Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica

William A. DiMichele[a] and Tom L. Phillips[b]

[a]*Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA*
[b]*Department of Plant Biology, University of Illinois, 505 South Goodwin Ave., Urbana, IL 61801, USA*

ABSTRACT

DiMichele, W.A. and Phillips, T.L., 1994. Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica. Palaeogeogr., Palaeoclimatol., Palaeoecol., 106: 39–90.

The dominant plants of the Late Carboniferous lowland tropics were taxonomically and structurally distinct from those of any later time periods. Dominance was distributed among lycopsids, ferns, sphenopsids, pteridosperms and cordaites, and each of these groups had distinctive and different ecological preferences and amplitudes. Peat-forming habitats were dominated by lycopsids throughout the Westphalian, with a significant cordaitean element in the middle Westphalian; during the Stephanian tree ferns were dominant, following major extinctions near the Westphalian–Stephanian transition.

Each of the major plant groups had distinctive architectures and tissue composition. Trees contributed up to 95% of the peat biomass and tree forms of lycopsids, *Psaronius* and *Medullosa* lack good modern analogues. The cordaites were the only woody plant group to contribute significantly to peat, and then only during the mid-Westphalian. Structurally wood-like lycopsid bark is the major "woody" tissue encountered in most Westphalian coals. Tree ferns and pteridosperms were largely parenchymatous in construction; the stigmarian root systems of lycopsids also were largely parenchymatous. The tissue structure of these dominant plants suggests the need for extreme caution in the inference of mire ecological conditions or vegetational structure from coal petrographic data. Peat formed under arborescent ferns or pteridosperms, or peat repeatedly exposed to decay and rerooting by stigmarian root systems of lycopsids, would have a distinctly non-woody signature and yet would have formed in a forested environment. A summary is presented of the autecology and synecology of mire plants, emphazing the structural framework provided by lycopsids during the Westphalian. Certain constraints in the links between peat biomass and miospore palynology are discussed in terms of over-representation, under-representation and non-representation. The formulation of Smith's four-phase hydroseral model is discussed and compared with more recent data available from plant paleoecology.

The current debate over an ombrotrophic vs. rheotrophic origin of Late Carboniferous peats relies in large part on paleobotanical data, almost entirely palynological, in combination with petrographic analyses. Ecological studies of miospores and of coal-ball and compression macrofossils, and the linkage of miospores to source plants, permit the re-evaluation of mire successional models. Evidence for tree lycopsids, sphenopsids, pteridosperms and cordaites suggests growth mainly in rheotrophic mires. Tree ferns are likely candidates for growth in domed mires, although evidence is ambiguous and some tree ferns clearly grew under rheotrophic conditions. Densospores, produced by at least *Sporangiostrobus* lycopsid subtrees, have been considered diagnostic of ombrotrophic conditions; abundant evidence refutes this simplistic interpretation and suggests broad ecological amplitudes for densospore producers, including growth under rheotrophic conditions.

Although plant fossils alone can not resolve most of the major debates in modern coal geology, paleobotany does contribute significantly to our understanding of ancient mires. An approach combining paleobotanical data with petrography, sedimentology and geochemistry, on a case by case basis, is most likely to produce a clear picture.

Introduction

A coal bed, as evidence of an ancient peat-forming mire, represents a complex environmental mosaic. Detailed studies of petrography, geometry, sedimentary context and paleobotany of coal seams reveal a variety of subhabitats within any given coal. Many of the inferred conditions within

ancient mires appear to have parallels in modern habitats. Various lines of evidence suggest that peat surfaces in Late Carboniferous mires ranged from continuously flooded to exposed, with extensive subaerial decay of organic matter; nutrient status possibly varied from exceedingly low in areas where nutrients entered with rain fall to high in areas subject to flooding from streams. Study of the distribution of ancient plants within coal seams, either through palynological or macrofossil analyses, reveals distinct patterns of species association, positive correlation of associations with physical indicators of environment, and life histories and morphologies consistent with habitat differentiation among the plants.

Although much can and has been learned through direct comparisons of modern and ancient peat-forming habitats, our desire to analogize pattern and process must be tempered by recognition of clear differences between the Late Carboniferous tropical flora and those of later time periods (Collinson and Scott, 1987a,b; DiMichele et al., 1992). Dominance in Late Carboniferous lowlands was distributed among five distinct tree groups: two seed-plant and three lower-vascular plant lineages, each with different architectures, tissue structure, ecological and preservational tendencies. This pattern differs distinctly from any post-Carboniferous landscape, particularly in the tropics, where woody seed plants have dominated nearly all habitats since the Late Permian (earlier in Gondwana and Angara). As a consequence, peat-formation models that purport to explain the Late Carboniferous must be consistent with the unique attributes of the archaic plants and vegetation.

There are distinctive patterns of stratigraphic distribution among Late Carboniferous plants that complicate environmental inferences. The most notable event is the extinction in North America of most major lycopsid tree taxa at the Westphalian–Stephanian boundary (Phillips et al., 1974, 1985; Phillips, 1980). This extinction also may have included the majority of tree-fern (Lesnikowska, 1989) and medullosan (Taylor, 1965; Phillips, 1981) species. Westphalian coals are dominated by, or are rich in, lycopsids, and during the middle Westphalian cordaites also were abun-

dant to locally dominant. In contrast, Stephanian coals are nearly uniformly dominated by tree ferns, rarely medullosans. This Westphalian–Stephanian dichotomy complicates ecological inferences because we know much more about the ecologies of individual species and community dynamics of the Westphalian. Such stratigraphically based "taphonomic megabiases" must be considered when using plant data in a comparative manner.

Sources of paleobotanical data

Evidence of the floras of ancient mires comes primarily from two sources: microfossils, largely pollen and spores, and coal-ball macrofossils. Coal-ball peats serve as the most direct evidence of the structure, life-history biology, and relative biomass of the original vegetation. Linkage of pollen and spore taxa to the parent plants permits inference of the parent vegetation from microfossils, and greatly expands paleoecological interpretations. Megaspores have been used sparingly as an index to original vegetation (Winslow, 1959; Scott and King, 1981; Bartram, 1987), but appear quite promising. Macroscopic plant remains also have been identified in polished-etched blocks of coal, a technique made use of by Winston (1986) and called "coal anatomy". In exceptional circumstances the final flora of the mire may be preserved as compression or impression fossils in the roof rock of a coal bed, usually if it was buried rapidly and by sediments that did not bring in plant parts from nearby environments (e.g., Wnuk and Pfefferkorn, 1987; DiMichele and DeMaris, 1987; Gastaldo et al., 1991). Great caution must be used in relating roof floras to mire environments; in most cases the roof preserves a post-mire flora from a considerably different physical setting (Scott, 1977, 1978; DiMichele et al., 1991).

Coal balls

Coal balls are concretions containing the structurally preserved peat stages of coal (Scott and Rex, 1985), in which plant tissues can be exceptionally well preserved even though organics are coalified to the same rank as the surrounding coal (Lyons et al., 1985). The mode of coal-ball forma-

tion remains problematic, and several models have been suggested (Stopes and Watson, 1909; Mamay and Yochelson, 1962; DeMaris et al., 1983). Field observations indicate considerable variation in the timing and spatial pattern of coal-ball formation within and between coal beds; it is improbable that one model can explain or predict all occurrences or taphonomic consequences. Coal balls preserve the details of plant anatomy and reproductive organs, from which whole plants and their biologies and ecologies can be inferred (e.g., Rothwell, 1981; Rothwell and Warner, 1984; Costanza, 1985; DiMichele and Phillips, 1985).

As with pollen and spore data, repeatedly recurring assemblages can be recognized in coal-ball peats and correlated with physical indicators of environmental conditions. Such correlations have revealed considerable physical differentiation within peat-forming environments (Phillips and DiMichele, 1981; Raymond and Phillips, 1983; DiMichele and Phillips, 1988; Raymond, 1987, 1988; Feng, 1989; DiMichele et al., 1991). Analysis of root abundances and patterns of root penetration can suggest vegetational successional sequences and provide a rough index of the amount of tissue decay (Phillips et al., 1977; Raymond and Phillips, 1983; Raymond, 1988; Feng, 1989). Coal balls also preserve a record of peat diagenesis—decay, degree of rerooting, activity of invertebrate decomposers. This valuable source of environmental information has been exploited marginally (Mamay and Yochelson, 1962; Perkins, 1976; DeMaris et al., 1983; Scott and Taylor, 1983; Raymond, 1987; Covington and Raymond, 1989; Phillips and DiMichele, 1990).

The effects of peat decay, including differential preservation, are a major obstacle to inferring parent vegetation from coal-ball peat (and hence from maceral-based methods). Differential litter production by parent plants further affects such inferences. In essence, with coal balls one attempts to infer the parent vegetation from its litter and root systems. Studies of modern temperate and tropical forests suggest that litter is a fairly accurate representation of the standing forest (Burnham et al., 1992). Shoot/root ratios in peats, however, indicate considerable loss of aerial debris, in many instances well over one-half (Phillips et al.,

1977, 1985; Raymond, 1987; Feng, 1989; Covington and Raymond, 1989). For these reasons we generally factor out roots (except for those of tree ferns) when attempting to reconstruct parent vegetation from coal-ball zones (Phillips and DiMichele, 1981; DiMichele and Phillips, 1988; DiMichele et al., 1991), thereby eliminating the potential intrusion of biomass from younger vegetation into older litter horizons.

All biases considered, it is our belief that coal balls are the best reference base of parent vegetation for a given coal seam. They include the full spectrum of plant growth forms, from ground cover to canopy trees, and usually preserve tissues well enough to permit a high degree of taxonomic resolution. In addition, coal balls are fundamentally autochthonous accumulations distributed physically within seams so that patterns of intra-seam vegetational change can be studied. Contrary to some assertions, such as that of Bartram (1987, p. 197: "...coal balls formed in water-logged anaerobic conditions and the plants within them represent only the communities adapted to such environments"), comparative petrographic (coal anatomy), miospore, and coal-ball analyses from the same coal seams show that coal balls accurately represent the parent vegetation of those coals in which they occur, and do not misrepresent abundances of or fail to sample major groups of plants (see Winston, 1986, 1989; Willard, 1992). Coal balls from coals throughout the Westphalian and Stephanian indicate several distinct plant assemblages in every coal, each associated with diagnostic indicators of physical environments.

Coal balls are known to occur in more coal beds in the Upper Carboniferous of Euramerica than in any other coal age (Phillips et al., 1985). However, their absence or apparent paucity in most coal beds, perhaps a product of the interaction of paleoclimate and geochemical factors (Cecil et al., 1985; Cecil, 1990) emphasizes the need to view them as reference bases. As a consequence, palynological and petrographic approaches to reconstructing vegetation should be "calibrated" in coals where a coal-ball reference frame is available (e.g., Winston, 1986, 1989; Willard, 1992).

Palynology

Palynology provides access to vastly more coal beds and sampling sites than coal-ball analyses. Consequently it permits integrated studies of vegetation, petrography, and geochemical analyses, and thus a broad base of data from which to infer habitat conditions. Miospore analyses have proven to be the backbone of Late Carboniferous "coal paleobotany", and have contributed fundamentally to models of peat accumulation and vegetational dynamics.

Pollen and spores provide evidence of plant associations only, which can then be correlated with physical attributes of coal beds (e.g., Mahaffy, 1985, 1988; Eble, 1990; Grady and Eble, 1990; Willard, 1992; Calder, 1993). To be exploited fully palynological data must be referenced to source plants (Courvoisier and Phillips, 1975; Willard, 1989a,b; Calder, 1993) and then to the biologies of these plants (e.g., DiMichele and Phillips, 1985; Trivett and Rothwell, 1985). Quantitative palynological data need to be normalized, even if only broadly, to account for the differential microfossil production by different species (Willard, 1992), and the effects of transport over distances that may exceed the areal extent of a mire (Peppers, 1982).

Clastic compressions

Compression–impression floras from coal roof shales or from clastic beds within coal-bearing sequences frequently have been used as a source of information on the ecologies of mire communities (e.g., Teichmüller, 1952, 1989; Jennings, 1986). Although we can learn much about autecologies from such studies, detailed comparisons suggest that most compression floras poorly represent peat-forming habitats taxonomically and quantitatively [compare Pfefferkorn and Thomson (1982) with Phillips et al. (1985), Peppers and Pfefferkorn (1970) and DiMichele et al. (1991)]. Compression floras are typically dominated by medullosan pteridosperms, ferns, or sphenopsids (Scott, 1977; Pfefferkorn and Thomson, 1982). Where mire and clastic floras share species, the local mire subenvironments usually are enriched in clastics, rendering

local conditions more like those outside of the peat-substrate areas (DiMichele et al., 1985). Peat substrates often have low pH, long periods of flooding or high water tables, and low or inaccessible nutrients (due to chelation) (Schlesinger, 1978), which make them physically "stressful" and inaccessible to most terra firma plants (DiMichele et al., 1987). Consequently mires tend to accumulate species that can tolerate the physical conditions, many of which are uncommon in the associated clastic environments. We do not intend to imply an absolute barrier to species exchange; the differences are quantitative for most plant groups.

Coal petrography

Petrographic study provides direct access to the structural fabric of coal, and thus represents an enormous and valuable source of data on the parental vegetation and taphonomy of Carboniferous mires. Petrographic characteristics of coal are, however, considerably more removed from attributes of the parent vegetation than either coal-ball macrofossils or pollen and spores due to the post-depositional effects of diagenesis (decay, coalification). Consequently the lithotype and maceral composition of a coal sample is a complex product derived from the interaction of plant-tissue composition, the original environment of peat accumulation, and the effects of post-depositional decay and physical–chemical modification of the organic detritus. Use of petrographic data to infer characteristics of parental vegetation or environments of plant growth, therefore, must be tempered by the recognition of the diagenetic overprint such data bear.

Most of the important kinds of trees in Late Carboniferous mires were distinct from those of younger mire settings. The woody seed-bearing trees that dominate most Holocene and Recent peat-forming habitats are particularly poor analogues for most Carboniferous trees. Important groups produced no wood (tree ferns) or a very limited amount of parenchymatous wood (medullosans), despite having tree habits. In addition, root systems of the lycopsids, abundant in most Westphalian mires, were largely parenchymatous,

and in some peats made up more than 50% of the biomass (Phillips et al., 1985). Thus, it is critically important that petrographic studies of the Euramerican Carboniferous recognize and accommodate the original botanical composition of the mires in attempting to reconstruct vegetation.

Petrography intersects or overlaps with paleobotany in three major ways, each of which we will discuss briefly. The first, and most directly applicable to purely botanically based approaches, is "coal anatomy" (Thiessen, 1920; Thiessen and Sprunk, 1942; Winston, 1986), in which plant tissues are identified and quantified in thin sections or polished-etched blocks of coal. The second is the neutral use of petrographic data in conjunction with analyses of microfossils (and occasionally macrofossils), ash yield, and mineralogy of coal to develop an integrated picture of trends and parallel patterns in the independent sets of data (e.g., Smith, 1962; Grady and Eble, 1990). The third is the use of petrographic data alone, usually through the construction of complex indices based on maceral ratios (e.g., Diessel, 1986; Kalkreuth et al., 1991), to infer characteristics of the parental vegetation and mire hydrologic conditions. The first two of these approaches we find promising, empirically based means to estimate mire vegetation and/or environmental conditions. The third we find problematical and, in some of the inferences drawn from the data, simply unaccceptably and unproductively speculative, unconstrained by external sources of independent data, and inconsistent with more direct means of estimating the parent vegetation.

Macerals and macrofossil data

One of the most important contributions coal-ball analyses can make to the study of coal is to emphasize that Late Carboniferous mires were populated by plants that were mostly taxonomically and structurally distinct from mire vegetation of later time periods. There are no existing modern (or post-Paleozoic) mires capable of serving as acceptable vegetational analogues for peat-forming habitats of the Late Carboniferous. The closest parallels may be found between modern mangrove peats and Westphalian cordaite-dominated mire

floras (Raymond, 1988), but even in these cases the comparisons require many caveats (Raymond, 1987; Covington and Raymond, 1989). Unlike modern tropical landscapes, which are largely seed-plant dominated, those of the Late Carboniferous tropics were co-dominated by several plant groups, each uniquely constructed and contributing different ratios of wood, parenchyma and "bark" (Fig. 1).

Wood, in the form of vitrinite or fusinite, is often discussed as a major element in Late Carboniferous mires. Yet, only one group of plants, cordaitean gymnosperms, was both abundant in mires and woody. Even at the zenith of their importance, in the late Westphalian C and early D (Phillips and Peppers, 1984), cordaite wood rarely accounted for more than 45% of the total tissue in peats; on average, cordaite wood accounted for < 1 to 20% of peat biomass, with a median on the low side (DiMichele et al., 1986). True wood in Westphalian peats, estimated from coal balls, generally averaged 5–10% of peat biomass in those coals with a small cordaite element, and much of this "wood" was dispersed as small bundles in roots, leaves and small stems, rather than occurring as massive sheets.

Most of the "wood" described by petrographers is likely to be lycopsid periderm (bark), which was the major support tissue of lepidodendrid trees (Fig. 2). *Lepidophloios*, *Lepidodendron*, *Sigillaria*, *Paralycopodites* and *Diaphorodendron* produced periderm that was totally or partially massive and wood-like in appearance (DiMichele et al., 1986). The tissue appears to have been particularly impervious to decay; it is rarely root penetrated, even in heavily rooted peats, and some may be well preserved, even in peats that otherwise are rotted to a high degree. The chemical composition of lepidodendrid bark is not known, particularly the degree to which it was lignified, if at all (A.C. Scott and colleagues are currently investigating the chemistry of several fossil plant tissues: A.C. Scott, pers. commun., 1992; Collinson et al., 1992). During the Westphalian, before the extinction of the major lepidodendrid trees within mires, lepidodendrid bark accounted for 20–45% of the tissue of most coals, and often occurred as thick sheets (Fig. 3). Tree-fern-dominated Stephanian mires had few

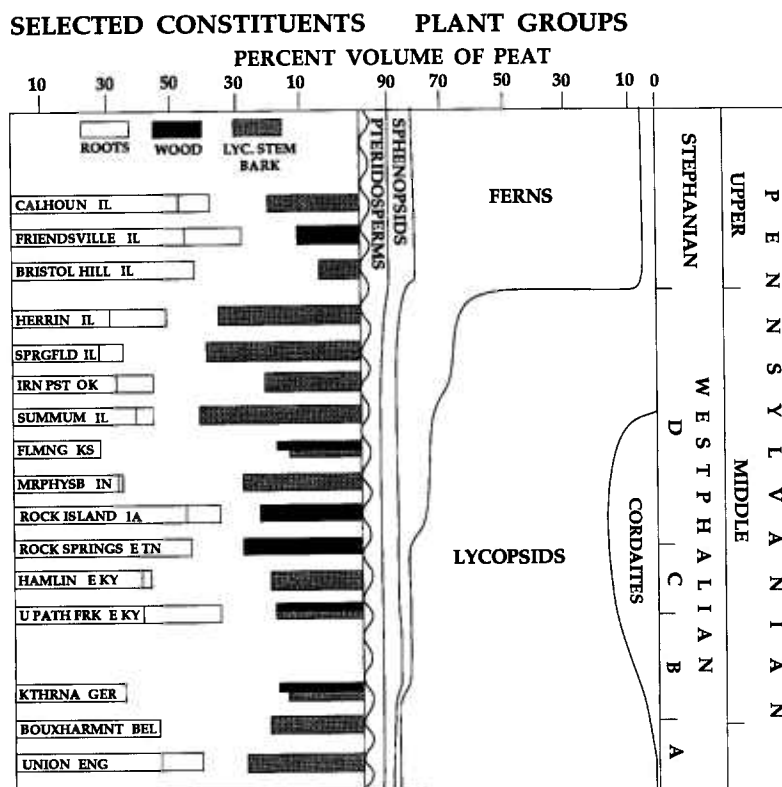SELECTED CONSTITUENTS   PLANT GROUPS

PERCENT VOLUME OF PEAT

Fig. 1. Changes in proportions of major plant groups in Late Carboniferous (Pennsylvanian) mires, and correlation with patterns of relative abundances of major organs and tissues types, on a seam average basis, in selected coals. Coals in sequence from oldest to youngest: Union seam of England, Bouxharmont seam of Belgium, Katharina seam of Germany, Upper Path Fork coal of Kentucky, Hamlin coal of Kentucky, Rock Springs coal of Tennessee, unnamed coal of Iowa equivalent to the Rock Island coal of Illinois, unnamed coal of Indiana equivalent to the Murphysboro coal of Illinois, Fleming (or Mineral) coal of Kansas, Summum coal of Illinois, Iron Post coal of Oklahoma, Springfield coal of Indiana, Herrin coal of Illinois, Bristol Hill coal of Illinois, Friendsville coal of Illinois, Calhoun coal of Illinois. See Phillips et al. (1985) for discussion of stratigraphy.

potential sources of wood or wood-like tissues: *Sigillaria* bark, and wood from calamites and cordaites, all of which were only sporadically and locally abundant. Note that not all lepidodendrid bark was wood-like in character. That of *Diaphorodendron* and *Synchysidendron* was anatomically complex and the bulk of it was composed of alternating bands of thick-walled and thin-walled cells.

Considerable importance has been placed by some petrographers (e.g., Diessel, 1982; Calder et al., 1991) on the relative abundance of cellulosic to lignified tissues as an index of the "woodiness" of the parent vegetation. A high content of presumably cellulose-rich tissues is taken to indicate herbaceous vegetation or vegetation containing proportionally few trees. In some cases such sup-

posedly herbaceous vegetation has been analogized to low-nutrient, ombrotrophic parts of modern mires. Coal-ball quantitative studies provide little support for the occurrence of extensive stands of herbaceous plants, in the sense of ground-cover ferns or lycopsids as a major biomass source of peat. The largest groups of supposedly "herbaceous" lycopsids, densospore producers (*Sporangiostrobus*) and *Endosporites* producers (*Chaloneria*) appear, in fact, to have been small subtrees with heights measured in meters rather than centimeters, supported by bark with a less dense texture than that of the large lepidodendrids (Wagner and Spinner, 1975; DiMichele et al., 1979; Pigg and Rothwell, 1983; Wagner, 1989).

Furthermore, as discussed above, an "herbaceous" signature can be derived from a fully

Fig. 2. Coal-ball peat from the Westphalian D Herrin coal of Illinois illustrating partially decayed, uncompressed wedges of lycopsid bark (*Paralycopodites* and *Lepidophloios* in this instance) within matrix of other aerial litter and roots. Specimen USNM 458417, magnification 1 ×.

forested mire. Low percentages of wood or wood-like tissues would be expected in detritus formed of debris from medullosan trees (with some exceptions in the Stephanian), *Psaronius* tree ferns, or from some of the lycopsid subtrees (Fig. 4). Intensive peat decay and particularly rerooting by either the highly parenchymatous stigmarian systems of lycopsids, or the aerenchymatous (air-chambered) roots of tree ferns also would greatly augment the "cellulosic" content of a peat, a taphonomic effect whereby a forested Late Carboniferous mire could produce a petrographic signature similar to that of herbaceous vegetation in a modern mire. Such heavily rooted and rerooted peats (Fig. 5) have been identified at numerous points in the Late Carboniferous of Euramerica, both in Westphalian and Stephanian mires (Phillips et al., 1985; Raymond, 1987, 1988).
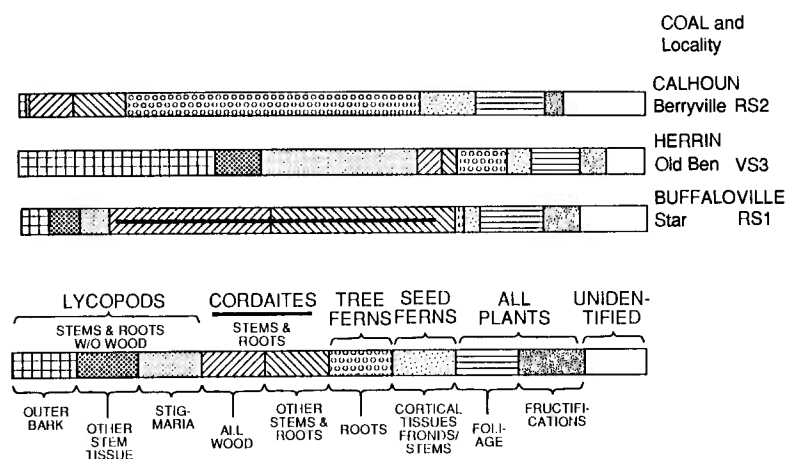
Fig. 3. Comparison of plant and tissue composition of three coals from different stratigraphic intervals. The unnamed Iowa coal (Star mine random sample 1) equivalent to the Buffaloville coal of Indiana is of early Westphalian D age and is dominated by cordaites; woody tissues from cordaites are a major component of peat biomass. The Herrin coal of Illinois (Old Ben No. 24 mine, vertical section 3) is of late Westphalian D age and is lycopsid dominated. The Calhoun coal of Illinois (Berryville random sample 2) is of Stephanian age and is tree-fern dominated. A major extinction of mire taxa occurred between the Herrin and Calhoun coals. All three coals formed under forested vegetation, yet relative abundances of wood, wood-like tissues (lycopsid bark), and parenchymatous tissues differs greatly, a function of species composition of the original forest.

These caveats emphasize that we must never lose sight of the distinctive taxonomic and tissue composition of the mire vegetation (see comments of Collinson and Scott, 1987). Truly herbaceous plants of low, ground-cover stature account for < 5% of the biomass of most coal-ball peats; these plants are largely ferns, and although they account for much of the taxonomic diversity of Late Carboniferous peat-forming communities this does not translate into importance in the sense of biomass.

Charcoal is a third type of preservation for which macrofossil evidence suggests cautious use in ecological inference (Scott, 1989). Inertinite in general, and fusinite in particular, have been treated as important indicators of "dry" conditions within mires in some petrographically based reconstructions of environments (Hacquebard and Donaldson, 1969; Gelification Index of Diessel, 1982, 1986; Harvey and Dillon, 1985; Grady and

Eble, 1990; Eble and Grady, 1990; Lamberson et al., 1991; Kalkreuth et al., 1991 but not by Calder et al., 1991 or Calder, 1993). For fusinite, this inference appears to be based on the assumption that burning is likely to be more frequent in parts of mires with exposed, even if wet, substrates. However, as Calder (1993) points out, fires may be tied to short-term climatic excursions and not be reflective of long-term hydrologic trends within a mire. Furthermore, fires are not limited to areas with exposed substrates, and can include crown fires in standing vegetation (see Scott and Jones, 1994). Burned trees may take years to disintegrate, and charcoal is subject to transport and remobilization after deposition within an ecosystem due to its inert character. All of these characteristics confound simple interpretations.

These factors alone suggest potential problems with ratios of vitrinite to inertinite (e.g. Harvey and Dillon, 1985; Eble and Grady, 1990) and the

Fig. 4. Examples of mostly parenchymatous peats formed under arboreous vegetation. (A) Medullosan dominated peat from the Westphalian D Herrin coal of Illinois. Medullosan foliar debris (*M*, at arrow) contains only scattered vascular bundles. A woody calamite stem (*C*, at arrow) forms a small part of the total peat. Specimen USNM 458418. (B) *Psaronius* tree-fern, root-dominated peat from the Stephanian Calhoun coal of Illinois. Peat is virtually all tree-fern roots, which contain very little woody tissue. Specimen USNM 458419. Both specimens magnified 1 ×.
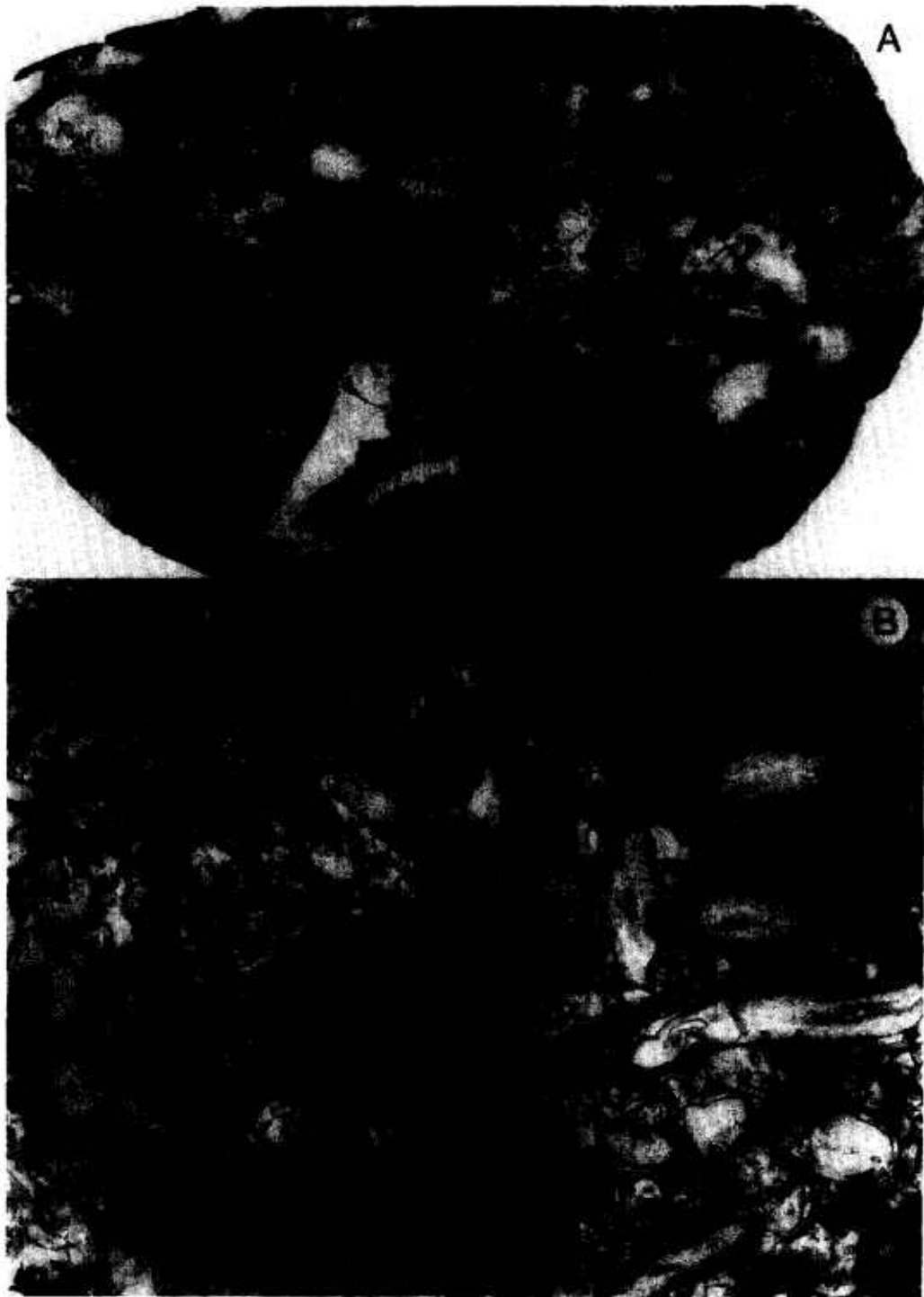
Fig. 5. Rotted peat penetrated by stigmarian appendages ("rootlets"), from the Westphalian D Herrin coal of Illinois. A large piece of *Lepidophloios hallii* periderm crosses the center of the peat mass; although cracked and obviously decayed the bark remains histologically identifiable and unpenetrated by roots. The stigmarian appendages are largely parenchymatous and serve to inflate the apparent "cellulosic" aspect of this peat, formed under arboreous vegetation. Specimen USNM 458420, magnified 1 ×.

related Gelification Index of Diessel (1982, 1986), which pit gelified macerals, presumably indicative of wet, anaerobic conditions, against inertinite macerals including fusinite, presumably indicative of dry, aerobic conditions (see Lamberson et al., 1991, for discussion). The process of gelification and the formation of fusinite (from among the other macerals in these indices) appear to be fundamentally independent processes, not part of a taphonomic or ecological continuum, and thus not readily and meaningfully juxtaposed in a ratio. Gelification is largely a tissue-specific, biochemical, diagenetic process unrelated to the formation of or environmental distribution of many inertinite macerals, and certainly charcoal. The formation of charcoal by fire, on the other hand, is the result of an active ecological process with the potential for strong environmental and taphonomic modifi-

cation; charcoal, due to its inert character, should not be a candidate for diagenetic gelification. In general, macerals of the inertinite group have diverse and often unproven or debated origins. The use of inertinite as diagnostic of dry conditions should, therefore, be accorded great caution.

In Late Carboniferous mires the most commonly encountered fusinized tissues are those of lycopsids (DiMichele and Phillips, 1988; DiMichele et al., 1991), a simple consequence of the high relative abundances of these plants. In coals such as the Herrin coal of Illinois, even though the most common lycopsid is *Lepidophloios*, and all biological and physical indicators suggest growth of this plant in standing water, it is one of the most common sources of fusinized tissue (DiMichele and Phillips, 1988). The medullosans and sphenopsids contribute much less total fusain to coal-ball

peats than do the lycopsids. However, a high proportion of medullosan and sphenopsid tissues are preserved as charcoal (DiMichele and Phillips, 1988; DiMichele et al., 1991). This may be a consequence of the environments in which they grew. It also may relate in part to properties intrinsic to these plant groups that predispose them and the litter they produced to fire. Medullosans in particular bore crowns of large leaves that remained adherent to the stems (Pfefferkorn et al., 1984), and may have formed thickets filled with large amounts of dead, dry foliage (Wnuk and Pfefferkorn, 1984). Furthermore, medullosans were rich in resins, which may have further enhanced their combustibility. These observations suggest again that charcoal has a complex relationship to environment, plant biology, and taphonomic processes, that it is not a simple indicator of environmental conditions, and that it should be used conservatively as an accessory to other kinds of information rather than as a primary indicator.

Coal anatomy

Plant remains can be identified to major taxonomic groups (lycopsids, tree ferns, medullosans, etc.) and in some instances to genus through the study of coal anatomy ("phyteral analysis"), cellular patterns on polished and etched coal surfaces (Winston, 1986). The approach is very similar to the quantitative analysis of macrofossils preserved in coal balls, but without the constraints on sampling location imposed by coal-ball deposits. Results are expressed in the form of relative abundances of plant taxa by sampling increment, lending themselves to ecological and stratigraphic analyses similar to those performed on other kinds of purely quantitative botanical data (Winston, 1986, 1989, 1990). Taxonomic identifiability of remains is considerably less than in coal-ball studies, so results must be reported at relatively high taxonomic levels with a large unidentifiable fraction remaining. Nonetheless, coal anatomy has the potential to expand the macrofossil sampling base greatly. Winston's studies also suggest that coal balls are an accurate representation of the vegetation of those coal beds in which they occur and, as such, expand our confidence in coal-ball data.

Petrographic data in an integrated approach

The use of petrographic data in combination with other sources of environmental and biological information can greatly enhance utility and help reduce biases derived from peat taphonomy and diagenesis. All data on coal floras and ecology have biases that can be partly circumvented by integration or comparison with independent sources of information (see Eble and Grady, 1992). The early work of Smith (1962) combined micro-lithotype descriptions and palynological analyses in the development of his domed-peat model. Hacquebard and Donaldson (1968) expanded the used of petrography, but based their inferential framework on planar peat models of Von Karmasin (1952) and Teichmüller (1952). Recent studies by Esterle and Ferm (1986), Helfrich and Hower (1989, 1991), Staub (1991), Eble and Grady (1990, 1992), Grady and Eble (1990), Pierce et al. (1991), Staub and Esterle (1992) and Calder (1993) herald an expanded approach to the integrative use of petrographic data. These studies combine petrography with other aspects of Late Carboniferous coal beds, including palynology, mineral matter content, low-temperature ash mineralogy, coal-body geometry, and sedimentological analysis of the associated rocks. The results demonstrate distinct patterns of correlation between many of the data sources and suggest environmental interpretations much more strongly than any of the approaches used in isolation. It is data from these kinds of studies that feed back most strongly into our own investigations of the autecology and community ecology of mire plants. We find substantial overlap between interpretations based on integrated use of spore–pollen and physical data, and inferences based on macrofossil coal-ball data.

Petrography as a direct measure of vegetation and paleoenvironment

Most scientists hope that their own special area of expertise will prove the key to understanding problems of importance in a broader area of research. Coal geology is no exception, and practioners of macrofossil paleobotany, palynology, sedimentology and petrography are all guilty at

some level of trying to infer too much from their limited data sets. Petrography, because of its special importance to the coal and steel industries, long has strived for means to interpret the genesis of coal from petrographic data. When petrographic studies lead to inferences about mire vegetation and vegetational structure they become directly comparable to data and inferences drawn from paleobotany on the same issues.

There is a distinctive school of thought in petrography that attempts to use ratios of supposedly "environmentally diagnostic" macerals to infer characteristics of the parental vegetation (e.g., Diessel, 1982; Teichmüller, 1989; Kalkreuth et al., 1991). This approach relies on the generally unspoken belief that there is a relationship between physical environment and vegetational architecture that is independent of time, geographical location, or taxonomic composition, an assumption that is unsupported by paleobotanical data. Teichmüller (1952, 1962), based largely on the study of Tertiary brown coals, identified four major environments in mires: dry terrestrial forest moor, wet forest moor (both with largely exposed peat substrates), limno-telmatic reed moor (intermittently flooded substrate), and open moor lake, forming a gradient within a mire. These concepts have been extended into the Paleozoic and force-fit by petrographers to Euramerican coals where there were no "reeds", and where woody, long-lived forest trees appear to have played little role in mires dominated by small or rapidly growing, non-woody trees. Gondwanan vegetation of the Permian, apparently rich in woody glossopterids (see Gould and Delevoryas, 1977), may be somewhat more amenable to these interpretations (Diessel, 1982), but there the composition of mire vegetation is too poorly known to provide an adequate test of petrographic inference. Consequently the "four moor" concept has been overlooked almost entirely in palynological and macrofossil studies of Euramerican coals, even where integrated with petrographic data (e.g., Smith, 1962; Grady and Eble, 1990; Eble and Grady, 1992; Helfrich and Hower, 1991). Current debate is focused on mire hydrologic models, contrasting domed (ombrotrophic) vs. planer (rheotrophic) peats (Moore, 1987; Calder, 1993).

The classic environmental reconstruction of Teichmüller (1952, p. 608) demonstrates clearly the attempt to draw a direct analogy between Tertiary and Carboniferous coals. The botanical composition of most Carboniferous landscape reconstructions is, in fact, a composite of information drawn from clastic-compression fossils, coal palynology and morphological analogy. For example, calamites are often indicated to be major constituents of Late Carboniferous mires, and analogized to "reeds" of a Tertiary swamp. In fact, calamites are quite distinct structurally from reeds, and by most sources of evidence, were scattered and usually minor components of mire habitats (Phillips and Peppers, 1984; Phillips et al., 1985). They were, however, more common in clastic compression floras and may have occupied a number of habitats in the landscape, particularly those in which sediment aggradation was common (stream sides, flood-basin backswamps; Scott, 1978). Standing water habitats in Late Carboniferous mires appear to have been occupied during the Westphalian by *Lepidophloios* and *Lepidodendron*, with subdominants of various types.

At the ultimate limit of inference by *any* form of indirect data are estimates of tree density and forest cover (Diessel, 1982, p. 479, 1986, p. 21). Petrographic-based conclusions about forest density, based on analogies from modern or Tertiary mires to those of the Paleozoic, particularly of tropical Euramerica, are simply fanciful extrapolations beyond reasonable levels. Direct paleobotanical measurements of in situ lepidodendrid tree stumps (Gastaldo, 1986a,b; DiMichele and DeMaris, 1987) or of mixed forests including lepidodendrids and medullosans (Wnuk and Pfefferkorn, 1987), indicate wide variations in tree densities, and a complex interaction between local environment and stand composition (see also DiMichele and Nelson, 1989). Lepidodendrids, for example, can be virtually randomly distributed, regardless of size, indicating little intertree interaction, a result of both the low-nutrient status of the substrate and the lack of a light intercepting crown for most of the life of an individual tree (DiMichele and Phillips, 1985). Evidence of high disturbance levels in parts of mires (Phillips and DiMichele, 1981; Raymond, 1988; DiMichele and

Phillips, 1988; Eble, 1990), sharp vegetational dis-continuities (DiMichele and Nelson, 1989), habitat patchiness (Wnuk and Pfefferkorn, 1987), and occasional long gradients (Gastaldo, 1987; Eble, 1990), suggest complex spatial patterns resulting from the interaction of plants and environmental
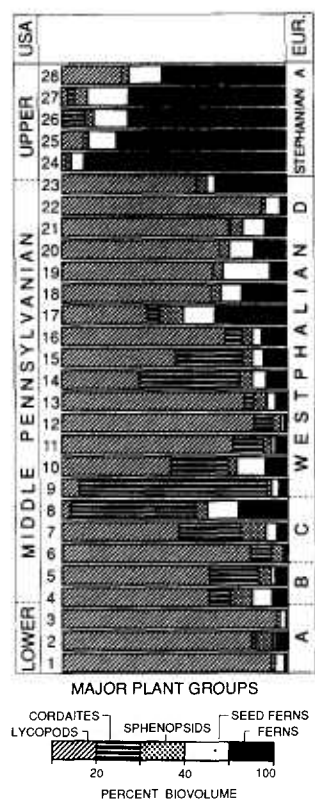

MAJOR PLANT GROUPS

Fig. 6. Plant composition on a seam-average basis of 28 selected Upper Carboniferous (Pennsylvanian) coals of Euramerica. Coals in stratigraphic order are: *1* = Union, England; *2* = Bouxharmont, Belgium *3* = New Castle, Alabama (Winston and Phillips, 1991); *4* = Katharina, Germany; *5* = Upper Path Fork, Kentucky; *6* = Hamlin, Kentucky; *7* = Rock Springs, Tennessee; *8* = Iowa (Urbandale-Shuler; Rock Island equivalent); *9* = Iowa (Star mine; Buffaloville equivalent); *10* = Iowa (Weldon; Buffaloville equivalent); *11* = unnamed, Indiana (Murphysboro equivalent); *12* = unnamed, Indiana (Staunton Formation); *13* = Secor, Oklahoma; *14* = Fleming (Mineral), Kansas; *15* = Bevier, Kansas; *16* = Summum, Illinois; *17* = Iron Post, Oklahoma; *18* = Springfield, Illinois and Indiana; *19* = Middle Kittanning, Pennsylvania (from Feng, 1989); *20* = Herrin, Illinois and Kentucky; *21* = Baker, Kentucky; *22* = Upper Freeport, Ohio; *23* = Danville, Indiana; *24* = Parker, Indiana, *25* = Bristol Hill, Illinois; *26* = Friendsville, Illinois; *27* = Duquesne, Ohio; *28* = Calhoun, Illinois. Based on 9214 coal balls, 453,718 cm² of coal-ball surface. See Phillips et al. (1985) for discussion of stratigraphy.

conditions. Environmental models therefore must be driven by the data, not by the a priori expectation of a fixed set of possible landscapes into which data must be fit.

Until we understand the relationship between maceral type and potential source plant or plants, and the relationship between maceral suites and floras (and through linkage to other kinds of data to other means of inferring vegetational structure) in ancient mires, it is the plants that are most diagnostic of the forests, not the macerals. This fact strongly recommends coal anatomy over maceral counts if inferences about vegetation are to be made directly from coal.

Stratigraphic patterns

The major biomass producers in most Pennsylvanian peat-forming mires (terminology of Gore, 1983; Moore, 1987) were trees. Five major groups of plants were present, lycopsids, ferns, sphenopsids, pteridosperms and cordaites, representing all of the contemporary evolutionary lineages except conifers. Trees of these groups usually account for about 95% of the peat biomass based on estimates from coal balls.

There are distinctive patterns of dominance and diversity that characterize different time intervals in the Late Carboniferous (Fig. 6). These result from extinctions and changing climatic conditions, resulting in the rise of new groups within ecological conditions similar to those of the previously dominant forms. These patterns complicate interpretations of paleoenvironment based on paleobotanical data, and limit ecological extrapolations, particularly between the Westphalian and Stephanian. During the Westphalian there were only minor extinctions, although several groups rose in ecological importance during that time and were subdominants or dominants for a part of the interval. Similarly, during the Stephanian there were only minor extinctions, with some changes in relative abundances of the subdominant taxa. However, the Stephanian ushered in a major change in dominance patterns. Most of the principal wetland-centered Westphalian tree species were extirpated in North America (Phillips et al., 1974), and underwent a steep decline in Europe

(Stschegolev, 1975). Some survived in China until the end of the Permian (Phillips et al., 1985). The Euramerican extinctions included all major arborescent to subarborescent lycopsid genera except *Sigillaria*, *Chaloneria*, and *Sporangiostrobus*, although small numbers of other Westphalian genera evidently survived in parts of Europe (e.g., Lorenzo, 1979). In North America, for which data have been tabulated, it also appears that many species of medullosan pteridosperms (Taylor, 1965), tree ferns (Lesnikowska, 1989), ground cover and vines (Phillips, 1980) disappeared from mires. In the ensuing Stephanian swamps tree ferns were the dominants, with subdominant medullosans, and, in some coals, sigillarians, cordaites, or calamites (e.g., Phillips et al., 1985; Pryor, 1988; Rothwell, 1988).

Most peat-forming mires were dominated on average by lower-vascular (non-seed-producing) plants. Exceptions to this pattern include cordaite abundance during the Westphalian B and C, and dominance in some coals during the Westphalian C–D transition in Iowa (Phillips et al., 1985; Raymond, 1988). Pteridosperms apparently domi-

nated some mires of the Namurian (Josten, 1983), and Stephanian (latest Virgillian; Phillips et al., 1985).

Until more detailed studies are carried out on Stephanian mire communites and the constitutent species, care should be used when drawing environmental conclusions based on analogy to Westphalian plants. Stephanian plants do not appear to translate directly into the habitat categories defined by plants of the Westphalian. Tree ferns had much higher dispersal potentials and were far more cheaply constructed as trees than were any of the other major Westphalian tree taxa. The biologies and spatial distributions of tree ferns suggest extremely broad ecological amplitudes, little affected by fine-scale environmental variability. Thus, the dominant plant group in Stephanian mires, if treated at the generic or familial level, and even the species level in most instances, is remarkably unrevealing of local habitat conditions. Ecologies of sigillarian lycopsids, medullosans and sphenopsids are understood to varying degrees and suggest habitat partitioning in Stephanian mires, but within a matrix of tree ferns.

TABLE 1

Glossary of botanical terms

Aerenchyma	Parenchyma tissue with abundant air-filled chambers
Apical (dichotomous) branching	Division of the apical meristem into two new growth areas
Apical meristem	Growth area at the tip of a stem
Autecology	Study of the ecological characteristics of individual species
Axillary branching	Branches resulting from apical meristems that form at the juncture of leaf and stem (the node, or leaf axil)
Cambium	A lateral meristem that produces secondary tissues, which add to the girth of a plant
Epiphytic	Growing perched on another plant, without ground contact
Lepidodendrid	Lycopsid trees with stigmarian root systems
Liana	Vine
Meristem	Growth point or region where active cell division occurs
Parenchyma	Tissue composed of thin-walled cells
Peduncle	Branch, generally short, that bears a reproductive organ at its tip
Phloem	Specialized tissue that conducts food (sugars produced in photosynthesis)
Primary body	Cells and tissues produced by cell divisions in the apical meristem
Secondary tissues	Those tissues produced by cell divisions in a cambium
Succession	Turnover in species composition of a site or habitat through time
Synecology	Study of the ecologies of groups of species (communities)
Taphonomy	Study of the processes attendant death, decay, burial, and lithification of organisms; the processes involved in the formation of fossils
Vegetative propagation	Growth of new axes from existing stems or parts of fronds
Wood	Secondary xylem; water-conducting tissue, produced laterally by a cambium
Xylem	Water-conducting tissues composed of thick-walled cells

Ecologies of dominant plants in Late Carboniferous mires

The ecologies of peat-forming plants form the basis of more derived inferences that may be of value in constraining models of peat formation. Inferences about the ecologies of individual whole-plant species derive from several sources. Foremost is comparative morphology and functional interpretation of plant organs and tissues, reconstruction of growth habit, and determination of life history (botanical and ecological terms are defined in Table 1). Biological data are amplified by correlation of species distributional patterns with physical indicators of the environment of growth, including data from peat taphonomy, the study of post-mortem processes in fossilization. Additional environmental inferences come from community ecology, through which patterns of species association can be assessed and correlated with life-history distributions (e.g., presence or absence of ground cover, abundance of species with life histories requiring exposed substrate for an extended period, or abundance of species with leaves indicating exposure to high light levels).

Most groups of plants had their peak diversities outside of peat-forming environments or associated clastic swamps. Only the lepidodendrids appear to have been centered in "swamps" sensu lato, and they had finely partitioned their amplitudes and strategies roughly along generic lines. Of the other plant groups, sphenophylls (Batenburg, 1982), cordaites (Rothwell and Warner, 1984; Costanza, 1985), and possibly tree ferns (Lesnikowska, 1989), may have had some swamp-centered lineages, but most species of these groups are known as compression–impression fossils from other kinds of clastic lowland habitats. Medullosans in particular seem to have had few lineages restricted to mires; the centers of diversity and dominance in this group were found among the clastic, terra firma lowlands (Scott, 1978; Pfefferkorn and Thomson, 1982).

The objectives of the remainder of this section are to outline in brief the ecological amplitudes of the major species or species groups in peat-forming environments. This should provide access to the major literature sources supporting ecological interpretations and point to those taxa important for assessing paleoenvironments.

Lycopsids

The tree lycopsids evolved in wetland environments in the Late Devonian (Scheckler, 1986), and became dominants in these habitats during the Carboniferous. By the onset of the Westphalian they had finely partitioned resources within the wetlands along taxonomic (generic) lines, and can serve as the best proxies for physical habitats among the dominant lowland plant groups (DiMichele and Phillips, 1985). All the trees and subtrees were constructed on the same theme, a basic pole architecture (Fig. 7) with a limited (determinate) period of growth (Andrews and Murdy, 1958; Eggert, 1961; Bateman and DiMichele, 1991). Two basic kinds of branching and reproduction characterize the trees: production of small, deciduous, cone-bearing, lateral branch systems throughout the life of a tree (polycarpic), or production of a cone-bearing crown only in the final phases of growth (monocarpic) followed by tree death. In either case, the trees did not have a conventional "crown" adapted for light capture; rather, the branch systems were directly associated with reproduction.

Lycopsids attained the tree habit independently of woody seed plants, and have a basic architectural plan that is "peculiar" when compared to any living trees (Fig. 8). Trees were supported by a thick rind of bark (periderm). The bark was mostly wood-like in appearance, and probably makes up the bulk of "wood" identified petrographically in Late Carboniferous coals (Winston, 1986). Production of wood actually was very limited, and the tissue was capable of rapid water conduction (Cichan, 1986). Ratios of bark to wood average about 4 or 5 to 1 based on cross-sectional measurements (e.g., Fig. 8). As such, lycopsid trees had separated the support and water conduction functions, and consequently avoided the structural compromises entailed in having wood serve both purposes, as in most seed plants.

All lepidodendrid trees appear to have had rapid growth and to have reached sexual maturity in a matter of years to a few tens of years at most.
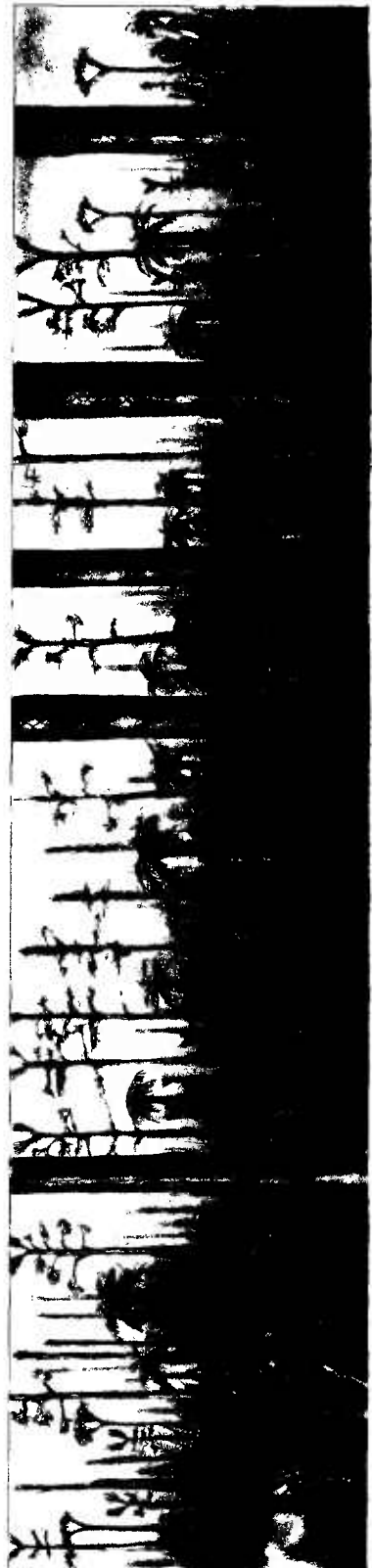
Fig. 7. Reconstruction of late Westphalian D mire vegetation from inner mire swamps to clastic back swamp-levee fringe. Four panels (A–D) form a continuous landscape. Compare with Fig. 9. (A) *Lepidophloios hallii*-dominated vegetation in area of persistently standing water, isolated from influx of clastics. Other plants, particularly pteridosperms, may have occupied hummocks within low-diversity, high-dominance stands with little ground cover and few free-sporing plants. (B) *Diaphorodendron scleroticum*-dominated vegetation in area of fluctuating water table. Complex understory of medullosans and tree ferns occurs in areas of wet but exposed peat. Scattered *Synchysidendron resinosum* trees also present (shown in background at right margin of panel; poles with determinate open crowns). (C) Mixed vegetation in exposed peat habitat, grading to open water peat-clastic backswamp. Left side to center of panel illustrate *Paralycopodites brevifolius* (foreground), tree ferns, and medullosans in an area subject to fires and clastic-rich flood waters. Sphenopsids fring open water in area subject to flooding from nearby streams. (D) Clastic backswamp on left of panel grading to levee with stream on far right. Sigillarian lycopsids, medullosans and ground cover dominate on the levee, with calamites most abundant along the water bodies.
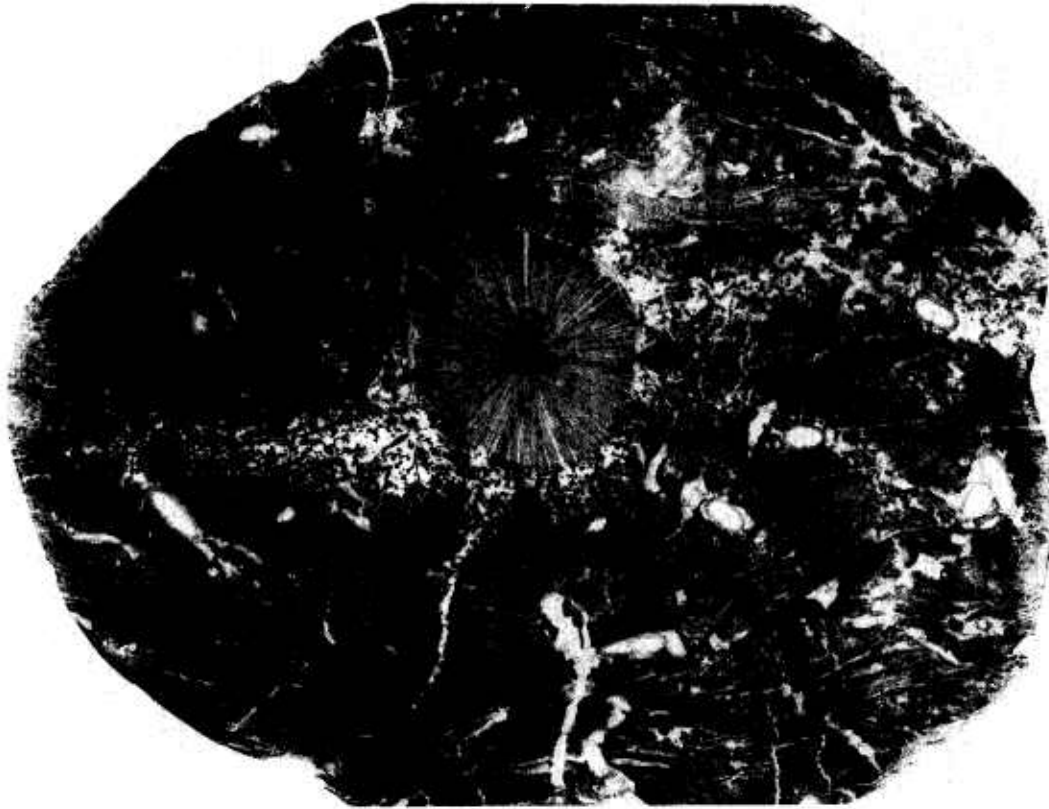
Fig. 8. Cross-section of lycopsid (*Diaphorodendron vasculare*) stem at stem base, demonstrating maximum development of wood (*W*, at arrow); tissue surrounding wood is nearly all periderm. Supporting periderm is somewhat compressed, suggesting a larger stem diameter than shown. Unnamed Indiana coal equivalent to the Murphysboro coal of Illinois. Specimen USNM 458421, magnified 1 ×.

This is suggested by a number of attributes: limited wood production; entirely terminal apical growth, with lack of lateral buds, and consequent inability to recover from damage to the main growth points; massive primary bodies in large diameter axes, suggesting either enormous apical meristems or some sort of primary thickening meristem (Rothwell and Pryor, 1991; Bateman et al., 1992; Phillips and DiMichele, 1992), either one capable of generating massive stems over short vertical distances; lack of secondary phloem, thus limiting the potential for translocation of photosynthetically derived sugars, resulting in modular physiological organization (Phillips and DiMichele, 1992); evidence of limited cambial activity both in the production of wood and periderm; and determinate growth, which in combination with monocarpic reproduction requires a habitat with no severe disturbances that would disrupt such a

reproductive cycle. In addition, plants in edaphically stressful habitats, such as swamps, bogs and fens, must compromise between stature and the physiological costs of root growth needed to sustain a large aerial biomass (Stevens and Fox, 1991). In summary, the basic construction of a lepidodendrid tree emphasizes tissue function during an uninterrupted time interval, lack of regular addition to or replacement of support and nutrient transport tissues, limited intervals of semi-aquatically dependent reproduction, and peculiar physiological constraints resulting from tree architecture. These combined factors demand short life spans, perhaps a decade or less, particularly in monocarpic forms (Phillips and DiMichele, 1992).

Reconstructions of lepidodendrid-dominated swamp forests have proven to be extremely misleading, both in showing crowns as analogous to those of dicots or conifers, and in illustrating

enormous trunk heights and girths. Certainly lycopsid trunks from coal roof shales, and other clastic-influenced habitats were large, reaching heights of 40 m and basal diameters of over 1 m (Thomas and Watson, 1976; Wnuk, 1985; Gastaldo, 1986a,b; DiMichele and DeMaris, 1987). Mire lepidodendrids, based on basal trunk segments found in coal balls, appear to have been considerably smaller (DiMichele, 1979, 1981), probably as a response to nutrient limitation on the peat substrate. Basal diameters of 15–35 cm seem more reasonable than one meter, based on current evidence. Despite smaller size than generally depicted in reconstructions, lepidodendrids appear to have been the tallest trees in mire environments (Fig. 7).

Lepidodendron and Lepidophloios

These two genera were closely related evolutionarily (Bateman et al., 1992), exhibited similar developmental and reproductive patterns, and occupied similar kinds of habitats in which long periods of standing water were an important defining characteristic. Within mires, data from palynology and coal petrology (Eble, 1990; Calder, 1993; Willard, 1992) suggest that Lepidodendron overlapped to some degree with Lepidophloios, but may have favored areas with higher levels of nutrient flow. Both genera spanned the Westphalian.

Lepidodendron hickii (Lycospora pusilla, Willard, 1989a) is the only species of the genus formally recognized in Westphalian peat-forming environments (DiMichele, 1983), but numerous species have been described from compression fossils, indicating that the genus was distributionally centered in clastic swamps (Willard, 1989b). Lepidodendron macrofossils and spores are encountered most commonly, and are apparently most abundant, in coals of Europe and the Appalachians; abundances in mid-continent coals seem to be relatively low, based on coal balls and on those palynological studies that separate Lycospora species (e.g., Willard, in press). However, Lepidodendron remains a common component of mid-continent clastic-swamp deposits, particularly in rocks of pre-Westphalian D age.

By contrast, Lepidophloios is one of the less abundant lycopsid genera in compression floras.

It is commonly represented in mires by two species, L. harcourtii (Lycospora pellucida, Willard, 1989a), particularly in the early Westphalian, and L. hallii (Lycospora granulata, Willard, 1989a) particularly in the late Westphalian. Lepidophloios occurred mostly in peat-substrate habitats, and the environmental differences between the two species of this genus are unclear despite stratigraphic differences in their relative abundances in both the peat and spore records (Phillips and Peppers, 1984).

Ecological evidence of the habitats of Lepidodendron and Lepidophloios in mires are drawn, in part, from the extensive anchorage systems (Stigmaria ficoides type), which had the largest lacunae (air chambers) of any of the lycopsids, indicative of aquatic submergence requiring gas exchange. In both genera the trunk exhibited determinate terminal branching only in the final growth phase, resulting in a single interval of massive cone production (monocarpic reproduction) prior to death. Both produced a seed-like "aquacarp" (Phillips and DiMichele, 1992), which is a megasporangiate unit (sporangium and leaf) that was probably fertilized and dispersed, boat-like, in water (Phillips, 1979). The aquacarp of Lepidophloios, known as Lepidocarpon, has the largest food-storage capacity of any lower-vascular plant megaspore in plant history; that of Lepidodendron (Achlamydocarpon takhtajanii) was about half as large. In both instances, the megaspores are assignable to Cystosporites giganteus.

In addition to the extensive stigmarian material buried in the peat substrate, the support bark of these trees was a major litter component. The bark was thick, yellowish in color in low-rank coal balls, extremely resistant to decay, and probably impregnated with water-proof chemicals. Bark fragments are very rarely root-penetrated, and survive histologically in some litter that is otherwise decayed mostly beyond taxonomic recognition (e.g. Fig. 5).

Lepidophloios occurs widely in mires and is associated with different species. However, L. hallii (we have less evidence for L. harcourtii) commonly dominates the lowest diversity assemblages, namely those with few or no ground-cover or free-sporing plants. This is consistent with a flooded peat surface. Some Lepidophloios litter assemblages are well preserved; others are reduced to mostly

bark. *Lycospora granulata* and *L. pellucida* (or *Cystosporites giganteus*) are consistently most abundant in vitrinite-rich coals that have moderate ash yields (Mahaffy, 1985; Esterle and Ferm, 1986; Bartram, 1987; Winston, 1990; Helfrich and Hower, 1991; Calder, 1993). Vitrinite is thought to form under subaqueous conditions (Teichmüller, 1989), consistent with moderate levels of particulate and dissolved minerals introduced in floods. *Lepidophloios* maxima commonly occur proximate to contemporaneous channels (Phillips and Peppers, 1984, p. 238; DiMichele and Phillips, 1988; Willard, 1992; Calder, 1993), or in interior parts of apparently planar, flooded peat swamps (Figs. 7A, 11; Bartram, 1987; Eble, 1990; Winston, 1990).

Lepidodendron dominated assemblages, while encountered less often in mid-continent coal-ball studies thus far, generally tend to be poorly preserved. They are frequently associated with mineral partings in the bed or with areas of split coal. This is consistent with palynological analyses that indicate highest abundances of *Lycospora pusilla* in parts of coal bodies with clastic partings and elevated amounts of mineral matter (Eble, 1990), inferred to represent rheotrophic mires (Calder, 1992).

Synchysidendron and Diaphorodendron

These two genera had been variously described as *Lepidodendron* or "coal-swamp" *Lepidodendron* until the establishment of *Diaphorodendron* (DiMichele, 1985). *Synchysidendron* (DiMichele and Bateman, 1992), a generic segregate from *Diaphorodendron*, has the same kinds of microspores (*Granasporites medius*), megaspores (*Cystosporites varius*), and aquacarps (*Achlamydocarpon varius*) as *Diaphorodendron*, but differs in structural anatomy. The two species of *Synchysidendron*, *S. dicentricum* and *S. resinosum*, are monocarpic with terminal-phase branching (Figs. 7B, 11; DiMichele and Phillips, 1985; Phillips and DiMichele, 1992). By contrast, *Diaphorodendron* consists of a central columnar trunk bearing rows of deciduous lateral branches (Figs. 7B, 11). Cones were borne at the tips of the lateral branches conferring the plants with continuous (polycarpic) reproduction (DiMichele and Phillips, 1985). The

three described species, *D. vasculare*, *D. phillipsii*, and *D. scleroticum* are similar in general habit but differ in size and anatomical detail (DiMichele, 1981; Wnuk, 1985).

Synchysidendron and *Diaphorodendron* apparently grew on exposed to partially submerged peat substrates and are associated with diverse kinds of assemblages, including ground cover. Relative abundance distributions of the two genera, determined from coal-ball studies, are quite different, and are extremely difficult to track with miospores due to the low spore output (Phillips and DiMichele, 1992). *Synchysidendron* was large (Wnuk, 1985) but cheaply constructed with much parenchyma in the wood and a thick inner bark that included bands of thin-walled cells. *Synchysidendron resinosum* occurs widely in the late Westphalian, but usually at low abundances both in peat-forming habitats (DiMichele and Phillips, 1985) and in clastic swamps (Wnuk, 1985: "*Lepidodendron*" *rimosum*). Plants occurred widely but in low abundances, suggesting diffuse distribution, perhaps in areas of minor disturbance in otherwise stable, mostly unflooded habitats. *Synchysidendron* appears to have been an ecological opportunist (DiMichele and Phillips, 1985). Its maximum biomass abundance in any coal-ball zone rarely reaches 20% and occurs in complex vegetational assemblages.

Diaphorodendron species rarely co-occurred, but were commonly dominant or co-dominant with a variety of other tree types. As a group, the species achieved greatest abundances in habitats with saturated, occasionally flooded peats. Exposure of the peat substrate is suggested by the moderate quality of peat preservation, which in coal balls often shows evidence of dessication but with minimal decay, and diversity of associated plants, including subcanopy, low, woody scramblers (cordaites), and herbaceous ground cover (Fig. 7B). Some populations may have been tolerant of brackish water (Eggert and Phillips, 1982; Lesnikowska, 1984; Raymond, 1988). *Diaphorodendron* species appear to have been site occupiers. Trees lived for several seasons or years during which they exhibited either continuous or repeated reproduction. In peat profiles *Diaphorodendron* is often abundant in numerous consecutive zones and, in some cases, may

dominate the entire profile, a successional pattern we have designated "repetitive". "*Lepidodendron*" *bretonense*, described by Wnuk (1985) from a clastic swamp, is the likely compression equivalent of *D. scleroticum*, indicating tolerance of a variety of swamp conditions, including flooding and mineral enrichment of the substrate.

Paralycopodites

There is just one described species of *Paralycopodites* (*P. brevifolius*) based on vegetative organs. Correlation with cone morphospecies suggests the existence of several natural species, with at least two in peat-forming habitats (DiMichele, 1980). In the compression fossil record, *Paralycopodites* is probably equivalent to *Ulodendron* sensu Thomas (1967). The name *Anabathra pulcherrima* has been applied to *Paralycopodites* vegetative remains by Pearson (1986), a name that would have nomenclatural priority if synonymy could be clearly established. Although both names are in use for this plant (Bateman et al., 1992; Phillips and DiMichele, 1992), we recently (September 1992) examined the type of *Anabathra* and found that it was too fragmentary to permit synonymy with *Paralycopodites*. Consequently, we prefer to use *Paralycopodites*, and suggest that the name *Anabathra* be restricted to the type material only.

Paralycopodites was a small tree that produced cones prolifically on short, lateral, deciduous branches that were borne in two opposite or subopposite rows on the trunk (Figs. 7C, 11) (Hirmer, 1927; DiMichele, 1980). The very small lateral branches shown by Hirmer (1927) are more like expanded cone peduncles than light-capture organs; Hirmer's reconstruction is strongly supported by studies of the anatomy. Cones were bisporangiate with megaspores (*Lagenicula*) in the lower half and microspores (*Lycospora orbicula* = *L. micropapillata*, Willard, 1990) in the upper half. Two "species" of the cone *Flemingites* can be attributed to Late Carboniferous *Paralycopodites*, suggesting that natural species of this genus differed in only minor details. Coal-ball and palynological studies indicate that *Paralycopodites* had distinct ecological characteristics and can be

detected readily wherever it occurs, even in modest abundances.

On the whole *Paralycopodites* is usually a minor component of most coal-ball assemblages. However, it was the dominant genus on a seam-average basis in several relatively thin coals (Hamlin coal of eastern Kentucky and Secor coal of Oklahoma; Phillips et al., 1985; DiMichele et al., 1991). *Paralycopodites* also exhibited limited dominance in some coal-ball zones of thick, widespread coals such as the Springfield and Herrin in the Illinois Basin (DiMichele and Phillips, 1985, 1988; Willard, 1992).

The life history and physical construction of *Paralycopodites* indicate a functional link to ecotonal environments with intermittent flooding, clastic input and peat exposure. The prolific spore production over its often short life time leaves behind an excellent record of its local distribution in coal (Bartram, 1987) and organic shales. This suggests both local dispersal as well as unusually strong restriction by environmental conditions.

Paralycopodites abundances are greatest in association with coal-bed seat earths, mineral partings or in other parts of coals near contemporaneous sediment-accumulating channels or other sources of groundwater recharge (Bartram, 1987; DiMichele and Phillips, 1988; Calder, 1992; Willard, 1992). Medullosan pteridosperms, plants consistently associated with peat-to-clastic transitional habitats, are common to dominant associates of *Paralycopodites* (DiMichele and Phillips, 1988). In numerous cases, *Paralycopodites*-rich assemblages exhibit elevated levels of fusain (DiMichele and Phillips, 1988) and peat preservation is quite variable and often quite heavily degraded (DiMichele et al., 1991), suggestive of nutrient-rich settings possibly abetted by post-fire runoff and nutrient cycling.

Sigillaria

As a group, the sigillarian trees are encountered far more commonly in clastic deposits than in peat, suggesting a center of distribution in wetlands surrounding peat-forming mires (Figs. 7D, 11). Common occurrences of *Sigillaria* trunks in channel lags and in organic shales suggest growth along

channel margins or on wet floodplains fringing channels.

Sigillaria has the most recognizably distinct anatomy, reproductive morphology, and ecology of the lepidodendrid trees, despite our limited understanding of whole plant assemblages. *Sigillaria* was a survivor of wetland extinctions near the Westphalian–Stephanian boundary; the best known organ assemblages occur in the Stephanian Calhoun coal of Illinois (Schopf, 1941; Delevoryas, 1957; Eggert, 1972). Sigillarian trees exhibited a pole habit, with "branching" confined to whorls of cones sporadically produced below the apex (Figs. 7D, 11). Upon reaching a near terminal phase of determinate growth the tip may have forked. As far as is known, all sigillarians bore monosporangiate cones, known as *Mazocarpon* if anatomically preserved. The microspores are identified as *Crassispora kosankei*. *Mazocarpon oedipternum*, the cone of *Sigillaria approximata* (= *S. ichthyolepis*), produced *Laevigatosporites glabratus* megaspores. Schopf (1941) suggested that these cones were shed intact and broke up mechanically in the surficial litter. Further distribution may have been effected by water flow, nearby streams, or floods (Phillips and DiMichele, 1992). A single scenario is inadequate to account for sigillarian reproductive biology. The occurrence of *Tuberculatisporites* megaspores in some Westphalian cones and anatomical differences between Westphalian and Stephanian cones points to the need for caution in making comparisons across the Westphalian–Stephanian boundary for this group.

In general, the Westphalian coal-ball record of *Sigillaria* suggests that most species occupied areas peripheral to mires, sparingly scattered within them, and rarely constituted a major biomass source within zones of otherwise thick peat profiles. Except for the decay-resistant bark, which constitutes the only bulk litter, *Sigillaria* is identified in peat largely from its characteristic "v"-veined leaves, scattered cone fragments, peduncles and/or megaspores. The stigmarian appendages are distinct from those of other lepidodendrid trees (Eggert, 1972). Plant assemblages associated with sigillarian litter are often high in diversity, poorly preserved, and commonly associated with abun-

dant fusain, observations consistent with fire-razed, rheotrophic mires, and seasonal climates. The greatest late Westphalian abundance of *Sigillaria* encountered thus far occurs in the Springfield coal of Indiana, proximate to an active channel (Eggert, 1982; Eggert et al., 1983; Phillips et al., 1985; Mahaffy, 1988), and apparently also near the outer margin of the mire (Willard, 1992). Abundances at the bases of Westphalian (Scott, 1978) and Stephanian coals suggests reliance on nutrient enrichment and a colonizing capacity.

Microspores (Eble, 1990) and megaspores (Bartram, 1987) from coal measures have been found in closest association with clastic partings in coals or with coal roof shales. *Crassispora* is most common in coals of the upper Westphalian A and B (Smith and Butterworth, 1967; Winston, 1990) and in the Stephanian (Peppers, 1964; Phillips et al., 1974), both identified as times of seasonally dry or reduced rainfall in the Euramerican tropics (Phillips and Peppers, 1984; Cecil, 1990; Winston, 1990).

Tracking the actual abundances of *Sigillaria* based on *Crassispora* is wrought with difficulties. As with *Granasporites*, the spores appear to under-represent the abundance of the parent plants.

Sub-arborescent lycopsids

Chaloneria and *Sporangiostrobus* are among the few lycopsids that survived the Westphalian–Stephanian extinctions in Euramerican wetlands. Both are known, in varying detail, from anatomical preservation and compressions or cast-mold specimens. The most abundant reported occurrences and best known assemblages for each genus occur in the Stephanian (Pigg and Rothwell, 1983; Wagner, 1989). *Sporangiostrobus* has not been verified yet from macrofossils in the Stephanian of North America. These two genera were essentially poles with extensive or concentrated reproductive regions, resulting in prolific microspore and megaspore output. It is their spore record, in combination with coal petrographic data, that has provided bases for most inferences or assertions regarding their paleoenvironmental implications

Chaloneria (= compression *Polysporia)* The unbranched stem of *Chaloneria* was probably 1–2

m in height with a diameter up to about 10 cm (DiMichele et al., 1979; Pigg and Rothwell, 1983). A rounded plant base with lacunose appendages provided the anchorage for this robust "stick-in-the-peat". The mostly thin-walled structure of the tissues and limited amount of wood suggest rapid growth, and are consistent with the typical frag-mentation, decay, and flattening of the litter. The microspores, *Endosporites* (*E. globiformis*, *E. orna-tus*), and the megaspores *Valvisisporites* (*Valvisporites*) *auritus*, were freely dispersed into the environment, a reproductive pattern requiring a wet-peat surface or some water cover.

Both coal-ball (DiMichele et al., 1979) and palynological data (Dempsey, 1964; Habib, 1968; Grady and Eble, 1990; Helfrich and Hower, 1989, 1991) suggest co-occurrences of *Chaloneria* with a variety of mire elements, but usually not with *Lycospora*-producing lycopsid trees. Association with cordaites, calamites and medullosans, often in coals enriched with clastics or in clastic swamps (Habib, 1968; Lamboy and Lesnikowska, 1988; Grady and Eble, 1990), places these plants in higher nutrient habitats of peat accumulation. The widespread distribution of *Endosporites* in Late Carboniferous coal-miospore floras (Smith and Butterworth, 1967; Peppers, 1970, 1979; Phillips et al., 1974) suggests a long-ranging, if quantita-tively minor role in most mires. However, after the extinctions of the dominant Westphalian trees, *Endosporites* producers became important in a number of thin, boney coals near the base of the Stephanian (Missourian) of the mid-continent United States (Phillips et al., 1974, 1985; Phillips and Peppers, 1984).

The importance of *Chaloneria* in patchy (Westphalian) to more extensive (Stephanian) marsh-like associations is suggested by the combi-nation of palynological and coal-ball studies. We use "marsh-like" to indicate mostly small-habit vegetation and probably fluctuating but ephemeral shallow-water habitats.

Sporangiostrobus (= *vegetative Bodeodendron*) *Sporangiostrobus* has been reconstructed by Wagner (1989); Fig. 9 is modified from Wagner's original reconstruction. Based on partially permin-eralized and compressed, nearly entire plants from
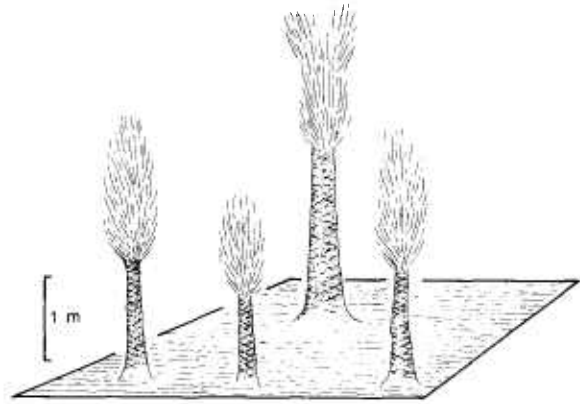

Fig. 9. Reconstruction of *Sporangiostrobus* from a Stephanian coal of Spain. Redrawn from Wagner (1989).

Stephanian volcanic-ash beds in central Spain, the plant was 3 m or more in height, 30 cm or so in basal diameter, with an unbranched or sparsely branched columnar trunk (Wagner and Spinner, 1975; Wagner, 1989). Sporangia were produced in fertile areas on the axis rather than in discrete cones, and massive numbers of spores were pro-duced. Anatomy of a fertile portion 16 cm long and 12 cm wide, and the associated vegetative remains have been described from Westphalian (Middle Pennsylvanian) coal balls by Leisman (1970). The basal anchorage system has not been established clearly as stigmarian (see Wagner, 1989).

Sporangiostrobus produced *Densosporites* (and related crassicingulate spore genera, e.g., *Cristatisporites*, *Radiizonites*) microspores (Chal-oner, 1962; Leisman, 1970; Courvoiser and Phillips, 1975; Wagner, 1989) and is considered to be the major densospore producer associated with dull coals and, in turn, Smith's (1957, 1962) pro-posed hydroseral succession (Wagner, 1989). There are other densospore producers, such as *Porostrobus* (Chaloner, 1962; Leary and Mickle, 1989). However, the consistent co-occurrences of megaspores, such as *Zonalesporites* from *Sporangiostrobus*, have aided significantly in sepa-rating the taxonomic source of densospores in coals and shales (Grebe, 1966; Corsin et al., 1967; Pierart, 1968; Scott and King, 1981; Bartram, 1987; Wagner, 1989). Given the environmental significance attributed to densospore producers, a

major study is needed in which megaspores are considered, and consequent finer taxonomic resolution used in making environmental inferences.

A direct correlation by Wagner (1989) between *Sporangiostrobus* and a dull, mineral-rich coal with a high densospore count emphasizes the need to distinguish among densospore source plants, which may have different environmental preferences. It is noteworthy that the largest discovered occurrences of *Sporangiostrobus*, including nearly entire plants, occurred in volcanic-ash beds associated with a Stephanian coal bed (Wagner, 1989). Volcanic-ash beds of Bohemia yielded similar specimens in the Westphalian D (Nemějc, 1931). The main source of anatomical information is derived from limited coal-ball specimens in Kansas coals (Leisman, 1970). However, Leisman (1970, p. 167) noted that *Sporangiostrobus* occurred in considerably higher numbers in some Iowa coals and such assemblages constituted a dominant component in one Iowa coal (Brotzman, 1974). The Kansas and Iowa occurrences are early Westphalian D in age. Despite the relative abundances of *Sporangiostrobus* in some coal balls from Iowa, the lack of whole-plant assemblage studies from these sources has permitted unconstrained inferences about its abundances at other sites based mainly on spore data.

If the *Sporangiostrobus* growth forms and sizes described from Stephanian specimens by Wagner (1989) are representative of Westphalian forms, this free-sporing, heterosporous lycopsid is more like the tree forms than any truly herbaceous lycopsid. The reproductive cycle would require wet-peat substrates or some surface water. The overall life history may have been broadly similar to that of *Paralycopodites*. This suggests a colonizing or opportunistic strategy, and the potential to spread through local habitats rapidly. Wagner (1989) could not clearly distinguish a polycarpic from a monocarpic life history for these plants.

The collective physical data on the environments of peat accumulation with which *Sporangiostrobus* is associated do not compel a simple interpretation. These plants obviously could tolerate a wide range of physical conditions, including nearly the full spectrum of nutrient conditions. The key to their success and survival may have been environments

in which competition was kept low, either by disturbance or by nutrient limitation. No compelling case can be made either from paleobotany or from physical data that *Sporangiostrobus* constituted a climax taxon in a hydroseral succession of a domed, fully ombrotrophic mire, as discussed later in our consideration of Smith's (1962) four-phase model.

Ferns

Ferns were a taxonomically diverse and structurally complex group of plants in Late Carboniferous tropical wetlands. Ecologically they fall into two broad groups, columnar trees and small ground-cover-to-vine habits. All were herbaceous and homosporous.

Small ferns

The small ferns account for most fern diversity but generally only a few percent of peat biomass (Phillips, 1974; Phillips et al., 1985). *Anachoropteris*, *Botryopteris*, *Psalixochlaena* and *Zygopteris*, among others, are collective indicators of ground cover and exposed peat substrates. *Psalixochlaena* and *Zygopteris*, in particular, appear to have been associated with exposed peat surfaces. All branched, and most had vegetative (non-sexual) means of propagation, permitting them to spread rapidly (Phillips, 1974). *Ankyropteris*, and a few species of the above genera were facultative climbers, commonly found in association with *Psaronius* tree-fern root mantles. Despite assertions (Rothwell, 1991), there is little data suggesting that any of these plants were truly epiphytic (living on other plants) rather than lianas (vines).

Marattialean ferns

Marratialean ferns varied in size from small, unbranched, recumbent plants, to large trees (Morgan, 1959; Mickle, 1984; Lesnikowska, 1989). *Psaronius* is the genus of stems described from anatomical preservation, and, by convention, the stem name is applied to the whole plant. Several stem genera have been described from compression or cast-mold preservation (Pfefferkorn, 1976), and most *Pecopteris* foliage is derived from such ferns.

Psaronius was the most important biomass producer among the ferns and such plants were "cheaply" constructed. The tree habit was achieved largely by root-mantle support of the stem (Figs. 7B, D, 10A), the crown of which was composed of large fronds. Thick-walled tissues were minimal in all organs, and most of the root biomass (subterranean and aerial) was composed of air-chambered tissues (Ehret and Phillips, 1977). Some species also exhibited aerenchymatous tissues in stems and frond bases. Such structure indicates both an extensive internal system of gas exchange, as well as low nutrient requirements for tree-sized development. Roots generally constituted most of the biomass in a *Psaronius*-dominated peat; foliage was the second most common tree-fern litter element. Peats composed mostly of tree-fern litter and roots would have had a distinctly non-woody texture despite the fact that they were derived from trees (Fig. 4B).

Most, if not all, *Psaronius* had massive reproductive output; spores were produced in sporangia on the undersides of pinnules. The mostly small spores, produced in large numbers, conferred on *Psaronius* the potential for wide dispersal and colonization of available sites within mire habitats. Lesnikowska (1989) has reconstructed eleven species from dispersed organs in coal balls and suggested several others. These can be clustered into five groups based on reproductive organs (Table 2; Millay, 1979; Lesnikowska, 1989).

There are distinctive patterns of taxonomic distribution, structure, and abundances of *Psaronius* assemblages, which have been documented in greatest detail by Lesnikowska (1989). *Psaronius* did not become important in mires until the Westphalian C, based on coal-ball evidence (Figs. 1, 6); the spore record, however, indicates an earlier establishment (Phillips and Peppers, 1984; Phillips et al., 1985). Such assemblages were commonly 12–15% of the biomass in the late Westphalian D (e.g., Fig. 3, Herrin coal). Westphalian–Stephanian extinctions eliminated nearly all of the Westphalian *Psaronius* species from mires (Lesnikowska, 1989); a mostly new suite of species colonized and dominated Stephanian mire vegetation (Galtier and Phillips, 1985; Phillips et al., 1985; Pryor, 1988).

Some of the earliest *Psaronius* species in mires appear to have been relatively small, ground-cover plants. Using Morgan's (1959) morphometric criteria, Lesnikowska (1989) computed maximum heights in the Westphalian of 3–4 m for the tree forms. Maximum known stem diameter in the Westphalian is 11 cm; such stems had relatively thin mantles of adventitious roots. In contrast, some Stephanian *Psaronius* species were large trees with maximum reported stem diameters of 19 cm, embedded in a massive root mantle. The basal trunk diameter commonly attained 1 m. Large tree ferns certainly had appeared in clastic substrates by mid-Westphalian (Pfefferkorn, 1976; Pfefferkorn and Thomson, 1982; Lesnikowska, 1989).

Psaronius species had limited ability to colonize flooded substrates because of their free-sporing life history, which required an exposed surface for completion of the sexual cycle, and because of their lack of vegetative propagation. Patterns of species distribution and co-occurrences with other plants also suggest a preference for substrates with periodic to full subaerial exposure (Figs. 7, 11). *Psaronius* species certainly are candidates for occupancy of low-nutrient, domed-peat surfaces. However, there are no qualities of their biologies or inferred physical tolerances that place them unequivocally in such habitats. By virtue of the adventitious root system with aerenchyma, once *Psaronius* became established it should have been quite tolerant of fluctuating water tables, including flooding.

A principal difficulty in sorting out ecological differences among individual species of *Psaronius* results from our limited ability to identify species from the fragments typically found in coal balls, particularly the roots (Ehret and Phillips, 1977). Thus, the bulk of the biomass has been identified to the generic level. In addition, the spores are often remarkably non-diagnostic of whole-plant species (Lesnikowska, 1989); many of the dispersed spore taxa are produced by different whole-plant species. In some cases, the same plant produced more than one spore type.

As a general observation, the occurrences and the relative abundances of species, based on macrofossils, sporangiate organs, or spores, appear to be

highly variable within and between coals. It is quite possible that many species had similar tolerances and that numerous differences in species composition may reflect the historical vagaries of colonization dynamics and ecological opportunity. In contrast, distinct, complementary patterns of abundances have been identified for *Thymospora pseudothessenii* ("layered cells" *Psaronius*; *Scolecopteris vallumii* of Lesnikowska, 1989) and *Laevigatosporites globosus* (produced by at least four species) in the Springfield and Herrin coals of the Illinois Basin (Mahaffy, 1985, 1988; Willard, 1992). This suggests that some *Psaronius* species had distinctive edaphic preferences.

Sphenopsids

Two major evolutionary lineages of sphenopsids are represented in Late Carboniferous tropical wetlands, arborescent calamites and shrubby to scrambling sphenophylls. Both were common elements and usually widespread in mires but were mostly minor sources of peat biomass. Both exhibited vegetative propagation and lived in mire and clastic substrate habitats. *Sphenophyllum* species were ground-cover plants and species of the mires appear to have been mostly different taxonomically from those typical of clastic habitats, as indicated by contrasts in growth form (Batenburg, 1982).

Calamites were woody and rhizomatous, with aerial shoots of subtree to tree size. They exhibited determinate apical growth (Eggert, 1962). Calamites were framework plants in some parts of the landscape, largely areas of substrate aggradation or instability, such as stream and lake margins, and clastic flood basins (e.g., Scott, 1978; Gastaldo, 1987). Calamites were generally more abundant in such habitats than in mires. The most complete

whole plants have been reconstructed from compressions (Barthel, 1980), although there are some based on coal-ball material (Good, 1975). The degree of species overlap between these different environments is unknown; we suspect that as with pteridosperms, a subset of species from mineral substrates may typify mire habitats.

Of three principal stem genera of calamites described from coal balls (Andrews, 1952), *Arthropitys* appears to be much more common than *Calamodendron* or *Arthroxylon*. Two major foliage forms are known from compressions and coal balls as *Annularia* and *Asterophyllites* (Good, 1971, 1976). Cones assignable to the genera *Calamostachys* and *Palaeostachya*, among others, also are known from both forms of preservation (see summary in Good, 1975). Calamites were both homosporous and heterosporous and produced dispersed miospores assignable to *Elaterites*, *Vestispora*, and *Calamospora* (Good, 1977) and *Reticulatisporites* (Ravn, 1986). Studies of calamitean cones suggest that all produced *Elaterites* with three, coiled "elaters" (humidity-sensitive appendages; Good and Taylor, 1975). *Calamospora* and *Vestispora* may be either developmental stages, or reflect the loss of elaters of *Elaterites*; hence Good (1977) suggests extreme caution when interpreting miospore species differences among calamitean spores.

Calamites appear to have preferred planar parts of peat bodies, especially those enriched in nutrients (Figs. 7C, D, 11). They have a common association with clastic partings (Phillips and DiMichele, 1981) and high differential fusinization (Phillips and Peppers, 1984; DiMichele and Phillips, 1988; DiMichele et al., 1991). Most calamite peat biomass is woody debris from stems, roots and rhizomes (Fig. 10B). Preservation is quite

Fig. 10. Cross-sections of plants from Westphalian and Stephanian peats. (A) *Psaronius blicklei* stem (tree fern). Cross-section near stem base illustrating small stem surrounded by complex root mantle. Inner root mantle of dense compact roots grades outward into free roots. "Woody" tissues represent a small part of total stem structure. Calhoun coal, Illinois. Specimen USNM 458422, Magnified 1×. (B) *Arthropitys* stem (calamite). Note distinct wedges of wood radiating from hollow pith. Wood is highly parenchymatous, but is the major stem support tissue. Upper Path Fork coal, Kentucky, magnified 10×. (C) *Medullosa* stem (pteridosperm). Wood is organized into several distinct bundles in center of stem. Leaf bases surround the stem. Leaves were the major organs of medullosans and are the most common kinds of litter; stems such as this contribute little wood to the peat. Springfield coal of Indiana. Specimen USNM 458423, magnified 1×. (D) *Pennsylvanioxylon* stem (cordaite). Dense wood forms the bulk of stem tissues. Remnants of cortical parenchyma and periderm surround the stem. Unnamed Indiana coal equivalent to the Murphysboro coal of Illinois, magnified 10×.

TABLE 2

Spore types of *Psaronius* reproductive organ groups

Scolecopteris minor and *Scolecopteris oliveri* groups
  Laevigatosporties minimus
  Punctatisporites minutus

Scolecopteris latifolia group
  Laevigatosporites globosus
  Anapiculatisporites saetiger
  Thymospora spp.
  Cyclogranisporites spp.

Scolecopteris bulbacea group
  Laevigatosporites minimus

Scolecopteris major group
  Punctatisporites aerarius
  Torispora–Laevigatosporites globosus

---

variable and litter often is fragmentary. In the Westphalian, calamites were generally rather small and not very abundant; biomass abundances of < 1 to 11% have been reported in the Westphalian (Figs. 1, 6) on an average whole-seam basis (Phillips et al., 1985; Raymond, 1988; Feng, 1989; Willard, 1992). They, therefore, usually contributed only small amounts of wood to the peat. Stephanian peats, in contrast, locally contain large amounts of calamite wood, if only because maximum sizes were much larger, 30–45 cm diameter (Andrews and Agashe, 1965). Some of the highest abundances of calamites are reported in the Stephanian Duquesne coal of Ohio (20%, Pryor, 1988), and in the Autunian of France (36%, Galtier and Phillips, 1985). Profile studies suggest very rare dominance of peat layers. In such cases, or
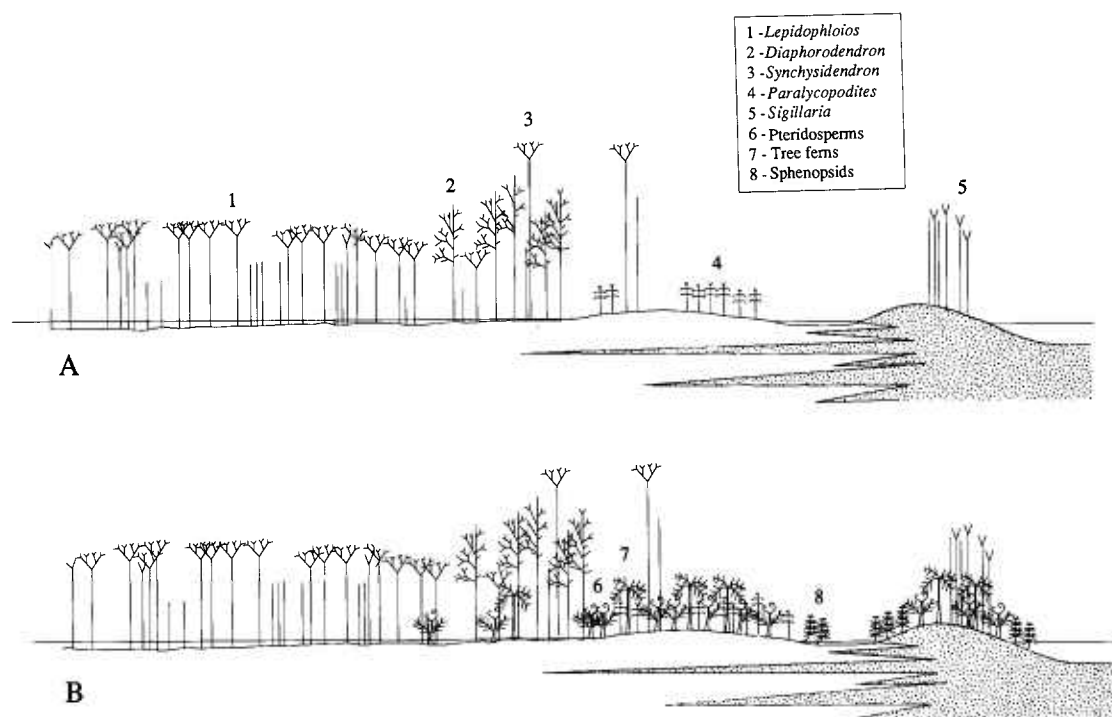

Fig. 11. Schematic transect through a planar, late Westphalian D mire. (A) Lycopsid-framework plants illustrating habitat partitioning among the major genera. Areas with standing water (left) are dominated by *Lepidophloios hallii*. These grade into habitats with wet, occasionally flooded peat, dominated by *Diaphorodendron scleroticum*, with scattered individuals or small stands of *Synchysidendron resinosum*. Areas where the peat substrate is mostly exposed, and subject to subaerial decay and floods from nearly clastic-rich streams, are enriched in *Paralycopodites (Anabathra)*. *Sigillaria* is most common in clastic substrate environments, on levees proximate to streams or in clastic swamps. (B) Same transect with addition of other major mire plants. Medullosans are most abundant in areas of peat exposure, particularly where nutrient levels are high, near areas of clastic influx. Sphenopsids are rare, and most abundant in areas of clastic influx at the margins of peat bodies. Tree ferns were widely dispersed throughout mires in all but habitats with persistent water cover. Tree ferns, pteridosperms and sphenopsids were common on levee and in clastic swamp settings. Cordaites were uncommon elements in late Westphalian D mires and are not shown.

where calamites were generally abundant, the associated plant assemblages are sometimes quite diverse and varied.

Palynological analyses in particular show calamite abundance peaks in association with clastic partings or high-ash coals (Mahaffy, 1985; Eble, 1990; Eble and Grady, 1990, 1992; Pierce et al., 1991; Calder, 1993). Such studies also suggest an inverse relationship between calamite and tree-fern abundances as well as associations of calamites with cordaites and *Chaloneria* (*Endosporites*). This pattern is evident when calamitean spores increase in the upper parts of coal beds. Calamite–cordaite–*Chaloneria* vegetation may have been relatively open to light penetration and of low stature.

Seed ferns (Pteridosperms)

Seed ferns constituted a broadly dominant group of lowland gymnosperms during the Late Carboniferous. Some of their considerable diversity in mires is reflected by the small scrambling, ground-cover plants, such as *Callistophyton*, and small vines, such as *Schopfiastrum*. These and other small seed ferns are important indicators of exposed peat substrates. All branched and most had means of vegetative propagation. Nevertheless, collectively, these small plants, like the small true ferns that shared their habitats, provided at most only a few percent of the biomass.

The principal pteridosperms in the lowlands were the robust medullosan seed ferns, represented by the small, monoaxial trees, *Medullosa* and *Sutcliffia*. *Medullosa* includes at least one small vine (Hamar and Rothwell, 1988), which exhibited axillary branching, and thus departs from the monoaxial habit. Architecturally, medullosans were complex; the stem consisted of several, centrally located wedges of wood embedded in a cortical ground mass of parenchyma, fibrous strands or fibrovascular bundles, and so-called "resin rodlets" (Fig. 10C). Most of the biomass of medullosans was allocated to fronds, which are thus the most commonly encountered organs in Westphalian peats; fronds contained only scattered bundles of woody tissue, and were mostly composed of cortical tissues. Within mires,

Westphalian seed ferns appear to have been smaller than those of the Stephanian.

Medullosan fronds were robust, and could be several meters in length. Based on compression fossils, two growth habits were common (Wnuk and Pfefferkorn, 1984; Pfefferkorn et al., 1984), both with somewhat larger dimensions than we estimate from coal-ball specimens. A free-standing form, up to 5 m in height, bore closely spaced fronds on straight trunks. Other medullosans had long, lax stems up to 10 m in height, but incapable of self-support. These forms grew in dense stands, probably thickets in which stems, adventitous roots, and fronds entangled and provided mutual support. Studies of coal-ball profiles indicate that some medullosans grew in local, patchy stands within Westphalian mires, and were commonly associated with diverse floras that included ground-cover plants, such as small ferns (Fig. 7B).

Medullosan litter, based on coal-ball studies (Phillips and DiMichele, 1981; DiMichele and Phillips, 1988; DiMichele et al., 1991) often is disproportionately fusinized compared with most other groups of trees and shrubs. In addition, medullosan-rich coal-ball zones have on average the highest fusain levels of the profiles in which they occur. Medullosans themselves may have increased the likelihood of conflagration; their tissues are infused with "resin-like" bodies and their fronds remained attached to stems after scenescence (Wnuk and Pfefferkorn, 1984; Pfefferkorn et al., 1984; DiMichele et al., 1992), providing copious quantities of highly flammable fuel. Combustion of plant materials releases nutrients into the substrate, and such nutrients may have enhanced recolonization of burned-over sites by pteridosperms.

Based on foliage as an indicator, there were three common groups of medullosans in mires, inferred from the most commonly encountered types of foliage: *Neuropteris* and *Alethopteris* from *Medullosa*, and *Linopteris* from *Sutcliffia*. Most of the foliage types reconstructed from coal balls have been described from compression–impression preservation (e.g., Baxter and Willhite, 1969; Stidd et al., 1975; Mickle and Rothwell, 1982; Reihman and Schabilion, 1976, 1978, 1985; Beeler, 1983; Schabilion and Reihman, 1985) and it is likely that

the mire representatives are a small subset of species known from the Late Carboniferous lowlands.

The pollen-bearing organs and seeds of medullosans are the largest of gymnosperms in the late Paleozoic. The principal prepollen of the medullosans is *Schopfipollenites* (*Monoletes*; Ravn, 1986, suggests use of the name *Zonalisporites*), which typically exceeds the 200 μm maximum diameter of standard miospore palynology preparation techniques (see dimensions in Taylor, 1982); *Sutcliffia* (bearing *Potoniea* pollen organs) produced *Punctatisporites kankakeensis* (Taylor and Taylor, 1987). The seeds were mostly large, some exceeding 5 cm in length. The large pollen organs, prepollen and seeds suggest heavy investment in sexual reproduction; medullosans lacked the potential for vegetative propagation. Animal pollination has been suggested in light of the large prepollen sizes (Dilcher, 1979; Scott and Taylor, 1983). Seed dispersal also may have been animal mediated or may have relied on water. Low dispersibility also must be considered, with consequent clumping of some species.

Medullosan species undoubtedly encompassed a range of ecological strategies, including different preferences for soil moisture and light intensity. Wnuk and Pfefferkorn (1984) identified different species in wet, topographic lows (*Neuropteris rarinervis* and *N. ovata*) and drier, topographic highs (*N. scheuchzeri*) within a clastic swamp. The patterns they identified are consistent with ecological inferences drawn from morphology of coal-ball specimens (Mickle and Rothwell, 1982; Reihman and Schabilion, 1985; Schabilion and Reihman, 1985).

Medullosan populations in mires appear to have required relatively high levels of mineral nutrients. In coal-ball profiles (Phillips and DiMichele, 1981; DiMichele and Phillips, 1988) and coal petrography (Johnson, 1979; Winston, 1990) medullosans closely correlate with elevated levels of mineral matter in coal, clastic partings, or split parts of coal beds proximal to contemporaneous channels (Fig. 11). This is amplified by medullosan abundance in clastic swamps that apparently were flooded for extended periods (Wnuk and Pfefferkorn, 1984, 1987), and by their general

dominance of compression-fossil assemblages from lowland–wetland habitats (Scott, 1978; Pfefferkorn and Thomson, 1982).

Cordaites

Cordaites were structurally similar to modern conifers, with dense wood (Fig. 10D), axillary branching, and strap-shaped leaves. Habits varied from scrambling ground cover to trees, although the largest forms appear to be from clastic environments. Cordaitean litter in mires is exceedingly distinctive, and includes leaves, woody stems and reproductive structures. Root systems were locally extensive, and were usually the major source of wood in cordaite-rich Late Carboniferous peats (Phillips et al., 1985; DiMichele et al., 1986). Cordaites were probably the slowest growing of the major tree types, which would have been a disadvantage in many mires where disturbance generally selected against slow-growing and potentially long-lived plants.

Cordaites were a diverse group and cumulatively encompassed a broad ecological amplitude (Raymond, 1988) ranging from dry substrates to brackish, waterlogged peats, perhaps as a result of tolerance of physiological drought (Wartmann, 1969). It is difficult to distinguish unambiguous environmental preferences for each of the known, or suspected, mire-dwelling cordaite species. There are, however, some distinctive patterns of relative abundance distributions for individual genera, or for the group as a whole, inferred from both coal-ball and miospore floras. Two stem genera have been recognized in mire habitats: *Mesoxylon*, with *Mitrospermum* seeds and *Felixipollenites* and *Sullisaccites* prepollen (Millay and Taylor, 1974; Trivett and Rothwell, 1985); and *Pennsylvanioxylon* (also called *Cordaixylon*, see Rothwell and Warner, 1984), with *Cardiocarpus* seeds and *Florinites* pollen (see Traverse, 1988, p. 193; Trivett, 1992). *Artisa*, a distinctive compression fossil, derives from the pith of cordaite stems, which is distinctly septate.

Studies of coals from the Westphalian A (Eble, 1990), Westphalian B (Calder, 1993; Eble and Grady, 1992), and early Westphalian D (Eble and Grady, 1992) find similar patterns of ecological

distribution. *Florinites* is most common in the marginal areas of coal bodies, subject to clastic influx from adjacent channels, or in association with mineral partings and adjacent high-ash coals, in some instances also elevated in sulfur. The most common plant associates are calamites, with some tree ferns and arborescent lycopsids at some localities. Coal-ball studies have found a cordaite–calamite association in the Summum coal of Illinois (Lesnikowska, 1984), and a consistent association of cordaites with lycopsids and tree ferns in a number of coals. Calder (1993) interpreted the patterns to mean that cordaites grew in planar swamps that had seasonally or periodically high water tables. Eble (1990) and Eble and Grady (1992) concluded that cordaites were most common in planar parts of peat bodies, subject to periodic flooding that in many areas rendered conditions poor for peat preservation.

Cordaites reached their zenith in middle Westphalian mires and, in turn, their greatest known diversity during the Westphalian C–D transition (Figs. 1, 3, 6). Although *Mesoxylon* and *Pennsylvanioxylon* occur throughout the Late Carboniferous, *Pennsylvanioxylon* appears to be far more abundant (dominant to subdominant) in the mid-Westphalian cordaitean interval. Cordaites as a whole diminished markedly near the middle of the Westphalian D, remaining a significant component of mire vegetation longest in mires of the Western Interior Coal Region.

Mesoxylon

Mesoxylon species were prominent cordaites in Westphalian A through late Westphalian C mires (Phillips and Peppers, 1984; Costanza, 1985). Small stature in mires is suggested by root and stem sizes (Costanza, 1985). So far as is known, the roots of *Mesoxylon* lacked aerenchymatous tissues, which were typical of *Pennsylvanioxylon* roots (Costanza, 1985). *Mesoxylon* roots commonly exhibit excentric growth rings in the wood suggesting interruptions of root growth. These anatomical features are consistent with growth in relatively exposed, well-drained peats that were occasionally flooded. Preservational quality of peats with locally abundant *Mesoxylon* is usually very poor, suggest-

ing heavy rotting, consistent with a seasonal climate.

Studies of cordaites in early Westphalian D coals of Iowa led Raymond and Phillips (1983) and Raymond (1988) to suggest that the *Mesoxylon* species (sources of *Mitrospermum compressum* and *M. leeanum* seeds) were intolerant of brackish-water conditions. This inference was based partially on patterns of shoot/root ratios, which Raymond (1987) argues permit brackish and fresh-water conditions to be distinguished, on patterns of species replacements as determined from root-penetration sequences in coal balls, and on multivariate analyses of species associations.

Pennsylvanioxylon

Species of *Pennsylvanioxylon* correlate readily with seed types (see Costanza, 1985; Trivett, 1992). The best understood species are *P. birame*, the source of two varieties of *Cardiocarpus spinatus* seeds, and *P. nauertianum* (= *Cordaixylon dumusum*, Rothwell and Warner, 1984), the source of *Cardiocarpus oviformis* seeds.

Pennsylvanioxylon birame, of the type with *Cardiocarpus spinatus* var. *corpulentus* seeds, was reconstructed by Cridland (1964) and later Costanza (1985) as a mangrove-like tree up to 5 m tall, supported by a sparse array of adventitous prop roots. Support for the mangrove-like hypothesis comes from studies of late Westphalian C Iowa coal balls. The shoot/root ratios are low (0.15), typical of plants growing in brackish to near-marine waters (Raymond, 1987, 1988), and pyrite rims can be found on roots attributable to *P. birame*, which suggests active root growth under salt-water conditions (Raymond, 1988). There also was associational evidence in combination with root-penetration sequence studies that place the plants in low-diversity assemblages, distinct from those rich in other cordaites, tree ferns or medullosans (Raymond, 1988). In some Kansas coals, *Pennsylvanioxylon* is closely associated with fusain (Phillips et al., 1985); the tissues are abundantly fusinized and occur in distinct layers in coal balls in association with many other kinds of fusinized plant debris.

A second type of *Pennsylvanioxylon birame* (source of *Cardiocarpus spinatus* var. *macilenta*)

occurs in assemblages with shoot/root ratios typical of freshwater peats (Eggert and Phillips, 1982). The plants were quite small and apparently constituted a persistent substory associated with *Diaphorodendron* forests.

Pennsylvanioxylon nauertianum (*Cordaixylon dumusum*) occurs throughout later Westphalian D and Stephanian coal-ball deposits in North America; however, it is quite scattered in occurrence and is typically a minor quantitative component of mire vegetation. Rothwell and Warner (1984) and Costanza (1985) independently reconstructed the plant as a small scrambling shrub, producing adventitous roots at the nodes as it sprawled across the peat surface. The aerenchymatous tissues in *Pennsylvanioxylon* roots suggest growth on water saturated to flooded substrates.

Common aspects of peat preservation in many types of cordaitean assemblages are extensive decay and evidence of peat exposure, even in some cases where the peat is dominated by roots. Where cordaitean wood is abundant, there is often evidence of tissue destruction by wood-boring or tunneling invertebrate detritivores, leaving dense accumulations of fecal pellets.

Ecological structure in Late Carboniferous mires

Stratigraphic patterns of vegetational composition and succession in the Westphalian indicate basic continuity in ecological structure, while at the same time demonstrating changes in diversity, ecological complexity, and some aspects of structure (Phillips et al., 1974; Phillips, 1980; Phillips and Peppers, 1984; Phillips et al., 1985; Cross and Phillips, 1990). The ecological framework of most mires was formed principally by arboreous plants, which contributed about 95% of the peat biomass. Lepidodendrids, among the tree forms, comprise the basic ecological framework from the lower Westphalian A through the upper Westphalian D (Fig. 11). Diversity and complexity of lepidodendrid forests expanded with the step-wise addition or expansion of *Psaronius* tree ferns, medullosan seed ferns, certain cordaites, and other plants. Divergence from a lepidodendrid-based ecological framework occurred mainly where cordaites constituted the dominant plants, particularly in associ-

ation with *Psaronius* and medullosans; exclusion of lepidodendrids may reflect edaphic conditions not generally encountered in most Westphalian mires (Raymond, 1988). However, most of the stratigraphic patterns of vegetational change do record an incorporation of diversity and complexity within the lepidodendrid ecological framework. Thus, in the upper Westphalian D (upper Middle Pennsylvanian), where the most diverse and structurally complex mires are found, the *relative* abundances of lepidodendrids are reduced. Nevertheless, it should not be assumed, based on miospore data, that the structural framework created by the lepidodendrids was spatially diminished, or that *Psaronius* tree ferns had become the numerical dominants in the mires. All coal-ball deposits from these coals clearly indicate continued lepidodendrid structure and dominance. It seems quite likely that the large mires represented in the upper Westphalian D of the eastern United States exhibited an increased productivity by virtue of their structural complexity and diversity, which, in turn, reflect both historical elements of vegetational change as well as prevailing environmental controls.

The Westphalian wetland lepidodendrids had partitioned wetland habitats along generic lines (Figs. 7, 11), a pattern that probably arose in an Early Carboniferous radiation of the group. Within mires lepidodendrids played a major role in colonizing, stabilizing, and expanding habitats of peat accumulation, without excluding most other plant types capable of living on such substrates. One of the most distinctive structural attributes of the lepidodendrids is their pole-like architecture, which casts little shade. Shading was further minimized by dropping of leaves and lateral branches, and the formation of a terminal, and relatively diminutive "crown", associated with the onset of reproduction in monocarpic forms. However, through their extensive stigmarian anchorage system, lepidodendrids tended to dominate the substrate environment, and hence stabilized the environment for other plants.

The principal lepidodendrids from the lower Westphalian A through the upper Westphalian D included *Lepidophloios* and *Lepidodendron* in the wettest, typically standing water habitats,

Diaphorodendron on exposed to partially submerged peat substrates, *Paralycopodites* on variably exposed to submerged peat, and *Sigillaria* on mostly emergent, better-drained substrates proximate to or within mires. Each of these edaphic habitats is associated with different levels of disturbance, mainly short-term fluctuations in the water table and the introduction of nutrients in floods. The relative gradient diagram (Fig. 11) conveys the basic patterns of dominance; the actual distributions were considerably broader, especially for *Lepidophloios* (Phillips and Peppers, 1984). The representation of such habitats is quite simplified in the figure; the mire was, in fact, a mosaic of habitat patches, and the landscape distribution of genera could be quite heterogeneous in any given area (e.g., DiMichele and Nelson, 1989). It is particularly important to note that exposed peat surfaces appear to have been common, based on taphonomic evidence, in association with *Diaphorodendron* (Fig. 7B), *Paralycopodites* (Fig. 7C), and *Sigillaria* (Fig. 7D). Smaller lycopsids also were basic components of mires, although their abundances were quite variable. *Hizemodendron* (formerly *Lepidodendron*) *serratum* (Bateman and DiMichele, 1991) occurred throughout the Westphalian; *Sporangiostrobus*-type plants and *Chaloneria* increased during the late Westphalian A to B, and continued into the Stephanian. There are other lycopsid genera, not dealt with here, in Westphalian A and younger rocks.

The continuity of lepidodendrid distribution throughout the Westphalian provides a stable baseline for models and general reconstructions of mire plant communities. From an ecological viewpoint, the continuity has permitted development and testing of autecological and synecological interpretations to the point where the lepidodendrids have become the most sensitive indicators of mire edaphic conditions. One outcome of ecological studies is the recognition that most of the structural complexity and taxonomic diversity is associated with habitats in which there is taphonomic evidence of periodic, substantial, substrate exposure, often in association with occasional clastic input (or the accumulation of mineral matter through peat degradation), habitats that we interpret as

elevated in available nutrients. Habitats in which *Lepidodendron* or *Lepidophloios* reach maximum abundances usually exclude most other species (Figs. 7A, 11), but particularly ground-cover and homosporous, free-sporing plants (ferns and sphenopsids). Some *Psaronius* species may have evolved the ability to tolerate these environments by the late Westphalian D, but the evidence is scant. It appears that entry to, or expansion within, the lepidodendrid-dominated framework was accelerated during episodes of extrinsic abiotic stress, such as climatic excursions in the early Westphalian; in addition, mires in general tended to accumulate species through geological time, a process that reached its maximum in the late Westphalian D. The lepidodendrids provide a semi-quantitative reference base for estimating the severity of environmental changes and help to frame such questions for other plant groups (e.g. Winston, 1990).

The extreme dominance of lepidodendrids in many Westphalian mires could, in part, be a reflection of taphonomic processes. Both coal-ball and independant coal-anatomical investigations indicate that most of the plant tissues that went into making coal came from lepidodendrids during the Westphalian, with the exception of some mires where cordaites were dominant (Fig. 6). Studies of plant organs, however, indicate that much of the aerial litter was lost to decay. Extensive decay may have led to enrichment of peat in lepidodendrid bark, and allowed roots of these plants to penetrate and repenetrate some peat layers.

Peat taphonomy in combination with studies of the vegetation indicate that the ecological circumstances attending peat accumulation could and did differ to varying degrees within and between mires. In the Westphalian, in particular, the short life spans and potential of the plants to respond rapidly to environmental fluctuations should closely link peat taphonomy and ecology, where peat accumulation rate and burial rate could have acted in concert. When taphonomic factors are added to vegetational patterns a complex picture emerges, one that suggests incomplete overlap of growth environments with those of peat accumulation and burial. The ecological and taphonomic realms are often not so closely linked as we would wish, either

in the Westphalian A–B of Western Europe, wherein Smith's model was developed, or in the Westphalian D of the USA, from which so much of the coal-ball data are derived.

An alternative model of Westphalian peat-forming ecosystems is desirable if we are to integrate data and inferences from community paleoecology with those derived from studies of peat burial and preservation. To a large extent coal geology, especially coal petrology, has spearheaded efforts to analyze and even model the paleoenvironmental controls on coal quality—the key environmental characteristics of coal deposits (Diessel, 1982; Cecil et al., 1985; Teichmüller, 1989). The combination of palynological and petrographic studies have energized the relationship between paleobotany and coal geology, but have also emphasized areas where inferences are in potential conflict.

The models of Smith (1957, 1962) represent an important integration of paleobotanical and petrographic data, but were developed at a time when little was known about the ecology of Late Carboniferous plants from peat-forming environments; most of the inferences about mire plants had, to that time, been drawn from studies of clastic compression floras, and most of the environmental interpretations had come from studies of coal petrology (e.g. Teichmüller, 1952). Our intent is to evaluate Smith's "miospore dominants" and "incursions" in light of more recent studies of mire paleoecology, using as much of the available evidence as possible.

Successional patterns in mires

Analyses of coal-ball patterns from numerous coals suggest several different types of "successional" patterns in Late Carboniferous coals (Table 3). We use the term succession in a broader sense than it is generally used in neoecology. Recoveries from disturbance and hydroseral patterns of vegetational change through time are combined when examining whole-seam patterns of vegetational change. The successional patterns are based on the dynamic distribution of the dominant framework trees and shrubs, and the patterns of diversity associated with them. Three basic pat-

terns suffice to describe the coals we have studied, and each is discussed in turn: repetitive, mixed and progressive. Different parts of a mire may exhibit different successional patterns, or successional dynamics may change through time depending on the prevailing groundwater and nutrient levels and directional or spatial changes in them.

Repetitive succession

Repetitive successional patterns involve repeated or continuous occupation of a part of a mire by essentially similar vegetation during the period of peat accumulation. Such patterns may be indicative of recurring, similar kinds of disturbances or persistence of particularly extreme physical conditions for most of a mire's history. Examples of mire dynamics apparently controlled by recurring disturbances or strongly rheotrophic conditions come from several Westphalian coals, including an unnamed coal of west-central Indiana equivalent to the Murphysboro coal of Illinois (Eggert and Phillips, 1982; Peppers, 1982), the Secor coal of Oklahoma (DiMichele et al., 1992), and the Summum coal of Illinois (Lesnikowska, 1984). All were dominated by lycopsids, either *Paralycopodites* or *Diaphorodendron*.

Most of the Stephanian coals we have analyzed from the Illinois basin seem to fit the repetitive pattern; the parent mires appear to have been nearly monotonously dominated by tree ferns (Phillips et al., 1985). There are at least two documented instances in the Stephanian where the basal peats were dominated by sigillarian lycopsids, and where tree-fern dominance then ensued: the Calhoun coal of Illinois (Phillips et al., 1985) and the Pittsburgh coal of the Appalachian basin (Grady et al., 1992). Because tree ferns are notably non-diagnostic environmental indicators, at our present levels of taxonomic resolution (particularly of macrofossils), it is unclear whether monotonously tree-fern-dominated Stephanian mires reflect harsh, unchanging physical conditions, or whether the tree ferns had particularly broad ecological amplitudes. There is little evidence of the extensive intramire disturbances typical of the Westphalian as the driving forces of repetitive succession. Self-replacement of tree ferns on sites

TABLE 3

Profile patterns of peat accumulation

Patterns	Examples	
	Tree types	Coals
I. Repetitive Same kinds of vegetation repeatedly recolonizing disturbed coal-swamp habitats resulting in similar kinds of peat composition	*Diaphorodendron* or *Paralycopodites*	Secor (OK) Murphysboro (IN) Summum (IL)
II. Progressive Changes in vegetation from closely related habitats due to slight to moderate shift in environmental conditions; peat composition changes some to much	*Lepidophloios* to *Diaphorodendron* to *Paralycopodites*	Herrin (IL) *in part* Springfield (IN) *in part*
III. Mixed Sharp differences in vegetation due to major change in environmental conditions; more rapid onset of severe disturbance results in distinctive peat composition and/or loss of peat record	*Lepidophloios* or *Lepidodendron* to cordaites	Upper Path Fork (east KY) Rock Springs (east TN)

over extended periods appears to have dominated patterns of vegetational dynamics.

Mixed succession

Mixed successions typically involve the alternation of two vegetation types, each characteristic of distinctively different physical environments. Such patterns suggest oscillations of physical conditions at the peat surface, particularly the alternation of standing water habitats with exposed peat surfaces. Two examples from the middle Westphalian are the Upper Path Fork coal of eastern Kentucky (Phillips and Chesnut, 1980), and the Rock Springs coal of eastern Tennessee (McLaughlin et al., 1985). In each case a lycopsid, either *Lepidophloios* or *Lepidodendron*, indicative of standing water environments, alternates with cordaite-dominated peats. The cordaite-rich peats typically evidence subaerial exposure, such as extensive decay, wood-boring by invertebrates, and associated floras rich in ground cover.

The Fleming and Bevier coals of Kansas, also rich in cordaites, display similar alternations of two basic vegetation types, one rich in monocarpic lycopsids, the other in cordaites, associated with medullosans, calamites and tree ferns.

Progressive succession

Progressive successions are those in which vegetational change proceeds through several stages from wet, flooded substrates to exposed peat surfaces, occasionally vice versa. This progression may be gradual or involve several distinct states in a series within a profile. We have detected this most frequently in Westphalian D coals dominated by lycopsids but with important medullosan and tree-fern elements. Examples include the Herrin and Springfield coals of the Illinois basin (Phillips and DiMichele, 1982; Eggert et al., 1983; DiMichele and Phillips, 1988; Winston, 1988; Willard, 1990), the Middle Kittanning coal of Pennsylvania (Feng, 1989) and an unnamed coal in Iowa (Raymond, 1988).

In most of the cited cases the succession is defined by lycopsids, typically proceeding from dominance by *Lepidophloios* in low-diversity assemblages, through assemblages with abundant *Diaphorodendron* and *Synchysidendron*, with a diversity of ground-cover and tree ferns, to assemblages dominated by *Paralycopodites* and medullosans, often with tree ferns and a diversity of other plants. The coal studied by Raymond (1988) was cordiate-dominated. She inferred a succession

among different cordaites to tree ferns and then to lycopsids, using root-penetration analyses.

Many palynological studies using high-resolution incremental analyses demonstrate directional (? hydroseral) successional changes, often repeating one or more times within a bed, or characterizing the overall history of the mire (e.g., Smith, 1962; Mahaffy, 1985; Bartram, 1987; Eble and Grady, 1990). Such patterns may reflect evolution from rheotrophic to domed, ombrotrophic mires. However, the biologies of the constituent plants must be considered; a weak progression involving plants tied to aquatic or high-nutrient conditions could be typically rheotrophic, and be driven by changes in mire hydrology related to flooding or disturbance (e.g., Calder, 1993).

Coal palynology: taphonomy and comparison with coal-ball patterns

Palynological taphonomic biases are few but critical in translating miospore abundances into vegetational patterns. Due to the sporopollenin chemistry of their walls many miospores are highly resistant to decay and tend not to suffer extensive differential decay. However, most miospore studies limit the size of spores analyzed to a maximum of about 200 μm, which eliminates large medullosan pteridosperm prepollen (*Schopfipollenites, Monoletes*) from analyses. Unless extraordinary methods are used, medullosans either are unrepresented in miospore counts or can be included only with difficulty through separate quantitative analyses of a course macerate fraction.
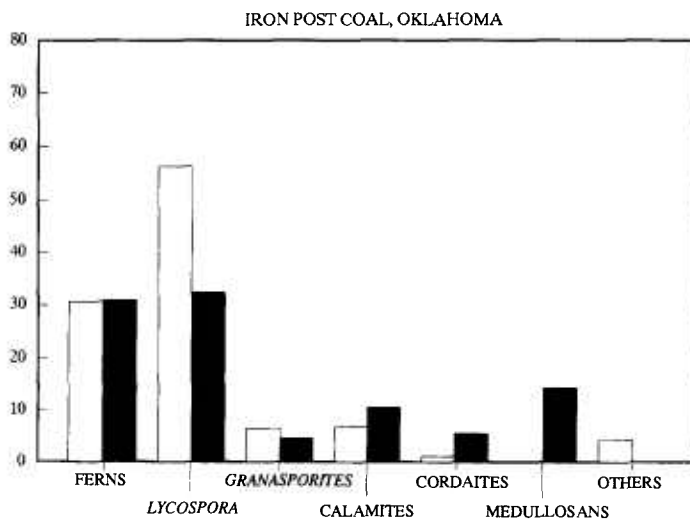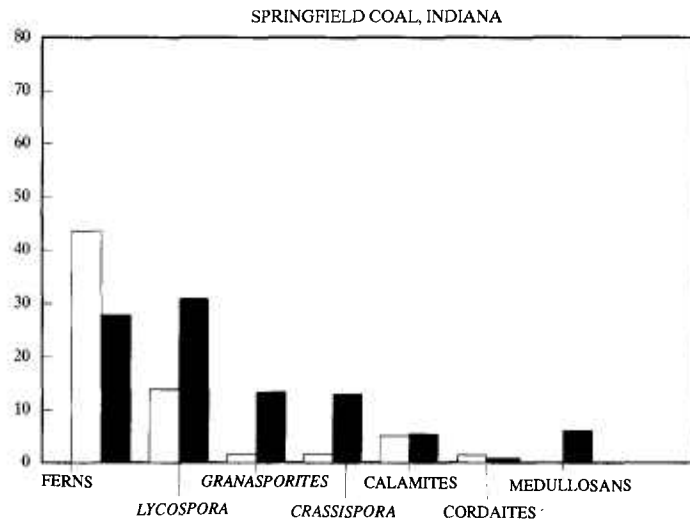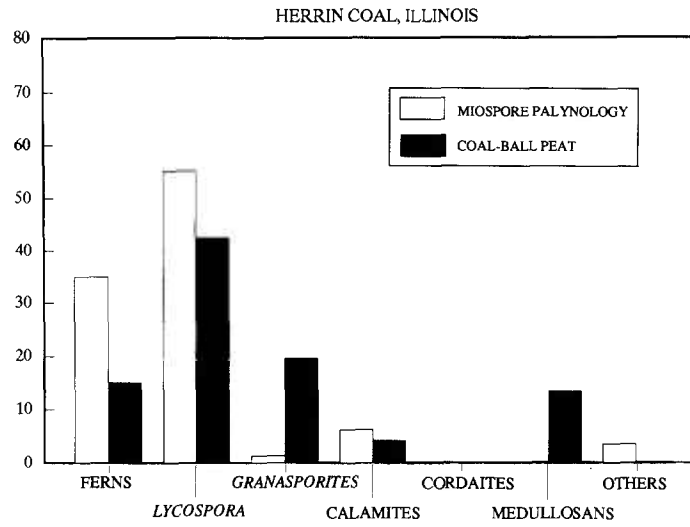
More serious concerns are the differential production of spores by source plants, the taxonomic level at which results are often reported, and the degree to which parent plants and miospores can be correlated. Differential spore production is a serious biological bias in palynology that can be addressed by direct comparison with macrofossil floras. Life history studies of plants from peat-forming habitats indicate that *Lycospora*-producing lycopsids (*Lepidophloios, Lepidodendron* and *Paralycopodites*), densospore-producing lycopsids (especially *Sporangiostrobus*), and many *Psaronius* tree-fern species, produced massive numbers of spores relative to other plants of greater, equal, or
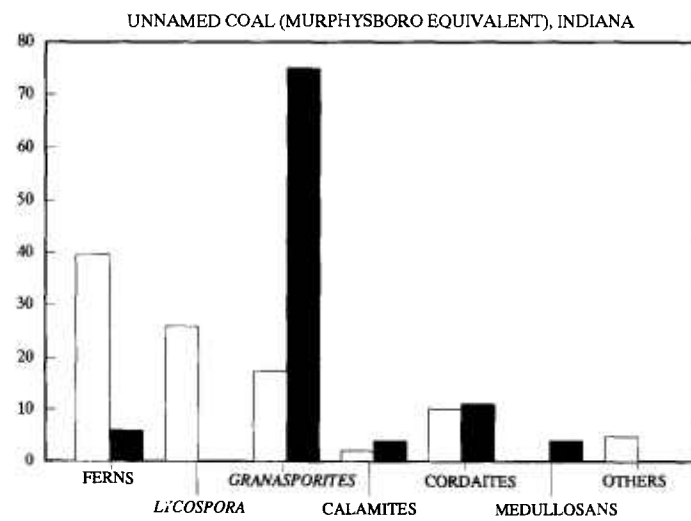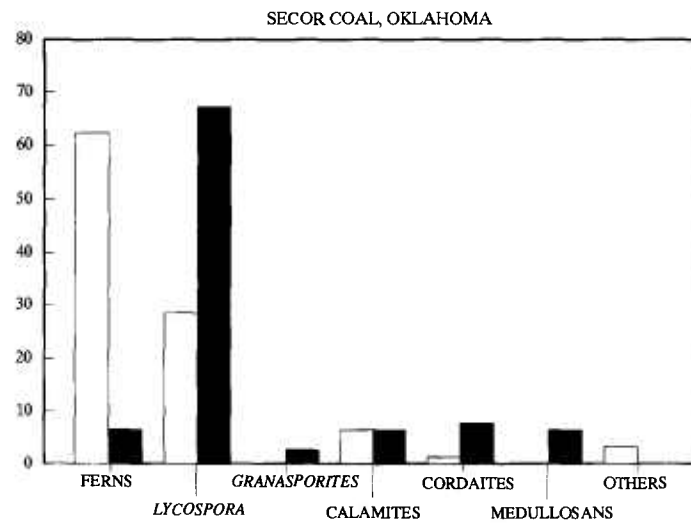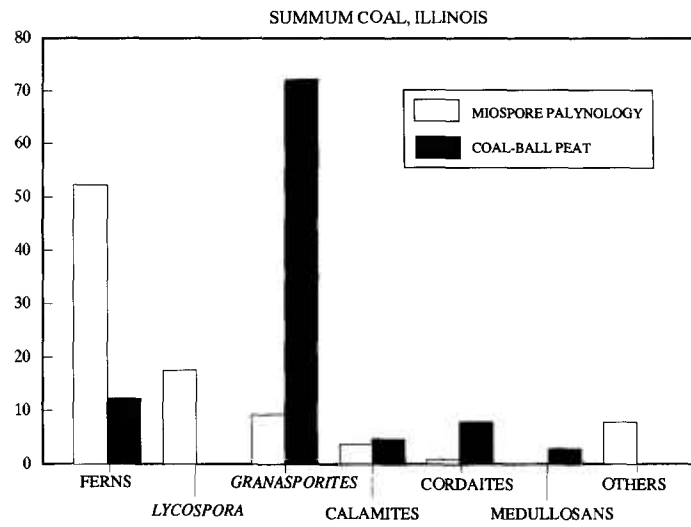
near equal abundance in the parent vegetation (Lesnikowska, 1989; Wagner, 1989; Willard, 1990, 1992). In contrast, lycopsids that produced *Granasporites* (*Diaphorodendron* and *Synchysidendron*) or *Crassispora* (*Sigillaria*), some tree-fern species, and cordaites produced fewer, often larger, miospores, or spread low levels of miospore production over an extended interval of tree growth (DiMichele and Phillips, 1985; Costanza, 1985; Trivett and Rothwell, 1985; Lesnikowska, 1989). This pattern of reproduction leads quantitative palynology to underestimate, sometimes severely, the standing biomass of important plant groups. The biases of relative spore production should not be taken lightly. Almost universally recognized by palynologists as a problem, it is often alluded to gravely in introductory remarks only to be seemingly forgotten in subsequent vegetational reconstructions.

The continued anonymity of some miospore taxa (relative to a parental plant) is a diminishing but real problem. There are now several significant summaries of miospore-plant correlations (Ravn, 1986; Lesnikowska, 1989; Willard, 1990; Calder, 1993). Remaining problems include discovery of source plants for abundant spores thought to be derived from ground-cover ferns or lycopsids (e.g., *Triquitrites, Anacanthotriletes*), and a solution to the complexities of tree-fern spore production patterns. A related problem, at least for those trying to use the palynological literature as a source of paleoecological data, is the level of taxonomic information presented in some palynological studies. Particularly for dominant lycopsids and tree ferns, specific-level spore identities are needed for ecological resolution. As an example, *Lepidophloios hallii, Lepidodendron hickii*, and *Paralycopodites* spp. have different ecological implications. Unfortunately, all produced *Lycospora* microspores; fortunately they produced different species of *Lycospora*, and species-level data are needed to reconstruct vegetational patterns in these instances.

Comparison of palynological and coal-ball patterns

We have chosen six Westphalian D coals to contrast patterns of plant abundance inferred from

HERRIN COAL, ILLINOIS

SPRINGFIELD COAL, INDIANA

IRON POST COAL, OKLAHOMA

SUMMUM COAL, ILLINOIS

SECOR COAL, OKLAHOMA

UNNAMED COAL (MURPHYSBORO EQUIVALENT), INDIANA

peat and miospores (Fig. 12A–F). All abundances are reported as coal-bed averages, which at present is the only practical means to compare coal-ball peat data with coal palynology due to the limited number of directly comparable incremental studies, and the existing abundance of literature at the scale of coal-bed summaries. Coal balls and coal samples for miospore analysis were collected from the same mines or mining areas, and in two instances were immediately adjacent (Herrin coal—Sahara; and Springfield coal—Island Creek), consequently the possibility of sampling different parent vegetations, or different physical environments was minimized. All coal-ball analyses were carried out or checked by one of us; palynological studies of four of the six samples were carried out by Russell A. Peppers (Illinois State Geological Survey), by Debra A. Willard (U.S. Geological Survey) or James F. Mahaffy (Dordt College), who interacted extensively with Peppers. Thus, investigator bias is minimized as much as possible.

Several patterns emerge. Most obvious is the lack of medullosans in miospore analyses, an artifact of preparation techniques. Second is the general under-representation of *Granasporites*-producing lycopsids (*Diaphorodendron* and *Synchysidendron*) in palynofloras, a function of spore productivity. This is particularly striking in the Summum and Murphysboro Equivalent coals (Fig. 12D, F). In both instances *Diaphorodendron* dominates the peat (Lesnikowska, 1984), but *Lycospora* dominates the palynoflora. No *Lycospora* producers were identified in either coal-ball profile. Cordaites and *Sigillaria* (*Crassispora*) are similarly under-represented in the palynoflora. Third, over-represented taxa include *Lycospora*, although this is highly variable, and tree ferns, the latter in almost every instance. Even such a coarse-grained analysis reveals some systematic differ-

ences between peat and palynology. Unfortunately, on a zone by zone basis within adjacent peat and palynological profiles, Willard (1992) found much greater variability in patterns of over- and under-representation than in time-averaged bed summaries; the problem is more complex than our summaries suggest. Thus, it may be best to use "rules of thumb" to paint a semiquantitative picture of parent vegetation, accounting for taphonomic biases.

Miospore palynology and the domed-peat model

A.V.H Smith developed a model of peat forest succession based on palynologic and petrographic analyses in the Lower and Middle Coal Measures of England (Smith, 1957, 1962, 1964a,b, 1968). Succession in his model is reflected by spatial and vertical variation among four distinctive, and repeatedly recognizable miospore assemblages, or phases, each of which is broadly associated with a petrographically distinctive type of coal. Three of the four phases, the Lycospore, Transition and Densospore (Smith, 1957) constituted a directional, successional order in which reversals were possible but without any direct change between Lycospore and Densospore phases (Smith, 1962). The Incursion phase was added (Smith, 1962) to account for irregular disruptions to the "normal" succession, and could occur at any stage. Smith (1964b) considered the sequence of miospore assemblages to reflect physical changes in the substrate as peat accumulated, from subaquatic (the Lycospore phase) to subaerial (the Densospore phase), in essence describing an evolution from a rheotrophic to an ombrotrophic mire.

The paleoenvironmental interpretations that evolved from this model have been used to expand and support paleoclimatic models. There has been less time devoted to re-examination of the design

Fig. 12. Comparisons of seam-average, quantitative biomass estimates of major plant groups based on miospore palynology (open bars) and coal-ball peat (black bars). Relative abundance is shown in percent on the vertical axis; computed separately for miospore and peat samples. Localities and sources of information: (A) Herrin coal, Illinois: coal balls, Phillips and DiMichele (1981); miospores, Mahaffy (1985). (B) Springfield coal, Indiana: coal balls and miospores, Willard (1990). (C) Iron Post coal, Oklahoma: coal balls and miospores, Phillips et al. (1985). (D) Summum coal, Illinois: coal balls, Phillips et al. (1985); miospores, Peppers (1970). (E) Secor coal, Oklahoma: coal balls, DiMichele et al. (1991); miospores, Phillips et al. (1985). (F) unnamed coal (Murphysboro equivalent), Indiana: coal balls, Eggert and Phillips (1982); miospores, Peppers (1982).

of the model and limited efforts to broaden it and integrate the model with data from other kinds of paleoecological studies. In this section we review the formulation of the "phase" concept in order to make some comparisons with ecologic structure inferred from other kinds of data.

The development of the concept of "dominant miospore phases" (Smith, 1957, 1962), and relationship of the phases to coal microlithotype characteristics are at once both simple and complex. In the late 1950s and early 1960s there was a paucity of ecological data on the vegetation of the peat-forming environments represented by Westphalian coals. Swamp reconstructions, such as that of Teichmüller (1962), served as general models, but in fact were not based wholly on the plants that colonized peat substrates. Certain spore types, however, were known to be associated with bright coals (Lycospora) and certain with dull coals (Densosporites in crassidurain).

On the basis of what was then known, Smith (1957, p. 346) set out a priori to distinguish miospore assemblages on the basis of "dominant miospores" and to establish that they occurred in a "...well defined and ordered sequence". According to Smith (1962, p. 432), "A miospore [Guennel, 1952, p. 10] phase is defined as that part of a seam profile which is characterized by the occurrence of a particular association of species comprising a dominant or group of dominant, species together with certain less abundant species." Smith's "dominant miospore species" were "...arbitrarily defined as the minimum number of species constituting fifty percent of the total number of spores counted." This was based on counts of 500 miospores from coal intervals 0.5 to 2.5 inches thick with uniform petrographic composition (lithotypes). Typically one, two, or three "dominant miospore species", about equally distributed, could be identified in 90% of the sampling intervals from coal profiles.

The original successional model was based on coal columns from selected upper Westphalian A (Silkstone, Thornecliffe, and Parkgate) and Westphalian B (Swallow Wood, Barnsley, and Hazel) coals of Yorkshire. These particular coals were chosen because they exhibited common petrographic types (except for cannels), and because

they contained horizons of crassidurain. Therefore, Smith considered these to be the most likely to yield evidence of the ecological succession he sought, but within a stratigraphic interval that was restricted enough to rule out changes in miospore composition due to plant migration or character evolution.

Based on the generally dulling upward petrographic character of these coals, Smith (1957) first established three "dominant miospore phases" (Lycospore, Transition and Densospore), which approximated relationships to coal microlithotypes. The first and third phases were named for the dominant miospore genus, and the Transition for its typically intermediate successional position; the Lycospore and Densospore phases were not observed to occur next to each other. In this generalized sequence of "dominant miospore phases" Laevigatosporites desmoinensis (L. vulgaris in Smith and Butterworth, 1967, p. 285) was generally the "dominant miospore species" in the Transition phase, but Calamospora was also important to dominant, and the relative proportions of these spores varied among Transition phase samples, hence the name (see discussion in Smith, 1962, p. 473). According to Smith (1962, p. 433) "The dominant species of a phase are, therefore, diagnostic of the phase and may be made the basis for its recognitition."

One of the inconsistencies of Smith's (1957) original succession model, aside from permissible reversions, was that the Lycospore and Transition phases, or parts of them, could be characterized by "dominant miospore species" other than Lycospora, or Laevigatosporites desmoinensis and Calamospora, respectively. Hence, Smith (1962, p. 434) introduced a new concept, the Incursion phase (Fig. 13), so named because of its supposed origin with periods of sudden flooding, bringing in a flora that did not occupy a unique position in the successional order. The taxa characteristic of an Incursion phase were Crassispora kosankei and Punctatosporites minutus, which had generally similar abundance fluctuations and occurred in association with Lycospora and Laevigatosporites. Incursion phases occurred in about equal numbers between Lycospore and Transition phases and between Transition and Densospore phases.
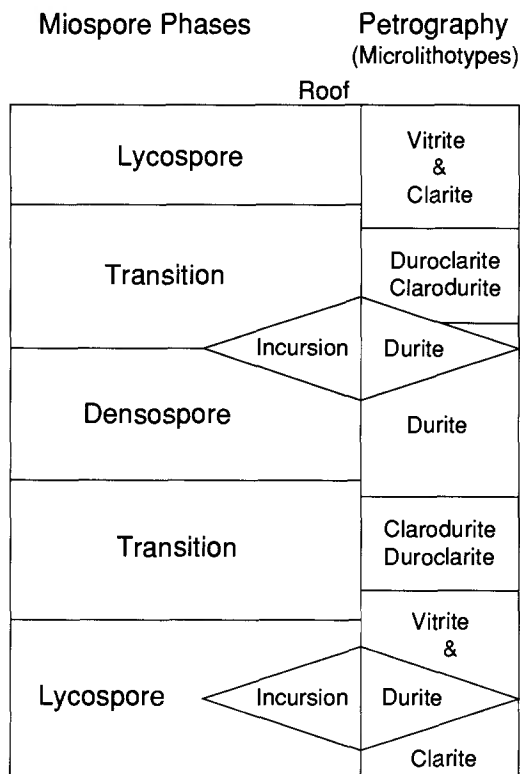
Miospore Phases

Petrography
(Microlithotypes)

Roof

Miospore Phases	Petrography (Microlithotypes)
Lycospore	Vitrite & Clarite
Transition	Duroclarite Clarodurite
Incursion / Densospore	Durite / Durite
Transition	Clarodurite Duroclarite
Lycospore / Incursion	Vitrite & Durite / Clarite

Fig. 13. Miospore-petrographic "phase" diagram modified from Smith (1962). See text for details.

Densospore phases often were terminated by Incursion phases (Smith, 1962, p. 459).

The Incursion phase was recorded wherever the combined total of *C. kosankei* and *P. minutus* exceeded 15% of the miospore count because "... although they are rarely numerous enough to dominate their associated assemblages, the palynological and petrological evidence suggests that the phase so defined does represent a distinct type of swamp environment" (Smith, 1962, p. 455). This seemingly random (Smith, 1964a, p. 59) fourth phase could occur anywhere except within a Densospore phase. The Incursion phase exhibits the highest level of miospore diversity; Densospore and Lycospore phases have the lowest diversity. Also occurring in abundance in some Incursion phase samples are *Fabasporites* and the highest levels of three species of *Florinites* (Smith, 1962, p. 455). The Incursion phase sometimes appears in association with an abrupt change in petrography at the termination of a Lycospore phase,

and may persist and end gradually. Tenuidurites are invariably associated with the Incursion phase (Smith, 1968, p. 36). The appearance of the Densospore phase is usually abrupt (Smith, 1964a, p. 59) and crassidurites are invariably associated with this phase. However, petrographic changes (see Fig. 12) do not necessarily occur at a phase boundary (Smith, 1964a, p. 60). It is also quite likely that further subdivisions of the miospore associations can be made (Smith, 1968, p. 36; see Fulton, 1987). Smith (1968, p. 37) states: "In a thick coal seam in a stable area, the full sequence of phases usually occurs with maximum development of the Densospore phase in the middle and/or upper positions of the seam."

Smith (1962, p. 430) clearly stated that "dominant miospore species" of a phase did not necessarily represent the dominant plants in the source vegetation, but that "... they may nevertheless be used to characterise a particular vegetation type, ... growing under a particular set of edaphic conditions, that is conditions relating to the soil environment" (1962, p. 432). This, in a sense, sums up the challenge for paleoecology. We must be able to relate what is known about the ecological structure of Westphalian mire vegetation and autecologies of individual species, to the palynological record. Furthermore, the effects of taphonomy on coal-petrographic and coal-ball characteristics need to be distinguished from the original ecological conditions of the peat-forming habitats.

The use of miospores to examine ecological patterns within mires over geological time relies on consistent taxonomic identifications. This is an area with many uncertainties, and only a few problems need be mentioned here with reference to lycopsids. *Lycospora* ?*granulata* Kosanke in Smith and Butterworth (1967, p. 247) is apparently not the same as the *Lycospora granulata* that is derived from cones of *Lepidophloios hallii* (C.F. Eble, pers. commun., 1992, believes this to be *L. torquifer*). This is relevant because Smith (1962, p. 433) includes his *L. granulata* in the Transition phase. Smith (1962, 1964b) reported exceptionally abundant occurrences of *Crassispora kosankei* (see stratigraphic plots in Smith, 1964b, p. 298; Smith and Butterworth, 1967, p. 73) and also recognized *Granasporites* (*Apiculatisporis*) *irregularis* (Smith

and Butterworth, 1967, plate 7, 18, 19), which is now *Granasporites medius* (*Cappasporites distortus*) (Ravn et al., 1986). Our concerns are two fold regarding *Crassispora kosankei* (*Sigillaria*) and *Granasporites medius* (*Diaphorodendron* and *Synchysidendron*). *Granasporites medius* (= *G. irregularis* in Smith, 1962) is associated with the Lycospore phase, occurring in 44% of the assemblages of that phase. *Crassispora kosankei* is much more abundant in the Incursion phase and Smith (1964b) documents oscillations in its stratigraphic abundance, which peaks at about the middle Westphalian B. Miospore abundances for both *Sigillaria* and *Diaphorodendron–Synchysidendron* tend to be relatively small in relation to actual plant abundances, based on comparisons between coal-ball and palynological patterns (Willard, 1992). Often the two miospore taxa have not been distinguished in the literature (see Smith, 1962, plate 30, e; Peppers, 1970, p. 120; Kosanke, 1988, p. 70); thus, there is some uncertainty and ambiguity in treating the relatively large abundances of *Crassispora kosankei* as representing *Sigillaria* only.

Quantitative data on the relative importances of the four miospore phases have been reported for coals (Clay Cross to Two-foot Marine Band) in the lower half of the Westphalian B of Yorkshire (Smith and Butterworth, 1967, p. 85). Diagrams indicate that, on average, nearly one-half of the bed was represented by the Lycospore phase, with about equal importances (about one-sixth each) of Incursion, Transition, and undetermined phases. Densospore phases were of minor importance, with one important exception in the Barnsley seam, where the Densospore phase was one-sixth of the total. In Britian, the oldest Westphalian deposits of crassidurain, in which the Densospore phase occurs, occur in the middle of the Westphalian A in all coalfields so aged, and are know from most beds and from all coalfields up to the Westphalian B/C boundary (Smith, 1964a). However, relatively few of these coals have abundances of the Densospore phase exceeding that of the Barnsley seam. Coals of late Namurian age from the Scottish Westfield Coal Basin exceed those of the early Westphalian in densospore abundances (A.C. Scott, pers. commun., 1992)

Comparison of Smith's Miospore phases with broader ecological inferences

Smith (1962) was able to develop a general model of Westphalian intramire ecological succession largely because of the conservatism and continuity of lepidodendrid ecological patterns. His Lycospore phase apparently incorporates most of the environmental range encompassed by *Lepidodendron–Lepidophloios*, *Diaphorodendron* and *Paralycopodites*. As a consequence of encompassing the most prolific *Lycospora* producers (Phillips and DiMichele, 1992), the importance of *Diaphorodendron* is masked and is impossible to assess without direct access to anatomically identifiable plant remains. Megaspore palynology of coal profiles (Bartram, 1987) aids substantially in documentation of patterns of generic co-occurrence and distribution, but also is difficult to relate to relative abundances of parent plants. Miospore and megaspore patterns both are consistent with Smith's coarsely resolved characterization of a complex of lycopsids, including *Hizemodendron* (*Lycospora*) and *Chaloneria* (*Endosporites*), as "associated species" in a larger lycopsid vegetation. However, Smith (1962, p. 436) characterized some species of *Lycospora* and *Endosporites* as "associated species" of the Transition phase. Some *Densosporites* also were "associated" with the Transition phase.

Incursion—Crassispora (Sigillaria)

The Incursion phase, which is defined differently from the other phases, encompasses the most diverse and varied miospore assemblages. Incursions, as with the more prominent phases, are identified from a combination of miospore-assemblage and coal-petrographic data. Within Incursion floras, lepidodendrids represent an important component, namely *Crassispora* (*Sigillaria*), along with *Psaronius* ferns (*Punctatosporites minutus* and sometimes *Fabasporites*), which have similar patterns of increase and decrease in abundance within profiles.

The appearance of abundant *Sigillaria* and *Psaronius* within Westphalian A and B mires has considerable ecological significance. *Sigillaria*, in particular, is considerably under-represented by

Crassispora miospores (Willard, 1992); if the relative abundances reported by Smith (1964b) and Smith and Butterworth (1967) do represent only *Sigillaria*, then sporadic expansions of these trees were more common in the Westphalian A and B than at later times. *Psaronius* also appears to be rare in mires from these times, so its occurrence in Incursions suggests ties to unusual edaphic conditions. Although Smith (1962) required a 15% combined abundance of *Crassispora* and *Punctatosporites minutus* for recognition of an Incursion, he (1962, p. 438) illustrated an impressive stepped profile of increase in *Crassispora–Punctatosporites* to almost 40% as an example of an Incursion within a Lycospore phase that then extended into a Transition phase.

The recognition by Smith (1962) of a *Sigillaria*-rich vegetation associated with intra-mire disturbance is an important early discovery that is consistent with general thinking about the ecology of most *Sigillaria* species. The genus is most common in marginal parts of mires and in clastic swamps, and is associated with high miospore diversity and high incidence of *Schopfipollenites* (*Medullosa*) in the Incursion and Lycospore phases. The Incursion miospore signature is associated with high tenuidurite (inertinite) and mineral content, which makes a good case for intramire disruptions exceeding those that typically occur within a Lycospore phase. Keeping in mind the taxonomic uncertainties of miospore identification that continue to surround *Sigillaria*, it appears that species of this genus signal a response to disturbance resulting in seasonally drier, more exposed peat surfaces, probably enriched in available nutrients, colonized by a greater diversity of plants than typical of most other lycopsid-dominated assemblages.

Incursion—Florinites (Cordaitales)

Florinites mediapudens, representative of cordaitean gymnosperms, also occurs in Incursions between the Lycospore and Transition phases (Smith, 1962, p. 438). Abundances exceeding 30%, increasing within the phase in a step-like manner, have been identified. As with many other large pollen and spore types *Florinites* under-represents the abundances of cordaites in the parent vegeta-

tion. Consequently, high *Florinites* abundances, particularly when associated with distinctive petrographic qualities, indicate a considerable change in environmental conditions from those typical of mires, particularly of lepidodendrid-dominated habitats.

At the time of Smith's studies there was a complex historical bias (Chaloner, 1958; Neves, 1958) against interpreting cordaites as lowland vegetational components, particularly as elements of peat-forming habitats. As a consequence, most of the *Florinites* or other miospore taxa attributed to cordaites were explained away as derivatives from "uplands" when encountered in coals or offshore sediments (see for example the interpretation of Gibson, 1961). We now know that cordaites were extremely diverse taxonomically and ecologically, and that they extended into many kinds of lowland–wetland habitats (Rothwell and Warner, 1984; Costanza, 1985; Trivett and Rothwell, 1985). Coal ball data from England, from continental Europe (Rhur, Donets), and from many coals in the United States, vindicate Smith's (1962) recognition of a cordaitean presence in mires, and show clearly that although cordaites may have occurred in "uplands", such occurrences do not preclude their importance in mires.

Within peat-forming habitats cordaites, as a group, did not encompass a breadth of physical conditions comparable to that of the lepidodendrids, but some apparently occupied portions of mires unfavorable to lepidodendrid colonization or growth. Based on what is currently known about the cordaites in Westphalian A and B coal-ball peats, many apparently could not tolerate wet mire conditions to the same degree that later species could.

Densospore phase

The empirical data on densospore-bearing plants and the marked variety of physical environments in which they occur suggest that considerable caution should be used in trying to ascribe a typical ecology and habitat to this "dominant miospore phase". The basic habitat is characterized on the basis of petrography, indicating severely decayed peat, represented by "crassidurites".

The relationship between densospore-bearing

plants, such as *Sporangiostrobus*, and other lepido-
dendrids is problematic. Whereas it seems that
Sporangiostrobus was a prolific spore producer and
probably associated with extremely stressful or
frequently disturbed conditions, these are
characteristics shared with *Chaloneria* and
Paralycopodites. At present we do not know if
Sporangiostrobus had a stigmarian system or an
unbranched basal rhizomorph, characteristics that
may have helped define its ecological amplitude.

Few environmental clues exist regarding den-
sospore producers, and those that do are largely
anecdotal, not welded into a complete picture.
Densosporites (or *Sporangiostrobus*) has been
found in shaley coals and in outright clastic depos-
its by several authors (e.g., Urban, 1962; Corsin
et al., 1967; Ravn, 1979; Wagner, 1989) and Smith
(1962) notes the high incidence of Incursions (with
associated clastics) following Densospore phases.
It has been suggested by Wagner (1989) that
Sporangiostrobus occurs in coal balls but has been
consistently overlooked, with exceptions (Leisman,
1970). This criticism has merit, particularly if the
plant is rare; however, where *Sporangiostrobus*
occurs in abundance the sporangia and megaspores
are scattered widely throughout the adjacent peat.
This should make it stand out much like
Chaloneria. Despite the Iowa occurrences, we sus-
pect that no coherent delineation of the habitats
of densospore-producing plants is likely to arise
until additional studies from coal balls are added
to analyses such as that of Wagner (1989). As
Smith (1962, p. 439) stated, "Little can be deduced
about the vegetation of the Densospore phase."
Extreme caution, therefore, is warrented in using
densospores as indicators of raised mire conditions.

Transition phase

The relationship between our understanding of
lepidodendrid ecologies and the composition of
the Transition phase is the most elusive of all of
Smith's phases. The Transition phase, as Smith
characterized it, has a higher miospore species
diversity than either the Lycospore or Densospore
phases, yet shared many species with both, depend-
ing on relative positions of the phases within the
bed profile. In general, the "dominant miospore"
species included *Laevigatosporites vulgaris* and

Calamospora, suggesting abundances of sphenop-
sid plants. Smith (1962, p. 430) observed that
among the top ten "dominant species" *L. vulgaris*
had by far the highest number of presence–absence
occurrences among the total profile samples he
examined, and reached a higher overall percentage
than any other spore in the Transition assemblages,
49%. The widespread distribution of calamites is
consistent with their ability to propagate vegeta-
tively. They are common but rarely abundant in
coal balls; for example, in the Herrin coal calamites
comprise only 5% of the peat biomass but occur
in 55% of profile coal balls.

To the extent that calamitean habitats can be
generalized, they are usually associated with vary-
ing degrees of exposed peat and litter decay. Litter
may be badly degraded, though not always, and
often rhizomes and root systems consititute the
bulk of the calamitean debris. Calamitean litter in
peat is consistently associated with a dispropor-
tionately high fusain content (Phillips and
DiMichele, 1981; DiMichele and Phillips, 1988;
DiMichele et al., 1991). Despite the widespread
occurrences of calamites, macrofossil evidence
from coal balls suggests that they did not dominate
extensive areas of mires; reconstructions
(Teichmüller, 1962, 1989) in which they are shown
as the dominants in standing-water habitats are
extrapolated from work on clastic-compression
floras. Calamites have been noted, from miospore
data, to be more abundant in the early Westphalian
than in the later Westphalian (Peppers, 1979;
Phillips et al., 1985). Nevertheless, the actual vege-
tation of the Transition phase and its ecological
setting remain only vaguely defined.

Miospore phases and environmental inference

The ecological structure of mires became more
complex during the Westphalian, meaning that
more discrete successional "phases" became
differentiable on the basis of "dominant miospore"
species and genera, or "bulk species composition"
(Fulton, 1987). The stratigraphic interval on which
Smith (1957, 1962) based his model, the
Westphalian upper A and B, was ecologically
stable enough to permit the recognition of similar,
coarsely resolved taxonomic assemblages through-

out the interval. More refined analyses (Smith and Butterworth, 1967) of this same interval have provided some important data on the relative abundances of the principal non-*Lycospora* miospores, many of which underwent significant increases in frequency and relative abundance following earlier, less conspicuous appearances. The pattern of initial appearance of miospore species or genera in small numbers, followed by expansion in frequency and abundance, is seen in taxa that occur later in the Westphalian as well, such as *Torispora*, *Thymospora* and others. In light of the temporal changes in "dominant miospore" species during the later Westphalian, and in the diversity of "phases" these spores are used to define, we need to distinguish as clearly as possible the implications of phase successions from the environmental inferences that can be deduced for any individual phase and its component species.

Smith (1962) clearly stated most of the premises of his research, so that it is possible to recognize two inferences of paramount importance. First, he considered that the upper Westphalian A and Westphalian B had extremely equable distributions of environmental "wetness". Second, he assumed that there was an inherent pattern of ecological succession in mires that could be defined and predicted. As a consequence of these assumptions he proceeded to develop the "dominant miospore" and incursion phase models based on a combination of palynological and coal petrographic data. His model led to the broad, and often uncritical acceptance of straight forward, consistent relationships between petrography and miospore composition, and thus to substitution of miospore "phases" for the broader miospore-petrographic complex of data (even though Smith had noted the need for subphase divisions). For the Lycospore phase in particular, the "dominant miospore" concept overshadows much more complex ecological structure within mires, and masks the contribution of lepidodendrids to other kinds of plant assemblages.

All of the phases described by Smith (1962) are inferred to have formed under continuously wet (rainfall or groundwater) conditions, whether peat was presumed to have accumulated under submerged or exposed conditions. The Lycospore phase was interpreted as developing under flooded conditions (high water table). The Transition phase was interpreted as the beginning of ombrotrophic elevation of the water table. The Densospore phase was inferred to represent a rainfed or ombrotrophic, domed-peat surface contributing to petrographic qualities indicative of substantial aerobic oxidation of accumulated peat. Incursion phases were proposed to represent sudden floods during the Lycospore or Transition phases, and often preceded and especially followed Densospore phases. Continuous, and largely invariable rainfall is the most important underlying thread in this model, based largely on the concept of hydroseral succession.

Smith's interpretations reflect the then prevailing view that the tropics of Westphalian times were everwet and ideal for the accumulation of peat. Certainly this is true in a broad sense, and most of the evidence suggests a humid climate in the tropics, on average, during most of the Late Carboniferous. More recent studies of Westphalian paleoclimate (Phillips and Peppers, 1984; Cecil et al., 1985; Cecil, 1990; Winston, 1990) suggest that there were considerable variations in wet and less wet intervals, some perhaps qualifying as "seasonally dry", and that the scale of variation may be smaller than the time necessary to accumulate a single coal bed. The general thinness of most Late Carboniferous coals, the strong evidences of intramire disturbance drawn from macro- and microfossils, coal petrology, and studies of the depositional environments of coal, point to climatic variability that in many instances may have placed strict spatial and temporal limitations on conditions for peat accumulation.

Summary—major points

There are several points we wish to make that underlie all the specifics and derived inferences presented in this paper.

(1) Most of the important tree types of Late Carboniferous mires were distinct taxonomically and structurally from those of later time periods. Lycopsids, pteridoperms and *Psaronius* tree ferns lack good modern structural or ecological analogues. Westphalian and Stephanian mires, consequently, were composed of tissue types and ratios

of woody to parenchymatous tissues vastly different from any post-Carboniferous mire. Most of the "wood" in Late Carboniferous mires was in reality lycopsid bark, which had a chemical structure distinct from that of wood (A.C. Scott, pers. commun., 1992), and was resistant to both decay and root penetration. True wood was contributed mostly by cordaites, which were usually subdominant elements of the vegetation in the middle Westphalian. Tree ferns and pteridosperms were largely of parenchymatous, non-woody construction, as were the root systems of lycopsid trees, all of which complicate petrographic inferences of ancient vegetation and environmental conditions.

(2) Macrofossil and palynological data, in combination with other indicators of physical environmental conditions such as presence or absence of clastic partings, fusain, ash content of coal, suggest a rheotrophic setting for the growth of most mire plant constitutents. Included are the lepidodendrids, *Lepidophloios*, *Lepidodendron*, *Paralycopodites*, *Diaphorodendron*, *Synchysidendron*, and *Sigillaria*, the calamites, medullosan pteridosperms and cordaites. Tree ferns appear to have had broad ecological amplitudes, as did densospore-producing lycopsid subtrees. Both of these groups could have been represented in low-nutrient ombrotrophic mires, as could some species of cordaites and pteridosperms; however, none of the existing paleobotanical evidence compels an ombrotrophic interpretation.

(3) In retrospect, we view the Westphalian as a period with significant environmental variability, manifested by high levels of abiotic disturbance of lowland habitats, including mires. This conflicts with the image of the first tropical "coal age" as a landscape of vast, quiescent, lush forests. Nonetheless, high levels of intrahabitat disturbance seem to be supported by empirical data from paleobotany, petrography, and stratigraphic patterns. As a consequence, many of the dominant Westphalian plants in mires either grew rapidly, were of small stature, or were cheaply constructed, adapted for the ecological constraints of mires as well as rapid exploitation of disturbed habitats. In addition, the simple, diorama-style reconstructions of Late Carboniferous mires fail to convey the complexity of the mire landscape, which appears to have had both vast tracts of monodominant lycopsid or tree-fern stands, and many areas of small-scale heterogeneity, combining localized flooding and peat exposure.

(4) There are distinctive patterns of temporal change in mire floras during the Late Carboniferous, including a major extinction during the Westphalian–Stephanian transition. Vegetational changes mark periods of change in mire community dynamics and dominance-diversity patterns. Change from lycopsid to tree-fern dominance in the Stephanian resulted in changed community structure and diversity, in concert with major changes in proportions of tissue types. Models of peat formation must consider the consequences of such changes.

(5) Petrographic data provide important information on peat chemistry and hydrology, but are not presently capable of reconstructing mire vegetation. Non-critical use of any unidimensional model, be it petrographic or based on plant fossils, is unlikely to advance our knowledge and understanding of Westphalian peat-forming ecosystems.

Acknowledgments

References

Andrews, H.N., 1952. Some American petrified calamitean stems. Ann. Mo. Bot. Gard., 39: 189–218.

Andrews, H.N. and Agashe, S.N., 1965. Some exceptionally large calamite stems. Phytomorphology, 15: 103–108.

Andrews, H.N. and Murdy, W.H., 1958. *Lepidophloios*—and ontogeny in arborescent lycopods. Am. J. Bot., 45: 552–560.

Barthel, M., 1980. Calamiten aus dem Oberkarbon und Rotliegenden des Thüringer Waldes. 100 Jahre Arboretum (1879–1979), pp. 237–258.

Bartram, K.M., 1987. Lycopod succession in coals: an example from the Low Barnsley Seam (Westphalian B), Yorkshire, England. In: A.C. Scott (Editor), Coal and Coal-bearing Strata: Recent Advances. Geol. Soc. Spec. Publ., 32: 187–199.

Bateman, R.M. and DiMichele, W.A., 1991. *Hizemodendron*, gen. nov., a pseudoherbaceous segregate of *Lepidodendron* (Pennsylvanian): phylogenetic context for evolutionary changes in lycopsid growth architecture. Syst. Bot., 16: 196–205.

Bateman, R.M., DiMichele, W.A. and Willard, D.A., 1992. Experimental cladistic analysis of anatomically preserved arborescent lycopsids from the Carboniferous of Euramerica: an essay on paleobotanical phylogenetics. Ann. Mo. Bot. Garden, 79: 500–599.

Batenburg, L.H., 1982. "Compression species" and "petrifaction species" of *Sphenophyllum* compared. Rev. Palaeobot. Palynol., 36: 335–359.

Baxter, R.W. and Willhite, M.R., 1969. The morphology and anatomy of *Alethopteris lesquereuxi* Wagner. Univ. Kans. Sci. Bull., 48: 767–783.

Beeler, H.E., 1983. Anatomy and frond architecture of *Neuropteris ovata* and *Neuropteris scheuchzeri* from the Upper Pennsylvanian of the Appalachian Basin. Can. J. Bot., 61: 2352–2368.

Bertram, U., 1989. Untersuchungen an coal balls aus dem Namur a von Ostrau unter berücksichtigung der Gattungen *Heterangium*, *Lyginopteris* und *Microspermopteris*. Palaeontographica, B, 214: 125–224.

Brotzman, N.L.C., 1974. North American petrified cordaitean ovules. Ph.D. Thesis, Univ. Iowa, 268 pp.

Burnham, R.J., Wing, S.L. and Parker, G.C., 1992. The reflection of deciduous forest communities in leaf litter: implications for autochthonous litter assemblages from the fossil record. Paleobiology, 18: 30–49.

Calder, J.H., 1993. The evolution of a groundwater influenced (Westphalian B) peat-forming ecosystem in a piedmont setting: the No. 3 seam, Springhill coalfield, Cumberland Basin, Nova Scotia. Geol. Soc. Am. Spec. Pap., in press.

Calder, J.H., Gibling, M.R. and Mukhopadhyay, P.K., 1991. Peat formation in a Westphalian B piedmont setting, Cumberland basin, Nova Scotia: implications for the maceral-based interpretation of rheotrophic and raised paleomires. Bull. Soc. Géol. Fr., 162: 283–298.

Cecil, C.B., 1990. Paleoclimate controls on stratigraphic repetition of chemical and clastic rocks. Geology, 18: 533–536.

Cecil, C.B., Stanton, R.W., Neuzil, S.G., Dulong, F.T., Ruppert, L.F. and Pierce, B.S., 1985. Paleoclimatic controls on late Paleozoic sedimentation and peat formation in the central Appalachian Basin (U.S.A.). Int. J. Coal Geol., 5: 195–230.

Chaloner, W.G., 1958. The Carboniferous upland flora. Geol. Mag., 95: 261–262.

Chaloner, W.G., 1962. A *Sporangiostrobus* with *Densosporites* microspores. Palaeontology, 5: 73–85.

Cichan, M.A., 1986. Conductance in the wood of selected Carboniferous plants. Paleobiology, 12: 302–310.

Collinson, M.E. and Scott, A.C., 1987a. Implications of vegetational change through the geological record on models for coal-forming environments. In: A.C. Scott (Editor), Coal and Coal-bearing Strata: Recent Advances. Geol. Soc. Spec. Publ., 32: 67–85.

Collinson, M.E. and Scott, A.C., 1987b. Factors controlling the organization and evolution of ancient plant communities. In: J.H.R. Gee and P.S. Giller (Editors), Organization of Communities, Past and Present. Blackwell, Oxford, pp. 399–420.

Collinson, M.E., Scott, A.C., De Leeuw, J.W. and Van Bergen, P.F., 1992. The evolution of plants and selected plant compounds relevant to the generation of oil from coal and coal-bearing strata. In: Coal and Coal-bearing Strata as Oil-prone Source Rocks. Geol. Soc. London, p. 6.

Corsin, P.M., Coquel, R. and Loboziak, S., 1967. Sur la composition palynologique verticale et horizontale d'un cycle sédimentaire du terrain Houiller. Palaeogeogr., Palaeoclimatol., Palaeoecol., 3: 167–184.

Costanza, S.H., 1985. *Pennsylvanioxylon* of Middle and Upper Pennsylvanian coals from the Illinois Basin and its comparison with *Mesoxylon*. Palaeontographica, B, 197: 81–121.

Courvoisier, J.M. and Phillips, T.L., 1975. Correlation of spores from Pennsylvanian coal-ball fructifications with dispersed spores. Micropaleontology, 21: 45–59.

Covington, D. and Raymond, A., 1989. Taxonomic uniformitarianism: the problem with shoot/root ratios of peats. Rev. Palaeobot. Palynol., 58: 85–94.

Cridland, A.A., 1964. *Amyelon* in American coal balls. Palaeontology, 7: 186–209.

Cross, A.T. and Phillips, T.L., 1990. Coal-forming plants through time in North America. Int. J. Coal Geol., 16: 1–46.

Delevoryas, T., 1957. Anatomy of *Sigillaria approximata*. Am. J. Bot., 44: 654–660.

DeMaris, P.J., Bauer, R.A., Cahill, R.A. and Damberger, H.H., 1983. Prediction of coal balls in the Herrin Coal. Ill. State Geol. Surv., Contract Grant Rep., 1982-3, 69 pp.

Dempsey, J.E., 1964. A palynological investigation of the Lower and Upper McAlester coals (Pennsylvanian) of Oklahoma. Thesis. Univ. Oklahoma, Norman, OK, 124 pp.

Diessel, C.F.K., 1982. An appraisal of coal facies based on maceral characteristics. Aust. Coal Geol., 4: 474–484.

Diessel, C.F.K., 1986. On the correlation between coal facies and depositional environments. Advances in the Study of the Sydney Basin. Proc. 20th Symp. Univ. Newcastle, pp. 19–22.

Dilcher, D.L., 1979. Early angiosperm reproduction: an introductory report. Rev. Palaeobot. Palynol., 27: 291–328.

DiMichele, W.A., 1979. Arbotescent lycopods of Pennsylvanian age coals: *Lepidophloios*. Palaeontographica, B, 171: 57–77.

DiMichele, W.A., 1980. *Paralycopodites* Morey and Morey, from the Carboniferous of Euramerica—a reassessment of the generic affinities and evolution of "*Lepidodendron*" brevifolium Williamson. Am. J. Bot., 67: 1466–1476.

DiMichele, W.A., 1981. Arborescent lycopods of Pennsylvanian

age coals: *Lepidodendron*, with description of a new species. Palaeontographica, B, 175: 85–125.

DiMichele, W.A., 1983. *Lepidodendron hickii* and generic delimitation in Carboniferous lepidodendrid lycopods. Syst. Bot., 8: 317–333.

DiMichele, W.A., 1985. *Diaphorodendron*, gen. nov., a segregate from *Lepidodendron* (Pennsylvanian age). Syst. Bot., 10: 453–458.

DiMichele, W.A. and Bateman, R.M., 1992. Diaphorodendraceae, fam. nov. (Lycopsida: Carboniferous): systematics and evolutionary relationships of *Diaphorodendron* and *Synchysidendron*, gen nov. Am. J. Bot., 79: 605–617.

DiMichele, W.A. and DeMaris, P.J., 1987. Structure and dynamics of a Pennsylvanian-age *Lepidodendron* forest: colonizers of a disturbed swamp habitat in the Herrin (No. 6) coal of Illinois. Palaios, 2: 146–157.

DiMichele, W.A. and Nelson, W.J., 1989. Small-scale spatial heterogeneity in Pennsylvanian-age vegetation from the roof shale of the Springfield Coal (Illinois Basin). Palaios, 4: 276–280.

DiMichele, W.A. and Phillips, T.L., 1985. Arborescent lycopod reproduction and paleoecology in a coal-swamp environment of late Middle Pennsylvanian age (Herrin Coal, Illinois, U.S.A.). Rev. Palaeobot. Palynol., 44: 1–26.

DiMichele, W.A. and Phillips, T.L., 1988. Paleoecology of the Middle Pennsylvanian-age Herrin coal swamp (Illinois) near a contemporaneous river system, the Walshville paleochannel. Rev. Palaeobot. Palynol., 56: 151–176.

DiMichele, W.A., Mahaffy, J.F. and Phillips, T.L., 1979. Lycopods of Pennsylvanian age coals: *Polysporia*. Can. J. Bot., 57: 1740–1753.

DiMichele, W.A., Phillips, T.L. and Peppers, R.A., 1985. The influence of climate and depositional environment on the distribution and evolution of Pennsylvanian coal-swamp plants. In: B.H. Tiffney (Editor), Geological Factors and the Evolution of Plants. Yale Univ. Press, New Haven, CT, pp. 223–256.

DiMichele, W.A., Phillips, T.L. and Willard, D.A., 1986. Morphology and paleoecology of Pennsylvanian age coal-swamp plants. In: R.A. Gastaldo (Organizer), Land Plants: Notes for a Short Course. Univ. Tenn. Dep. Geol. Sci. Stud. Geol., 15: 97–114.

DiMichele, W.A., Phillips, T.L. and Olmstead, R.G., 1987. Opportunistic evolution: abiotic environmental stress and the fossil record of plants. Rev. Palaeobot. Palynol., 50: 151–178.

DiMichele, W.A., Phillips, T.L. and McBrinn, G.E., 1991. Quantitative analysis and paleoecology of the Secor coal and roof-shale floras (Middle Pennsylvanian, Oklahoma). Palaios, 6: 390–409.

DiMichele, W.A. and Hook, R.W. et al., 1992. Paleozoic terrestrial ecosystems. In: A.K. Behrensmeyer, et al. (Editors), Terrestrial Ecosystems Through Time. Univ. Chicago Press, Chicago, IL, pp. 205–325.

Eble, C.F., 1990. A palynological transect, swamp interior to swamp margin, in the Mary Lee coal bed, Warrior Basin, Alabama. In: R.A. Gastaldo, T.M. Demko and Yuejin Liu (Editors), Carboniferous Coastal Environments and Paleocommunities of the Mary Lee Coal Zone, Marion and

Walker Counties, Alabama. Guideb. Fieldtrip 6, 39th Annu. Meet., Southeast. Sect., Geol. Soc. Am. Ala. Geol. Surv. Tuscaloosa, AL, pp. 65–81.

Eble, C.F. and Grady, W.C., 1990. Paleoecological interpretation of a Middle Pennsylvanian coal bed from the Central Appalachian Basin, U.S.A. Int. J. Coal Geol., 16: 255–286.

Eble, C.F. and Grady, W.C., 1992. Palynologic and petrographic characteristics of Middle Pennsylvanian coal beds and a probable modern analogue. Geol. Soc. Am. Spec. Pap., in press.

Eggert, D.A., 1961. The ontogeny of Carboniferous arborescent Lycopsida. Palaeontographica, B:, 108: 43–92.

Eggert, D.A., 1962. The ontogeny of Carboniferous arborescent Sphenopsida. Palaeontographica, B, 110: 99–127.

Eggert, D.A., 1972. Petrified *Stigmaria* of sigillarian origin from North America. Rev. Palaeobot. Palynol., 14: 85–99.

Eggert, D.L., 1982. A fluvial channel contemporaneous with deposition of the Springfield Coal Member (V), Petersburg Formation, northern Warrick County, Indiana. Ind. Geol. Surv., Spec. Rep. 28, 20 pp.

Eggert, D.L. and Phillips, T.L., 1982. Environments of plant deposition—Coal balls, cuticular shale, and gray-shale floras in Fountain and Parke Counties, Indiana. Ind. Geol. Surv., Spec. Rep. 30, 42 pp.

Eggert, D.L., Chou, C.-L., Maples, C.G., Peppers, R.A., Phillips, T.L. and Rexroad, C.B., 1983. Origin and economic geology of the Springfield Coal Member in the Illinois Basin. In: Guideb. Fieldtrip 9, Geol. Soc. Am. Annu. Meet., pp. 121–146.

Ehret, D.L. and Phillips, T.L., 1977. *Psaronius* root systems— morphology and development. Palaeontographica, B, 161: 147–164.

Esterle, J. and Ferm, J.C., 1986. Relationship between petrographic and chemical properties of coal seam geometry, Hance seam, Breathitt Formation, southeastern Kentucky. Int. J. Coal Geol., 6: 199–214.

Feng, B.-C., 1989. Paleoecology of an upper Middle Pennsylvanian coal swamp from western Pennsylvania, U.S.A. Rev. Palaeobot. Palynol., 57: 299–312.

Fulton, I.M., 1987. Genesis of the Warwickshire Thick Coal: a group of long-residence histosols. In: A.C. Scott (Editor), Coal and Coal-bearing Strata: Recent Advances. Geol. Soc. Spec. Publ., 32: 201–218.

Galtier, J. and Phillips, T.L., 1985. Swamp vegetation from Grand Croix (Stephanian) and Autun (Autunian), France, and comparisons with coal-ball peats of the Illinois Basin. Proc. 9th Int. Congr. on Carboniferous Stratigraphy and Geology, 4: 13–24.

Gastaldo, R.A., 1986a. Implications on the paleoecology of autochthonous lycopods in clastic sedimentary environments of the Early Pennsylvanian of Alabama. Palaeogeogr., Palaeoclimatol., Palaeoecol., 53: 191–212.

Gastaldo, R.A., 1986b. An explanation for lycopod configuration, "Fossil Grove" Victoria Park, Glasgow. Scott. J. Geol., 22: 77–83.

Gastaldo, R.A., 1987. Confirmation of Carboniferous clastic swamp communities. Nature, 326: 869–871.

Gastaldo, R.A., Demko, T.M. and Liu, Yuejin, 1991. A mechanism to explain persistent alternation of clastic and

peat-accumulating swamps in Carboniferous sequences. Bull. Soc. Géol. Fr., 162: 299–305.

Gibson, L.B., 1961. Palynology and paleoecology of the Iron Post Coal (Pennsylvanian) of Oklahoma. Ph.D. Thesis, Univ. Oklahoma, Norman, OK, 238 pp.

Good, C.W., 1971. The ontogeny of Carboniferous articulates: calamite leaves and twigs. Palaeontographica, B, 133: 137–158.

Good, C.W., 1975. Pennsylvanian-age calamitean cones, elater-bearing spores, and associated vegetative organs. Palaeontographica, B, 153: 28–99.

Good, C.W., 1976. The anatomy and three-dimensional morphology of *Annularia hoskinsii* sp. n. Am. J. Bot., 63: 719–725.

Good, C.W., 1977. Taxonomic and stratigraphic significance of the dispersed spore genus *Calamospora*. In: R.C. Romans (Editor), Geobotany. Plenum, New York, NY, pp. 43–64.

Good, C.W. and Taylor, T.N., 1975. The morphology and systematic position of calamitean elater-bearing spores. Geosci. Man, 6: 133–139.

Gore, A.J.P. (Editor), 1983. Ecosystems of the World. 4A. Mires: Swamp, Bog, Fen and Moor. Elsevier, Amsterdam.

Gould, R.E. and Delevoryas, T., 1977. The biology of *Glossopteris*: evidence from the petrified seed-bearing and pollen-bearing organs. Alcheringa, 1: 387–399.

Grady, W.C. and Eble, C.F., 1990. Relationships among macerals, minerals, miospores and paleoecology in a column of Redstone Coal (Upper Pennsylvanian) from north-central West Virginia (U.S.A.). Int. J. Coal Geol., 15: 1–26.

Grady, W.C., Fedorko, N., and Eble, C.F. 1992. Palaeoecology and palaeoenvironments of peat formation in the Pittsburgh coal bed, northern Appalachian Basin, U.S.A. Abstr. Geol. Assoc. Can., 1992 Annu, Meet., 17: AY2.

Grebe, H., 1966. Die Sporen flora der Flöze Ägir, Erda und Hagen 2 (ZB) aus den Bohrungen Prosper 4 und 5. Fortschr. Geol. Rheinld. Westf., 13: 705–730.

Guennel, G.K., 1952. Fossil spores of the Alleghenian coals in Indiana. Ind. Geol. Surv. Rep. Prog., 4, 40 pp.

Habib, D., 1968. Spore and pollen paleoecology of the Redstone coal (Upper Pennsylvanian) in West Virginia. Micropaleontology, 14: 199–220.

Hacquebard, P.A. and Donaldson, J.R., 1969. Carboniferous coal deposition associated with flood-plain and limnic environments in Nova Scotia. Geol. Soc. Am. Spec. Pap., 114: 143–191.

Hamar, J.J. and Rothwell, G.W., 1988. The vegetative structure of *Medullosa endocentrica* (Pteridospermopsida). Can. J. Bot., 66: 375–387.

Harvey, R.D. and Dillon, J.W., 1985. Maceral distributions in Illinois coals and their paleoenvironmental implications. Int. J. Coal Geol., 5: 141–165.

Helfrich, C.T. and Hower, J.C., 1989. Palynologic and petrographic variation in the Otter Creek coal beds (Stephanian, Upper Carboniferous), western Kentucky. Rev. Palaeobot. Palynol., 60: 179–189.

Helfrich, C.T. and Hower, J.C., 1991. Palynologic and petrographic variation in the Pond Creek coal bed, Pike County, Kentucky. Org. Geochem., 17: 153–159.

Hirmer, M., 1927. Handbuch der Paläobotanik. Oldenburg, Berlin, 708 pp.

Jennings, J.R., 1986. A review of some fossil plant compressions associated with the Mississippian and Pennsylvanian coal deposits in the central Appalachians, Illinois Basin, and elsewhere in the United States. Int. J. Coal Geol., 6: 303–325.

Johnson, P.R., 1979. Petrology and environments of deposition of the Herrin (No. 6) Coal Member, Carbondale Formation, at Old Ben Coal Company Mine No. 24, Franklin County, Illinois. Thesis. Univ. Illinois, Urbana-Champaign.

Josten, K.H., 1983. Die fossilen Floren im Namur des Rhurkarbons. Fortschr. Geol. Rheinld. Westf., 31: 1–327.

Kalkreuth, W.D., Marchioni, D.L., Calder, J.H., Lamberson, M.N., Naylor, R.D. and Paul, J., 1991. ·The relationship between coal petrography and depositional environments from selected coal basins in Canada. Int. J. Coal Geol., 19: 21–76.

Kosanke, R.M., 1988. Palynological studies of Middle Pennsylvanian coal beds of the proposed Pennsylvanian System Stratotype in West Virginia. U.S. Geol. Surv. Prof. Pap., 1455: 1–73.

Lamberson, M.N., Bustin, R.M. and Kalkreuth, W., 1991. Lithotype (maceral) composition and variation as correlated with paleo-wetland environments, Gates Formation, northeastern British Columbia, Canada. Int. J. Coal Geol., 18: 87–124.

Lamboy, W. and Lesnikowska, A., 1988. Some statistical methods useful in the analysis of plant paleoecological data. Palaios, 3: 86–94.

Leary, R.L. and Mickle, J.E., 1989. *Porostrobus nathorstii* sp. nov.: a new species of lycopsid cone from the Early Pennsylvanian of Illinois. Am. J. Bot., 76: 1638–1645.

Leisman, G.A., 1960. The morphology and anatomy of *Callipteridium sullivantii*. Am. J. Bot., 47: 281–287.

Leisman, G.A., 1970. A petrified *Sporangiostrobus* from the Middle Pennsylvanian of Kansas. Palaeontographica, B, 129: 166–177.

Lesnikowska, A.D., 1984. Two *Lepidodendron* coal-swamps in the Desmoinesean (Westphalian D) of the Illinois Basin. In: 2nd Int. Org. Paleobotany Conf., Edmonton, Alta., Abstr., p. 23.

Lesnikowska, A.D., 1989. Anatomically preserved Marattiales from coal swamps of the Desmoinesian and Missourian of the midcontinent United States: systematics, ecology, and evolution. Thesis. Univ. Illinois, Urbana-Champaign, 227 pp.

Lorenzo, P., 1979. Les sporophylles de *Lepidodendron dissitum* Sauver, 1848. Geobios, 12: 137–143.

Lyons, P.C., Hatcher, P.G., Brown, F.W., Thompson, C.L. and Millay, M.A., 1985. Coalification of organic matter in a coal ball from the Calhoun coal bed (Upper Pennsylvanian), Illinois Basin, United States of America. Proc. 10th Int. Congr. on Carboniferous Stratigraphy and Geology, 1: 155–159.

Mahaffy, J.F., 1985. Profile patterns of coal and peat palynology in the Herrin (No. 6) Coal Member, Carbondale Formation, Middle Pennsylvanian of southern Illinois. Proc. 9th Int. Congr. on Carboniferous Stratigraphy and Geology, 5: 25–34.

Mahaffy, J.F., 1988. Vegetational history of the Springfield coal (Middle Pennsylvanian of Illinois) and the distribution of the tree fern miospore, *Thymospora pseudothiessenii*, based on miospore profiles. Int. J. Coal Geol., 10: 239–260.

Mamay, S.H. and Yochelson, E.L., 1962. Occurrence and significance of marine animal remains in American coal balls. U.S. Geol. Surv. Prof. Pap., 354-I: 193–224.

McLaughlin, R.E., Phillips, T.L. and DiMichele, W.A., 1985. Middle Pennsylvanian coal-swamp vegetation in northeastern Tennessee. Geol. Soc. Am., Southeast. Sect., Abstr. Progr., 17: 124.

Mickle, J.E., 1984. Taxonomy of specimens of the Pennsylvanian age Marattialean fern *Psaronius* from Ohio and Illinois. Ill. State Mus. Sci. Pap., 19, 64 pp.

Mickle, J.E. and Rothwell, G.W., 1982. Permineralized *Alethopteris* from the Upper Pennsylvanian of Ohio and Illinois. J. Paleontol., 56: 392–402.

Millay, M.A., 1979. Studies of Paleozoic marattialeans: a monograph of the American species of *Scolecopteris*. Palaeontographica, B, 168: 1–69.

Millay, M.A. and Taylor, T.N., 1974. Morphological studies of Paleozoic saccate pollen. Palaeontographica, B, 147: 75–99.

Moore, P.D., 1987. Ecological and hydrological aspects of peat formation. In: A.C. Scott (Editor), Coal and Coal-bearing Strata: Recent Advances. Geol. Soc. Spec. Publ., 32: 7–15.

Morgan, J., 1959. The morphology and anatomy of American species of the genus *Psaronius*. Ill. Biol. Monogr., 27, 108 pp.

Němejc, F., 1931. A study on the systematical position of the fructification called *Sporangiostrobus* Bode. Bull. Int. Acad. Sci. Bohême, 1931: 1–13.

Neves, R., 1958. Upper Carboniferous plant spore assemblages from the *Gastrioceras subcrenatum* horizon, North Staffordshire, Geol. Mag., 95(1): 1–19.

Oestry-Stidd, L.L., 1979. Anatomically preserved *Neuropteris rarinervis* from American coal balls. J. Paleontol., 53: 37–43.

Pearson, H.L., 1986. Structure and taxonomy of the Carboniferous lycopsid *Anabathra*. Bull. Br. Mus. Nat. Hist., Geol., 40: 265–292.

Peppers, R.A., 1964. Spores in strata of Late Pennsylvanian cyclothems in the Illinois Basin. Ill. State Geol. Surv. Bull., 90: 1–89.

Peppers, R.A., 1970. Correlation and palynology of coals in the Carbondale and Spoon Formations (Pennsylvanian) of the northeastern part of the Illinois Basin. Ill. State Geol. Surv. Bull. 93, 173 pp.

Peppers, R.A., 1979. Development of coal-forming floras during the early part of the Pennsylvanian in the Illinois basin. Guideb. Fieldtrip 9th Int. Congr. on Carboniferous Stratigraphy and Geology, 9: 8–14.

Peppers, R.A., 1982. Palynology of the unnamed coal in the Staunton Formation, Maple Grove Mine. Ind. Spec. Rep., 30: 27–33.

Peppers, R.A. and Pfefferkorn, H.W., 1970. A comparison of the floras of the Colchester (No. 2) Coal and Francis Creek Shale. In: W.H. Smith et al. (Editors), Depositional Environments in Parts of the Carbondale Formation—Western and Northern Illinois. Ill. State Geol. Surv. Guideb. Ser., 8: 61–74.

Perkins, T.W., 1976. Textures and conditions of formation of coals balls of Middle Pennsylvanian age. Univ. Kans. Paleontol. Contrib., 82, 13 pp.

Pfefferkorn, H.W., 1976. Pennsylvanian tree fern compressions

Caulopteris, *Megaphyton*, and *Artisophyton* gen. nov. in Illinois. Ill. State Geol. Surv. Circ., 492, 31 pp.

Pfefferkorn, H.W. and Thomson, M., 1982. Changes in dominance patterns in Upper Carboniferous plant-fossil assemblages. Geology, 10: 641–644.

Pfefferkorn, H.W., Gillespie, W.H., Resnick, D.A. and Scheihing, M.H., 1984. Reconstruction and architecture of medullosan pteridosperms (Pennsylvanian). Mosasaur, 2: 1–8.

Phillips, T.L., 1974. Evolution of vegetative morphology in coenopterid ferns. Ann. Mo. Bot. Gard., 61: 427–461.

Phillips, T.L., 1979. Reproduction of heterosporous arborescent lycopods in the Mississippian–Pennsylvanian of Euramerica. Rev. Palaeobot. Palynol., 27: 239–289.

Phillips, T.L., 1980. Stratigraphic and geographic occurrences of permineralized coal-swamp plants—Upper Carboniferous of North America and Europe. In: D.L. Dilcher and T.N. Taylor (Editors), Biostratigraphy of Fossil Plants. Dowden, Hutchinson and Ross, Stroudsburg, PA, pp. 25–92.

Phillips, T.L., 1981. Stratigraphic occurrences and vegetational patterns of Pennsylvanian pteridosperms in Euramerican coal swamps. Rev. Palaeobot. Palynol., 32: 5–26.

Phillips, T.L. and Chesnut, D.R., 1980. Coal balls in lower Middle Pennsylvanian strata of Eastern Kentucky: occurrences and peat compositions. Geol. Soc. Am. Abstr. Progr., 12: 498.

Phillips, T.L. and DiMichele, W.A., 1981. Paleoecology of Middle Pennsylvanian age coal swamps in southern Illinois—Herrin Coal Member at Sahara Mine No. 6. In: K.J. Niklas (Editor), Paleobotany, Paleoecology, and Evolution. Praeger Press, New York, NY, 1, pp. 231–284.

Phillips, T.L. and DiMichele, W.A., 1990. From plants to coal: peat taphonomy of Upper Carboniferous coals. Int. J. Coal Geol., 16: 151–156.

Phillips, T.L. and DiMichele, W.A., 1992. Comparative ecology and life-history biology of arborescent lycopsids in Late Carboniferous swamps of Euramerica. Ann. Mo. Bot. Gard., 79: 560–588.

Phillips, T.L. and Peppers, R.A., 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climate control on coal occurrence. Int. J. Coal Geol., 3: 205–255.

Phillips, T.L., Peppers, R.A., Avcin, M.J. and Laughnan, P.F., 1974. Fossil plants and coal: patterns of change in Pennsylvanian coal swamps of the Illinois Basin. Science, 184: 1367–1369.

Phillips, T.L., Kunz, A.B. and Mickish, D.J., 1977. Paleobotany of permineralized peat (coal balls) from the Herrin (No. 6) Coal Member of the Illinois Basin. In: P.H. Given and A.D. Cohen (Editors), Interdisciplinary Studies of Peat and Coal Origins. Geol. Soc. Am. Microform Publ., 7: 18–49.

Phillips, T.L., Peppers, R.A. and DiMichele, W.A., 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. Int. J. Coal Geol., 5: 43–109.

Piérart, R. 1968. Les associations de microspores et de mégaspores dans une couche (couche 70 de Beeringen) du Westphalien A supérieur de la Campine (Belgique). Rev. Palaeobot. Palynol., 7: 275–283.

Pierce, B.S., Stanton, R.W. and Eble, C.F., 1991. Facies

development in the Lower Freeport coal bed, west-central Pennsylvania, U.S.A. Int. J. Coal Geol., 18: 17–43.

Pigg, K.B. and Rothwell, G.W., 1983. *Chaloneria* gen. nov.: heterosporous lycophytes from the Pennsylvanian of North America. Bot. Gaz., 144: 132–147.

Pryor, J.S., 1988. Sampling methods for quantitative analysis of coal-ball plants. Palaeogeogr., Palaeoclimatol., Palaeoecol., 63: 313–326.

Pryor, J.S., 1990. Delimiting species among permineralized medullosan pteridosperms: a plant bearing *Alethopteris* from the Upper Pennsylvanian of the Appalachian Basin. Can. J. Bot., 68: 184–192.

Ravn, R.L., 1979. An introduction to the stratigraphic palynology of the Cherokee Group (Pennsylvanian) coals of Iowa. Iowa Geol. Surv. Tech. Pap., 6, 117 pp.

Ravn, R.L., 1986. Palynostratigraphy of the Lower and Middle Pennsylvanian coals of Iowa. Iowa Geol. Surv. Tech. Pap., 7, 245 pp.

Ravn, R.L., Butterworth, M.A., Phillips, T.L. and Peppers, R.A., 1986. Pollen Spores, 28: 421–434.

Raymond, A., 1987. Interpreting ancient swamp communities: can we see the forest in the peat? Rev. Palaeobot. Palynol., 52: 217–231.

Raymond, A., 1988. The paleoecology of a coal-ball deposit from the Middle Pennsylvanian of Iowa dominated by cordaitalean gymnosperms. Rev. Palaeobot. Palynol., 53: 233–250.

Raymond, A. and Phillips, T.L., 1983. Evidence for an Upper Carboniferous mangrove community. In: H.J. Teas (Editor), Tasks for Vegetation Science, Vol. 8, pp. 19–30.

Reihman, M.A. and Schabilion, J.T., 1976. Two species of *Alethopteris* from Iowa coal balls. Proc. Iowa Acad. Sci., 83: 10–19.

Reihman, M.A. and Schabilion, J.T., 1978. Petrified neuropterid foliage from a Middle Pennsylvanian coal ball. Am. J. Bot., 65: 834–844.

Reihman, M.A. and Schabilion, J.T., 1985. Stomatal structure of *Alethopteris sullivantii* and *Neuropteris scheuchzeri*, Pennsylvanian pteridosperm foliage. Am. J. Bot., 72: 1392–1396.

Remy, W. and Remy, R., 1975. *Sporangiostrobus puertollanensis* n. sp. und *Puertollania sporangiostrobifera* n. gen., n. sp., aus dem Stefan von Puertollano, Spanien. Arg. Paleobot., 4: 13–29.

Rothwell, G.W., 1981. The Callistophytales (Pteridospermopsida): reproductively sophisticated gymnosperms. Rev. Palaeobot. Palynol., 32: 103–121.

Rothwell, G.W., 1988. Upper Pennsylvanian Steubenville coal-ball flora. Ohio J. Sci., 88: 61–65.

Rothwell, G.W., 1991. *Botryopteris forensis* (Botryopteridaceae), a trunk epiphyte of the tree fern *Psaronius*. Am. J. Bot., 78: 782–788.

Rothwell, G.W. and Pryor, J.S., 1991. Developmental dynamics of arborescent lycophytes—apical and lateral growth in *Stigmaria ficoides*. Am. J. Bot., 78: 1740–1745.

Rothwell, G.W. and Warner, S., 1984. *Cordaixylon dumusum* n. sp. (Cordaitales). I. Vegetative structures. Bot. Gaz., 145: 275–291.

Schabilion, J.T. and Reihman, M.A., 1985. Anatomy of petrified *Neuropteris scheuchzeri* pinnules from the Middle

Pennsylvanian of Iowa: a paleoecological interpretation. Proc. 9th Int. Congr. on Carboniferous Stratigraphy and Geology, 5: 3–12.

Scheckler, S.E., 1986. Floras of the Devonian–Mississippian transition. In: R.A. Gastaldo (Organizer), Land Plants, Notes for a Short Course. Univ. Tenn. Dep. Geol. Sci., Stud. Geol., 15: 81–96.

Schlesinger, W.H., 1978. Community structure, dynamics and nurtient cycling in the Okefenokee cypress swamp forest. Ecol. Monogr., 48: 43–65.

Schopf, J.M., 1941. Contributions to Pennsylvanian paleobotany: *Mazocarpon oedipternum*, sp. nov. and sigillarian relationships. Ill. State Geol. Surv. Rep. Invest., 75, 53 pp.

Scott, A.C., 1977. A review of the ecology of Upper Carboniferous plant assemblages with new data from Strathclyde. Palaeontology, 20: 447–473.

Scott, A.C., 1978. Sedimentological and ecological control of Westphalian B plant assemblages from west Yorkshire. Proc. Yorks. Geol. Soc., 41: 461–508.

Scott, A.C., 1989. Observations on the nature and origin of fusain. Int. J. Coal Geol., 12: 443–475.

Scott, A.C. and Jones, T.P., 1994. The nature and influence of fire in Carboniferous ecosystems. In: J.H. Calder and M.R. Gibling (Editors), The Euramerican Coal Province: Controls on Tropical Peat Accumulation in the Late Paleozoic. Palaeogeogr., Palaeoclimatol., Palaeoecol., 106: 91–112.

Scott, A.C. and King, G.R., 1981. Megaspores and coal facies: an example from the Westphalian A of Leicestershire, England. Rev. Palaeobot. Palynol., 34: 107–113.

Scott, A.C. and Rex, G., 1985. The formation and significance of Carboniferous coal balls. Philos. Trans. R. Soc. London, 311B: 123–137.

Scott, A.C. and Taylor, T.N., 1983. Plant/animal interactions during the Upper Carboniferous. Bot. Rev., 49: 259–307.

Smith, A.V.H., 1957. The sequence of microspore assemblages associated with the occurrence of crassidurite in coal seams of Yorkshire. Geol. Mag., 94: 345–363.

Smith, A.V.H., 1962. The paleoecology of Carboniferous peats based on miospores and petrography of bituminous coals. Proc. Yorks. Geol. Soc., 33: 423–463.

Smith, A.V.H., 1964a. Palaeoecology of Carboniferous peats. In: A.E.M. Nairn (Editor), Problems in Palaeoclimatology. Wiley, London, pp. 57–66.

Smith, A.V.H., 1964b. Zur Petrologie und Palynologie der Kohlenflöze des Karbons und ihrer Begleitschichten. Fortschr. Geol. Rheinld. Westf., 12: 285–302.

Smith, A.V.H., 1968. Seam profiles and seam characters. In: D. Murchison and T.S. Westoll (Editors), Coal and Coal-bearing Strata. Elsevier, New York, NY, pp. 31–40.

Smith, A.V.H. and Butterworth, M., 1967. Miospores in the coal seams of the Carboniferous of Great Britain. Spec. Pap. Palaeontol., 1: 1–324.

Staub, J.R., 1991. Comparisons of central Appalachian Carboniferous coal beds by benches and a raised Holocene peat deposit. Int. J. Coal Geol., 18: 45–69.

Staub, J.R. and Esterle, J.S., 1992. Evidence for a tidally influenced Upper Carboniferous ombrogeneous mire system: upper bench, Beckley bed (Westphalian A), southern West Virginia. J. Sediment. Petrol., 62: 411–428.

Stevens, G.C. and Fox, J.S., 1991. The causes of tree line. Annu. Rev. Ecol. Syst., 22: 177–191.

Stidd, B.M., Oestry, L.L. and Phillips, T.L., 1975. On the frond of *Sutcliffia insignis* var. *tuberculata*. Rev. Palaeobot. Palynol., 20: 55–66.

Stopes, M.C. and Watson, D.M.S., 1909. On the present distribution and origin of the calcareous concretions in coal seams known as "coal balls". Philos. Trans. R. Soc. London, 200B: 167–218.

Stschegolev, A.K., 1975. Die Entwicklung der Pflanzenbedeckung im Süden des Europäischen Tiels der UdSSR, vom Ende des Mittelkarbons bis zum Perm. Umfang und Gliederung des oberen Karbons (Stefan). Proc. 7th Int. Congr. on Carboniferous Stratigraphy and Geology, 4: 275–280.

Taylor, T.N., 1965. Paleozoic seed studies: a monograph of the American species of *Pachytesta*. Palaeontographica, B, 117: 1–46.

Taylor, T.N., 1982. Ultrastructural studies of Paleozoic seed-fern pollen: sporoderm development. Rev. Palaeobot. Palynol., 37: 29–53.

Taylor, T.N. and Taylor, E.L., 1987. The ultrastructure of fossil gymnosperm pollen. Bull. Soc. Bot. Fr., 134: 121–140.

Teichmüller, M. 1952. Vergleichende mikroskopische Untersuchungen versteinerter Torfe des Ruhrkarbons und daraus entstandenen Steinkohlen. Proc 3rd Int. Congr. on Carboniferous Stratigraphy and Geology, 2: 607–613.

Teichmüller, M., 1962. Die genese der Kohle. Proc. 4th Int. Congr. on Carboniferous Stratigraphy and Geology, 3: 699–722.

Teichmüller, M., 1989. The genesis of coal from the viewpoint of coal petrology. Int. J. Coal Geol., 12: 1–87.

Thiessen, R., 1920. Structure in Paleozoic bituminous coals. U.S. Bur. Mines Bull., 117: 1–296.

Thiessen, R. and Sprunk, G.C., 1942. Coal paleobotany. U.S. Bur. Mines Tech. Pap., 631: 1–56.

Thomas, B.A., 1967. *Ulodendron*: Lindley and Hutton and its cuticle. Ann. Bot. N.S., 31: 775–782.

Thomas, B.A. and Watson, J., 1976. A rediscovered 114-foot *Lepidodendron* from Bolton, Lancashire. Geol. J., 11: 15–20.

Traverse, A., 1988. Paleopalynology. Unwin Hyman, Boston, MA, 600 pp.

Trivett, M.L., 1992. Growth architecture, structure, and relationships of *Cordaixylon iowensis* nov. comb. (Cordaitales). Int. J. Plant Sci., 153: 273–287.

Trivett, M.L. and Rothwell, G.W., 1985. Morphology, systematics, and paleoecology of Paleozoic fossil plants: *Mesoxylon priapi* sp. nov. (Cordaitales). Syst. Bot., 10: 205–223.

Urban, J.B., 1962. Palynology of the Mineral Coal (Pennsylvanian) of Oklahoma and Kansas. Thesis. Univ. Oklahoma, Norman, 146 pp.

Von Karmasin, K., 1952. Deutung des Fazieswechsel in den Flözen Erda und Ägir auf Grund mikropetrographischer Schlitzprobenuntersuchungen. Bergbau Arch., 13: 74–100.

Wartmann, R., 1969. Studie über die papillen-förmigen Verdickungen auf der Kutikule bei *Cordaites* an material aus

dem Westphal C des Saar-Karbons. Arg. Paleobot., 3: 199–207.

Wagner, R.H., 1989. A late Stephanian forest swamp with *Sporangiostrobus* fossilized by volcanic ash fall in the Puertollano Basin, central Spain. Int. J. Coal Geol., 12: 523–552.

Wagner, R.H. and Spinner, E., 1975. *Bodeodendron*, tronc associé à *Sporangiostrobus*. C. R. Acad. Sci. Paris, Sér. D, 282: 353–356.

Willard, D.A., 1989a. Source plants for Carboniferous microspores: *Lycospora* from permineralized *Lepidostrobus*. Am. J. Bot., 76: 820–827.

Willard, D.A., 1989b. *Lycospora* from Carboniferous *Lepidostrobus* compressions. Am. J. Bot., 76: 1429–1440.

Willard, D.A., 1990. Palynology of the Springfield coal of the Illinois Basin (Middle Pennsylvanian) with quantitative comparison of spore floras and coal-ball peats and implications for paleoecological studies. Thesis. Univ. Illinois, Urbana-Champaign, IL, 133 pp.

Willard, D.A., 1992. Vegetational patterns in the Springfield coal (Middle Pennsylvanian, Illinois Basin): comparison of miospore and coal-ball records. Geol. Soc. Am. Spec. Pap., in press.

Winslow, M.R., 1959. Upper Mississippian and Pennsylvanian megaspores and other plant microfossils from Illinois. Ill. State Geol. Surv. Bull., 86, 135 pp.

Winston, R.B., 1986. Characteristic features and compaction of plant tissues traced from permineralized peat to coal in Pennsylvanian coals (Desmoinesian) from the Illinois Basin. Int. J. Coal Geol., 6: 21–41.

Winston, R.B., 1988. Paleoecology of Middle Pennsylvanian-age peat-swamp plants in Herrin Coal, Kentucky, U.S.A. Int. J. Coal Geol., 10: 203–238.

Winston, R.B., 1989. Identification of plant megafossils in Pennsylvanian-age coal. Rev. Palaeobot. Palynol., 57: 265–276.

Winston, R.B., 1990. Implications of paleobotany of Pennsylvanian-age coal of the central Appalachian basin for climate and coal-bed development. Geol. Soc. Am. Bull., 102: 1720–1726.

Winston, R.B. and Phillips, T.L., 1991. A structurally preserved, Lower Pennsylvanian flora from the New Castle coal bed of Alabama. Geol. Surv. Ala., Circ. 157, 21 pp.

Wnuk, C., 1985. The ontogeny and paleoecology of *Lepidodendron rimosum* and *Lepidodendron bretonense* trees from the Middle Pennsylvanian of the Bernice basin (Sullivan County, Pennsylvania, U.S.A.). Palaeontographica, B, 195: 153–181.

Wnuk, C. and Pfefferkorn, H.W., 1984. Life habits and paleoecology Middle Pennsylvanian medullosan pteridosperms based on an in situ assemblage from the Bernice Basin (Sullivan County, Pennsylvania, U.S.A.). Rev. Palaeobot. Palynol., 41: 329–351.

Wnuk, C. and Pfefferkorn, H.W., 1987. A Pennsylvanian-age terrestrial storm deposit: using plant fossils to characterize the history and process of sediment accumulation. J. Sediment. Petrol., 57: 212–221.