland *et al.* 1963). A wide collection of plants from many lithologies must be made to obtain a representative number of species to date a flora. As only genera of spores were identified they were not used in the stratigraphical determination, although Smith and Butterworth (1967) have set up palynological zones which are useful when there is no macrofossil flora or fauna, or to back up the data obtained from those groups. The great contrast between the flora, represented by spores from the coal, and the flora represented by macrofossils, from other lithologies, and their subsequent interpretation, might help explain the difficulty in matching Smith and Butterworth's (1967) spore zones and Dix's (1934) macrofossil zones.

The depositional environment. Depositional environments in the British Coal Measures have been reviewed by Duff *et al.* (1967), Hemingway (1968), and Elliott (1968, 1969), and facies analysis of West European sequences have been made by Reading (1970, 1971). These sequences may be compared to Recent peat-forming environments, and although detailed correlations are not possible, broad outlines have emerged (Fisk 1960; symposium papers in Dapples and Hopkins 1969; Coleman 1966; Reineck and Singh 1973). The succession at Annbank consists, at the base, of numerous small upward-fining units of micaceous silty shales and shaley silts with abundant plant fragments at the top of each, resting on a coal, shaley in part, underlain by a dark micaceous seatearth with *Stigmaria* (the bases of lycopods). Coal with an underlying seatearth represents an *in situ* peat deposit produced by 'swamp' vegetation (Elliott 1969). The area was subsequently inundated with detritus in irregular pulses which gave rise to each small upward-fining unit incorporating plant remains. This sediment may have been introduced in two ways: (1) by direct stream discharge into a now shallow lake or, (2) by the flooding of the swamp area by levée bank break (crevasse splay).

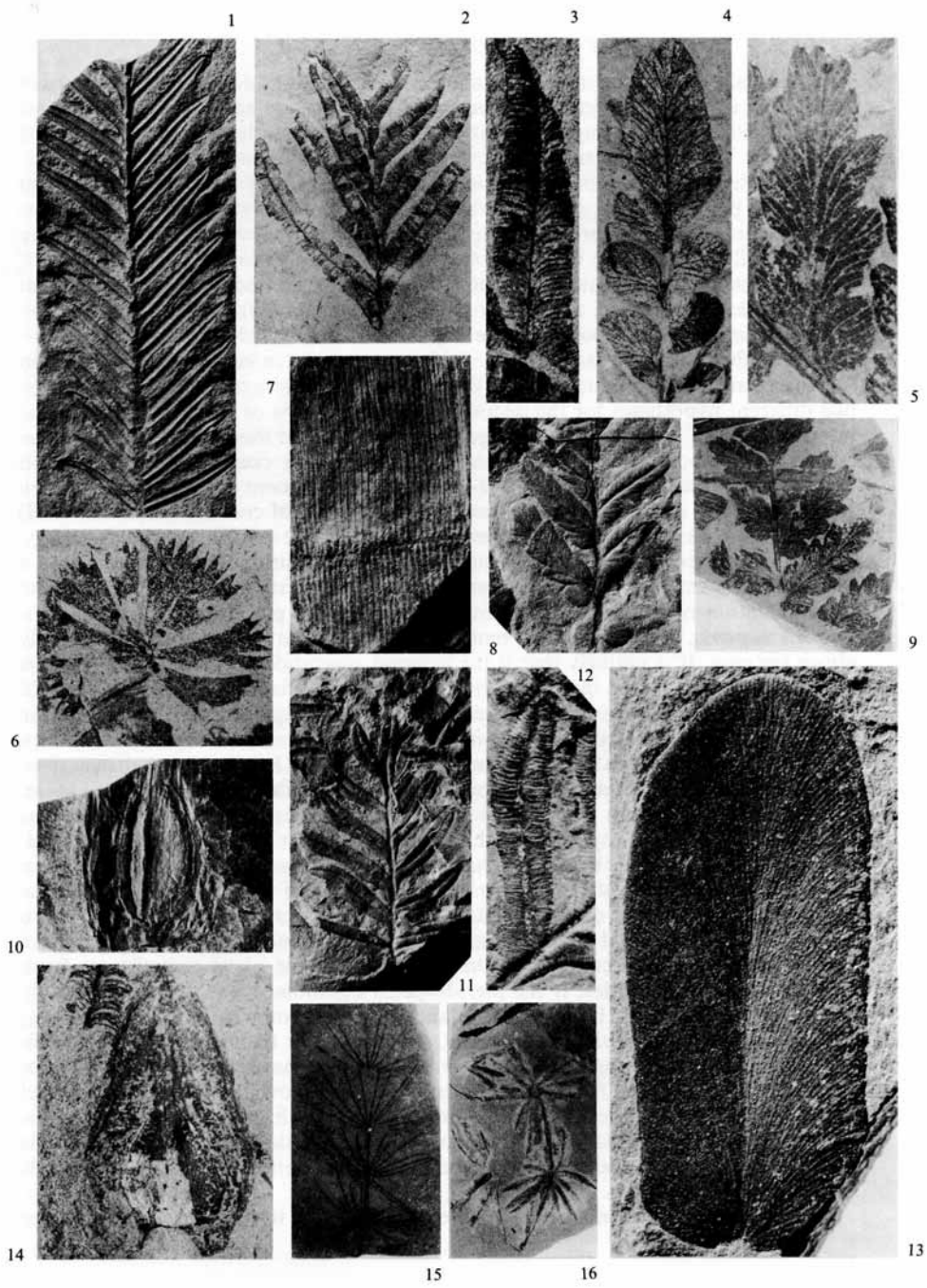
The lithologies above Bed 3 take on a coarser aspect and the *Pinnularia* horizons may have resulted from sphenopsids rooting in the sediment. These units are interpreted as being closer to the possible site of alluvial discharge. The mottled silty

EXPLANATION OF PLATE 51

Fossil plants from the Coal Measures (Westphalian B) of Annbank, Strathclyde.

- Fig. 1. *Alethopteris lonchitica*, $\times 1$, top illumination, Bed 4h, Pb 4449.
 Fig. 2. *Alethopteris lonchitica*, $\times 1$, under xylene, Bed 2j, Pb 4462.
 Fig. 3. *Alethopteris lonchitica*, $\times 3$, detail of fig. 2.
 Fig. 4. *Neuropteris cf. loshi*, $\times 3$, under xylene, Bed 3d, Pb 4454.
 Fig. 5. *Mariopteris muricata*, $\times 3$, detail of fig. 9, Bed 3, Pb 4465a.
 Fig. 6. *Sphenophyllum cf. cuneifolium*, $\times 2$, under xylene, Bed 4h, Pb 4443.
 Fig. 7. *Calamites cisti*, $\times 1$, top illumination, Bed 4g, Pb 4450.
 Fig. 8. *Mariopteris aff. saueri*, $\times 1$, top illumination, Bed 4h, Pb 4444.
 Fig. 9. *Mariopteris muricata*, $\times 1$, under xylene, Bed 3, Pb 4465a.
 Fig. 10. *Trigonocarpus* sp., $\times 1$, top illumination, Museum Collection Pb 4540.
 Figs. 11, 12. 11. *Alethopteris lonchitica*, $\times 1$, top illumination, Bed 4h, Pb 4446. 12, detail of fig. 11, $\times 13$.
 Fig. 13. *Neuropteris pseudogigantea*, $\times 3$, top illumination, Bed 4b, Pb 4440.
 Fig. 14. *Samaropsis pyriformis*, $\times 3$, under xylene, Bed 2d, Pb 4469.
 Fig. 15. *Asterophyllites equisetiformis*, $\times 1$, under xylene, Bed 4h, Pb 4442.
 Fig. 16. *Annularia radiata*, $\times 1$, under xylene, Bed 4h, Pb 4441.

All the figured specimens are in the Hunterian Museum, Glasgow (Pb).



SCOTT, Coal Measure plants from Ayrshire

sands with abundant rootlets (not stigmarian) and disseminated sphaerosiderite have been taken as an indication of frequent water-level change and exposure to the air (Elliott 1969) with resulting colonization by plants (possibly sphenopsids such as *Calamites*). There are alternative interpretations for the deposition of these rocks. With the stream (river) discharging into a shallow swampy lake, rapid silting up would take place (providing there was no subsidence), which would lead to colonization by plants with the periodic drainage (the intervals between flooding) causing rise and fall on the water table and frequent subaerial exposure. Alternatively, if the sediments represent genuine overbank deposits, then the sediments would coarsen towards the stream bank, and the coarser sediments with frequent exposure may represent actual levée deposits. These deposits are succeeded by small-scale cross-laminated fine micaceous sandstones. Such sequences have been reviewed by Allen (1965) and are also similar to many of the intradeltaic sequences of Elliott (1969). The two different hypotheses for the depositional environment of Beds 2 to 8 make the interpretation of the plant assemblages contained within them more difficult. The coal contains abundant lycopod spores which may have come from plants which lived *in situ* in the swampy peat- (coal-) forming environment or else may have been transported and deposited in that area. The palynology of coal-seams (Smith 1962) indicates that the spores chiefly represent the flora of the coal-forming community, although not necessarily the actual 'on-the-spot' composition. If this interpretation is correct for Annbank, then peat formation must have stopped in the area before the inundation of shaley-silts containing foliage of the pteridosperms *Neuropteris* and *Alethopteris*, since no lycopod remains are found in any of the units immediately above the coal. It is unlikely that if the lycopod vegetation was still thriving in the 'swamp' area during the initial flooding and sediment discharge, none of it would have been incorporated into the basal silty layer although much of it might have been transported out of the area. This discrepancy between the topmost coal flora and the roof-shale flora is frequently encountered in north Britain although occasionally abundant lycopod remains are found in roofs of shaley coal (Penny Hill seam, Ragpath, Co. Durham) and occasionally abundant upright trunks (Jongmans 1955; roof of Barnsley Top soft coal, Lowther North, near Wakefield) are preserved. Therefore the flora in the basal silty shales represents an assemblage of pteridosperm foliage with some *Cordaites* which may be the result of incorporation in detritus deposited by flooding or discharge into the area by a river or river system. The two hypothetical depositional environments postulated, although broadly similar, give rise to two hypotheses concerning the derivation of the plant assemblages from original plant communities. If the pteridosperm assemblage was deposited directly by a river into a shallow lake then the plants may have come from various sources; either from the edges of the swamp, lake, river banks, or from upstream. It is difficult to know from the fragmentation how far the plants have travelled. They do not appear to have travelled far, but Ferguson (1971) has shown that leaves may travel a considerable distance, even up to 50 km, without much damage, and even a few kilometres may encompass a wide variety of communities. The silting up of this shallow lake might have been accompanied by the colonization of mainly sphenopsids with some pteridosperms.

If the sediments were deposited by crevasse splay on to a floodplain then there

are other possible derivations for the plant assemblages. This detritus would include fragments of plants living around the swamp edge as well as perhaps some fragments of plants which had been incorporated in the sediment before flooding. Each pause in sedimentation would allow many of the plants to re-establish themselves on the floodplain only to be incorporated by the next flood. With meandering streams or rivers across the floodplain and a number of flooding episodes, levée bank deposits would be built up, upon which sphenopsids, such as *Calamites* might have grown, which would have been incorporated into the alluvium during flooding episodes. It is uncertain how *Cordaites* lived. The genus has been considered a pathological xerophyte (Wartmann 1969), as possibly inhabiting coastal plains (Cridland 1964; Peppers and Pfefferkorn 1970), or else living in the 'uplands' (Chaloner 1958; Peppers and Pfefferkorn 1970), which may have only been 10 m in height (Cridland and Morris 1963, p. 79). The occurrence of *Cordaitanthus* with long slender bracts in the basal silty shales (Pl. 50, figs. 1-3) would not indicate long transport as it would tend to break up easily.

CONCLUSIONS

Previous Upper Palaeozoic floral palaeoecological studies have shown the presence of three major swamp or lowland associations: lycopod, sphenopsid, and pteridosperm (Havlena 1971). However, there is not sufficient quantitative or sedimentological data to interpret these associations in terms of the plant communities from which they were derived. A quantitative study, using a point-quadrat technique, of a 'roof-shale' flora from the Westphalian B of West Scotland together with sedimentological observations and palynological data from the underlying coal has also shown the presence of such plant assemblages. The flora forming the coal is considered to represent an *in situ* community (as seen by the palynology) dominated by lycopods and sphenopsids. The roof-shale flora in contrast consists of two main assemblages; a lower one of mainly Pteridosperm foliage (*Neuropteris*, *Alethopteris*, and *Mariopteris*) with some *Cordaites* and an upper one which has in addition numerous Sphenopsids (*Calamites*, its foliage *Annularia* and *Asterophyllites* and its roots *Pinnularia*, as well as *Sphenophyllum*). These assemblages represent drifted accumulations, and the composition of these floral assemblages in terms of quantity of plant material and species content will be affected by both the different plant communities, or selections from them, which are being incorporated into the sediment, as well as the depositional history of the rocks themselves. The difference between the coal-forming flora and the roof-shale flora is emphasized. As the factors governing fossil plant assemblages are complex, their interpretation in relation to the fossil plant communities from which they have come is necessarily speculative. Changes, therefore, in the interpretation of the depositional environment of the plants, and their sedimentary history, must involve reconsideration of any plant-community model.

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