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STRATIGRAPHIC AND INTERREGIONAL CHANGES IN PENNSYLVANIAN COAL-SWAMP VEGETATION: ENVIRONMENTAL INFERENCES

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ABSTRACT

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Quantitative analysis of Pennsylvanian coal-swamp vegetation provides a means of inferring organization and structure of communities. Distribution of these communities further provides inferences about environmental factors, including paleoclimate. Our observations are based on in situ, structurally preserved peat deposits in coal-ball concretions from 32 coal seams in the eastern one-half of the United States and from several seams in western Europe and on spore assemblages from more than 150 seams.

There were three times of particularly significant and nearly synchronous vegetational changes in the Midcontinent and Appalachian coal regions during the Pennsylvanian Period. Each was different in kind and magnitude. The first marked changes occurred during the early part of the Middle Pennsylvanian with the fluctuating decline in the high level of lycopod dominance. The abundance of cordaites increased. There was a rise in the occurrences of the lycopod herbs to form intercalated marshlands and an overall increase in floral diversity. Changes ensuing from this time also include shifts in dominant species of lycopod trees and a sustained rise in abundance and diversity of tree-fern spores. The next significant time of change was during the middle part of the Middle Pennsylvanian, representing both a culmination of earlier trends and expansions of cordaites in the Midcontinent where there was a maximum change in species without net loss of diversity. Tree ferns and medullosan pteridosperms attained subdominant levels of abundance and diverse lycopod species dominated except in the Atokan-Desmoinesian transition of the Midcontinent. The third and sharpest break occurred near the Middle—Late Pennsylvanian boundary when extinctions of the dominant, coal-swamp lycopods allowed development of tree-fern dominance. The Late Pennsylvanian coal swamps apparently were colonized or recolonized mainly by species from outside coal swamps rather than by the survivor populations of the Middle Pennsylvanian swamps.

Paralleling the changes in floras through the Pennsylvanian are changes in preservational aspects of the peat. These include a decline in shoot/root ratios from approximately 1 to <1 during the first time of vegetational change and a rise in this ratio during the second; there was a parallel rise and fall in fusain abundance and a rise in wood/periderm ratios. The stratigraphic distribution of identified coal resources in the United States is

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interpreted as largely dependent on net changes in relative wetness of Pennsylvanian coal swamps, a pattern of drying during the first period of vegetational change, followed by a concomitant increase in continuous wet climate with brackish influence in the Midcontinent during the second; this was followed by a time of extreme moisture stress bringing on the third, and most severe, vegetational change.

INTRODUCTION

The plant ecology of Pennsylvanian tropical coal swamps is reconstructed in part by analyzing forest communities from permineralized peat deposits preserved in situ within coal-ball concretions. Species composition, vegetational structure, and relative dominance (abundance) patterns of species are the community traits in peats that allow us to recognize different and often specific kinds of environments. The growth, habits, and reproductive biology of the plants, primarily the trees, are major bases for reconstructing hypothetical habitats and environments of peat accumulation. Since most of the abundant spores in the coals can be related directly to parent species or genera, ecological information also can be derived from palynology. This is especially important for evaluating interregional similarities in vegetational change through time.

In this paper we outline the patterns of change in coal-swamp vegetation during the Westphalian and early Stephanian of western Europe and during the Pennsylvanian of the Appalachian and Midcontinent regions of the United States. The cumulative data provide a comparative and quantitative reference base that: (1) allow estimation of vegetational composition of coal swamps; (2) an evaluation of ecological interpretations on a geological time scale; and (3) the partial characterization of the major periods, kinds, and causes of vegetational change in coal swamps. It is our intent here to augment what is known of basinal geology with paleoclimatic and paleogeographic inferences, which also have significant bearing on the patterns of distribution of vegetation.

The names Lower (Early), Middle, and Upper (Late) Pennsylvanian are used in this report according to the recommendations of Bradley (1956) and as commonly used by the U.S. Geological Survey. The top of the New River Formation of West Virginia and equivalent strata mark the Lower—Middle Pennsylvanian boundary; the Allegheny—Conemaugh boundary of the northern part of the Appalachian region is equivalent to the Middle—Upper Pennsylvanian boundary.

Three major times of change in coal-swamp vegetation, each of different magnitude, are considered. Each was synchronous, or nearly so, across varying extents of the Euramerican paleotropical belt. The two most conspicuous times of departure from abundant moisture in the lowlands of the Euramerican coal belt began during the early part of the Middle Pennsylvanian (Westphalian B) and near the Middle—Late Pennsylvanian (Westphalian—Stephanian) transition and are referred to as the "first drier" and "second drier" intervals, respectively. At these times there were major changes in coal-swamp vegetation, especially during the early part of the Late Pennsylvanian. The significance of the latter was discussed earlier by comparing palynological and peat data (Peppers and Phillips, 1973; Phillips et al., 1974). The vegetational change during the Late Pennsylvanian, which was by far the most wide-reaching, was also detected in earlier studies of both clastic sediments and coal in the United States (White and Thiessen, 1913; Kosanke, 1947; Schemel, 1957; Winslow, 1959) and in Europe (Davies, 1929; Stschegolev, 1975). White, in particular (White and Thiessen, 1913, pp. 76—77), noted the same pattern apparently from field observations of compression floras, underclays, and coal partings long before extensive data from spore and coal-ball peat studies were available: "The Conemaugh (of lower Stephanian age) time witnessed several changes in the floras which may be of climatic cause. Most prominent among these are a rapid decrease, approaching extinction, of the colossal lycopods (Lepidodendreae), and the rapid development of the group of gigantic tree ferns, such as *Psaronius*, whose supposed fronds, *Pecopteris*, became highly varied, very large, and more or less distinctly villous in most species. The evidence therefore, points to the occurrence of short dry seasons." The absence of stigmarian seat-earths in the Upper Pennsylvanian has been noted many times (Huddle and Patterson, 1961). Similar observations by Feys (1964, p. 67) in the Stephanian of the Massif Central were attributed to the limnic nature of the basins in France.

A much more subtle series of vegetational changes occurred during the "first drier interval" than during the Middle to Late Pennsylvanian transition. These were documented first palynologically in the Illinois Basin Coal Field by Peppers (1979), subsequently compared with northeastern Tennessee (Phillips and Peppers, 1984) and now with eastern Kentucky by means of spore floras and peat. The drier intervals may be interpreted as two progressively-more-severe, pulse-like changes that most significantly altered the tropical coal-swamp vegetation of the Pennsylvanian. The Early Permian may be regarded as the beginning of the third and driest interval, essentially terminating the age of Euramerican coal swamps. Essential to our inference of "drier intervals" in the Pennsylvanian are interregional similarities of ensuing changes in the coal-swamp vegetation patterns that suggest widespread, nearly contemporaneous kinds of events.

The changes in coal-swamp vegetation between the "first" and "second drier intervals", in the middle part of the Middle Pennsylvanian, have been difficult to compare between the Appalachian region and the Midcontinent because of the dearth of permineralized peat deposits in coal balls in the Appalachian region. Differences in regional dominance patterns occurred during this time. This is due probably in part to regional geological controls that may overshadow the role of paleoclimate during this wet interval.

SOURCES OF DATA AND VARIABLE FACTORS IN RELATION TO METHODS

Information from in situ peat in coal-ball concretions is derived from 32 bituminous coal seams in the eastern one-half of the United States (Fig. 1) and from coals of Europe (Fig. 2). These provide a basis for the quantitative analyses of coal-swamp vegetation. Localities and pertinent geological information are given on the maps and in the text or can be found in the compilation by Phillips (1980). Determinations of major bituminous coal deposits in the Pennsylvanian System of the United States (Fig. 1) are based on identified bituminous coal resources compiled from reports by state geological surveys by Phillips et al. (1980).

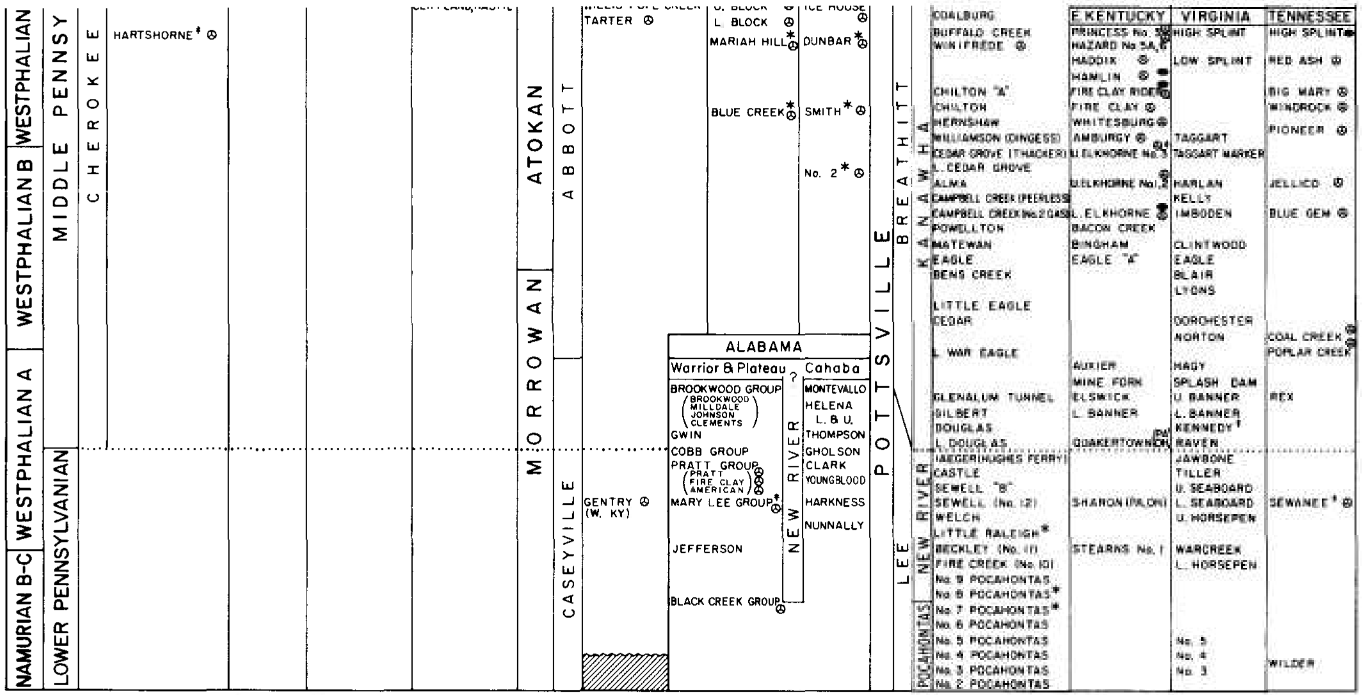
The quantitative data in the United States are derived mostly from the Paleobotanical Collections of the Department of Plant Biology, University of Illinois at Urbana. The collections from the Shuler and Urbandale Mines of Iowa were loaned by the Biological Laboratories of Harvard University; coal-ball peels were made available for the Weldon Mine of Iowa by the Department of Botany, University of Iowa, for the "High Splint Coal" of Tennessee by the Department of Geological Sciences, University of Tennessee, and for the coal above the Middle Kittanning of Pennsylvania by the Department of Geology, Michigan State University.

The data from western Europe were obtained from coal-ball peels from collections of the British Museum of Natural History (London) and University of Montpellier (coal balls from the Union Seam of Lancashire, England) and from the University of Liege (coal balls from the Bouxharmont Seam of Belgium). Slide collections utilized for quantitative analyses include the following: the Kidston Collection, Hunterian Museum at Glasgow, and the Scott and Oliver Collections, Palaeontology Department, British Museum (N.H.) (coal balls from the Upper Foot Seam at Shore-Littleborought); the Felix Collection, Humboldt-Universität zu Berlin, D.D.R. (coal balls from the Katharina Seam at Langendreer, Ruhr Coal Basin of North-Rhine Westphalia).

Spore analyses from more than 150 coals (Figs. 1, 4) in the eastern United States provide information on sequential coal-swamp floras including coals from which coal balls are not available. Coal samples were, in part, provided by the state geological surveys of Oklahoma, Kansas and Kentucky. Spore data from coals outside the Illinois Basin Coal Field are based usually on one channel sample from each coal. Slide preparations and residues are housed in the Coal Section, Illinois State Geological Survey at Urbana.

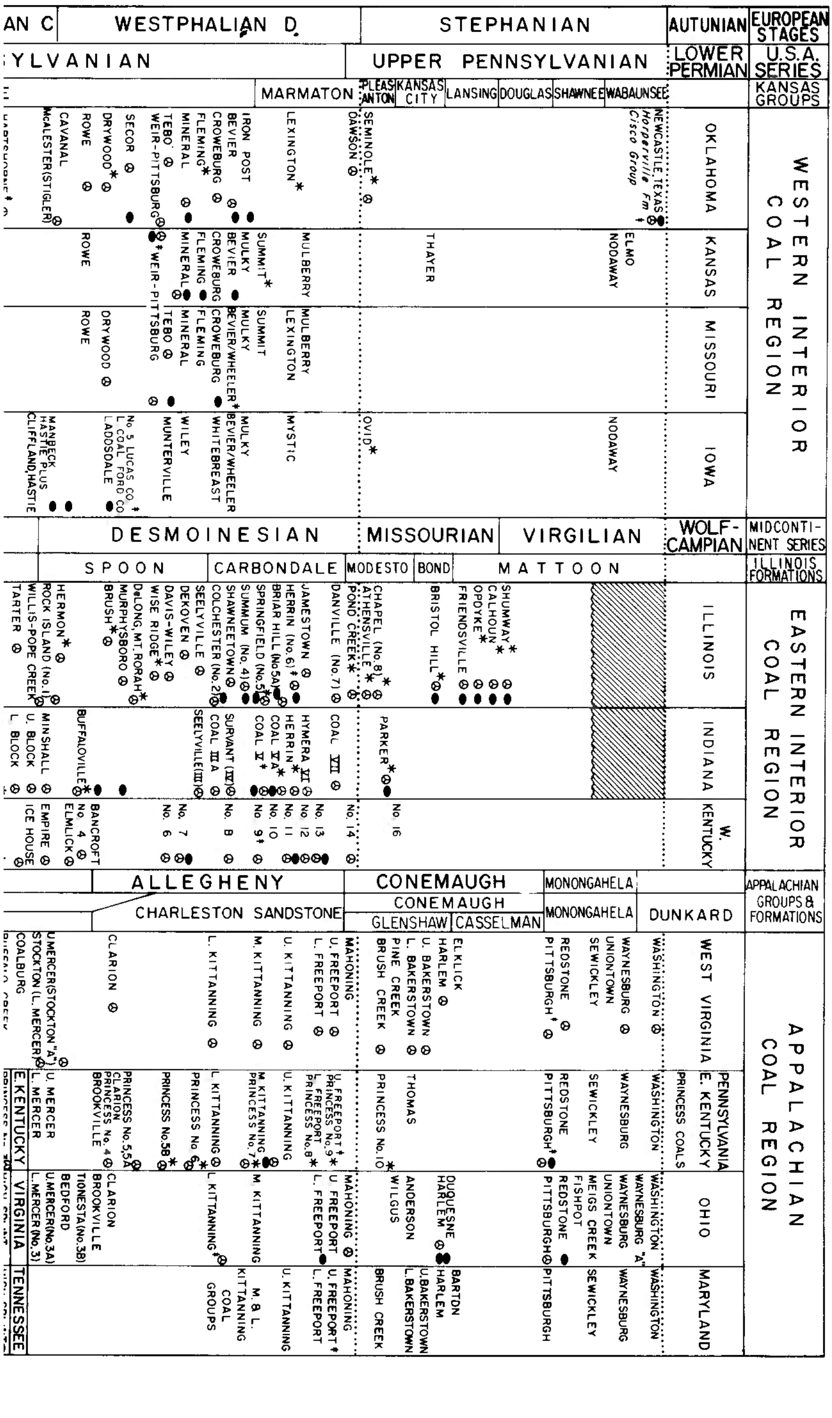
Techniques of analysis

The techniques for study and vegetational analysis of peat deposits are those given by Phillips et al. (1976, 1977) and by Phillips and DiMichele (1981). The coal-ball peats provide means of establishing whole plant assemblages including the plant sources of dispersed spores. Community analyses



1 Coals and approximate equivalents with totals of >100 million short tons (original or remaining identified resources)
* Coals and beds listed for stratigraphic references only
† Major coal resource for the state or region of state
● Occurrences of coal balls with reported or known vegetation
⊕ Palynological studies of spore floras of coal

Fig. 1. Stratigraphic distribution and approximate correlations of selected bituminous coals in the Pennsylvanian System of the United States with indications of those from which peat data and/or spore floras are derived. Dotted lines indicate boundaries of Lower and Middle Pennsylvanian and Desmoinesian—Missourian (Westphalian—Stephanian).



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DOUGLAS
SHAWNEE
WABAUNSEE
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MISSOURIAN
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WOLFCAMPIAN
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MATTOON
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CONEMAUGH
MONONGAHELA
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CASSELMAN
DUNKARD
APPALACHIAN GROUPS & FORMATIONS
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PENNSYLVANIA
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VIRGINIA
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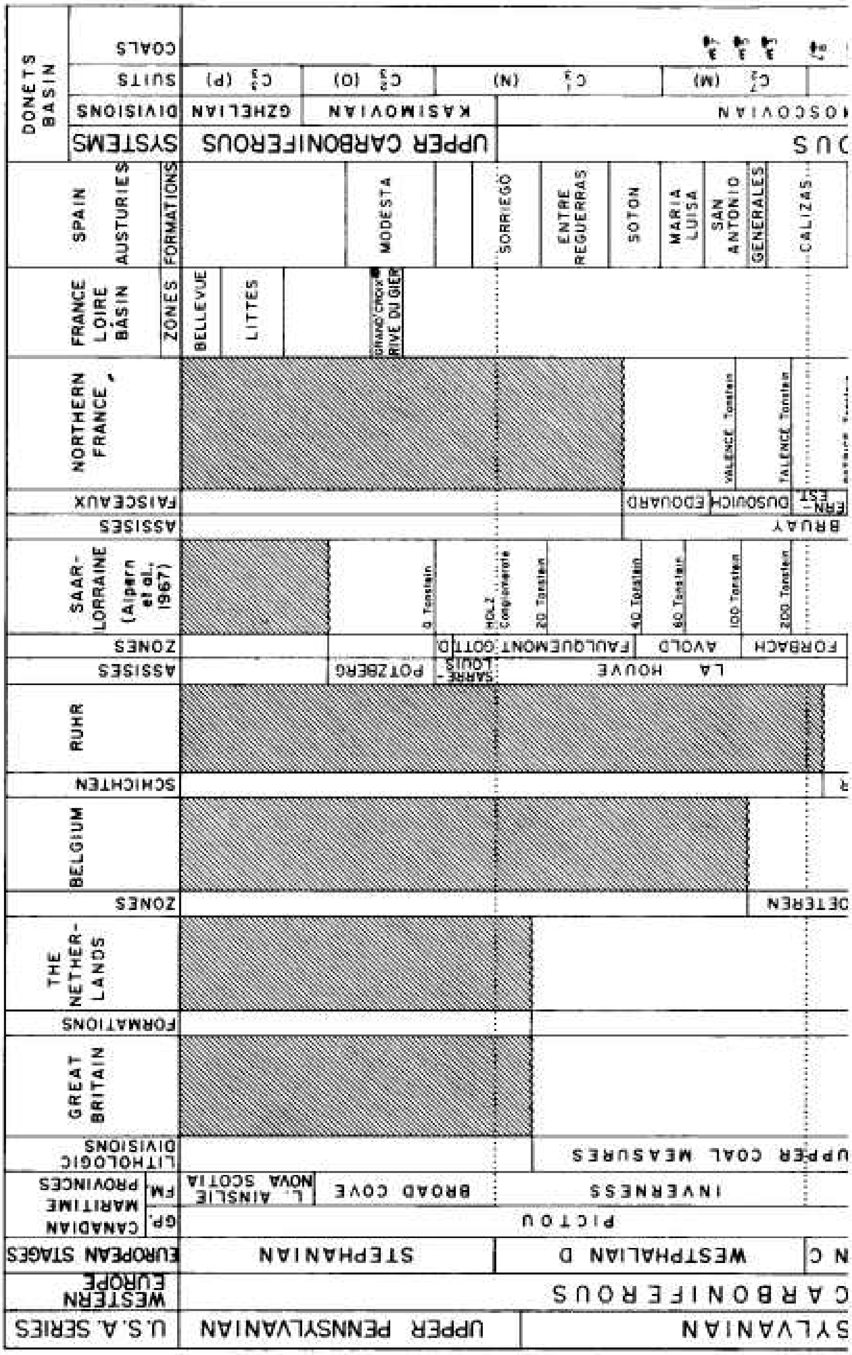
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GRAND'CROIX
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NORTHERN FRANCE
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ASSISES
EDOUARD
DUSOUICH
BRUAY
VALENCE Tonstein
SAAR-LORRAINE (Alpern et al., 1967)
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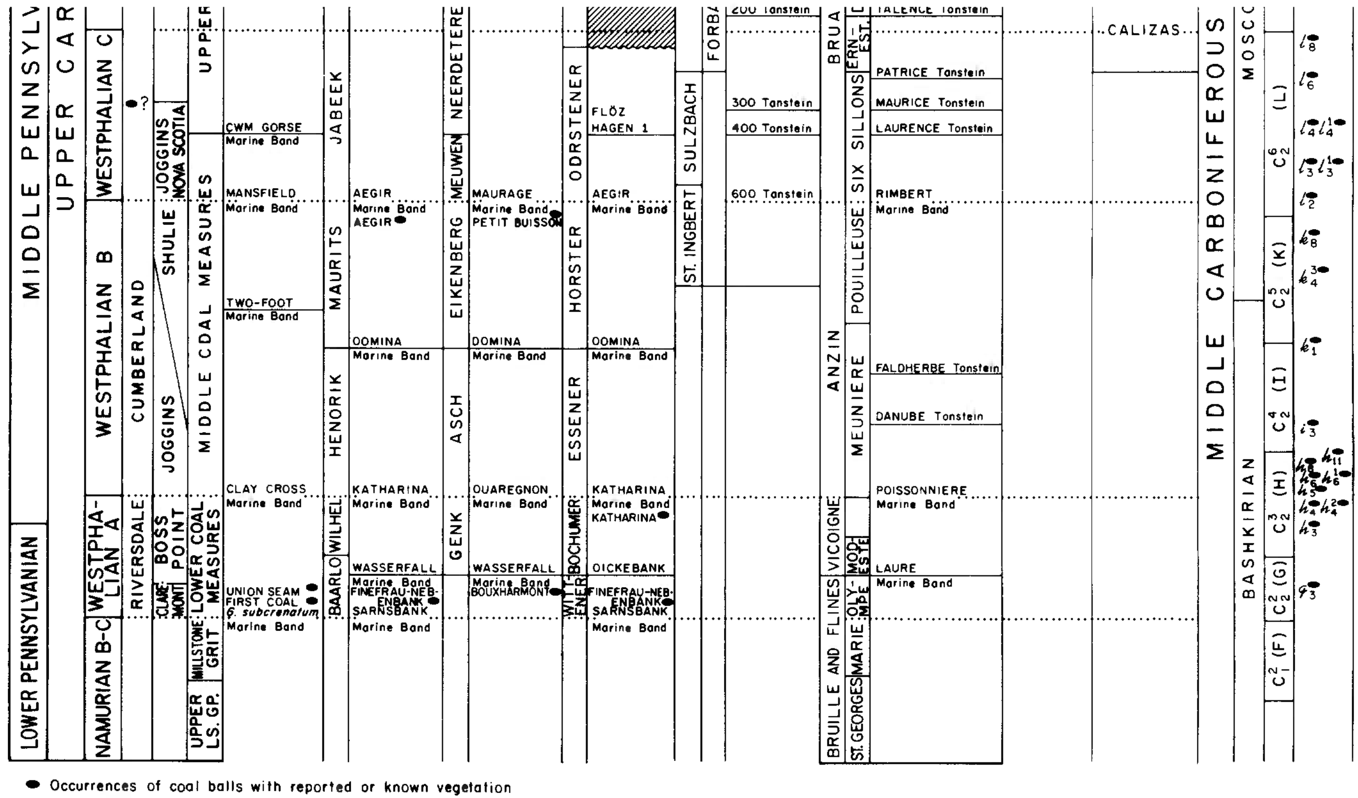


Fig. 2. Stratigraphic correlations of Upper Carboniferous strata in Canada and Europe with coal-ball occurrences compiled by Phillips (1980). Dotted lines indicate boundaries of Westphalian and Stephanian Stages.

determine dominance patterns, community structure and, in relation to evidence from many environmental indicators, relative ecological amplitudes (Phillips and Peppers, 1984) for dominant trees. The major factors that appear to have controlled plant distribution in coal swamps were relative wetness, brackish influences and nutrients.

One of the most significant limitations to community analysis, besides the difficulty of identifying dismembered plant parts, is reflected in the shoot/root ratio of peat. In many of the Lower and Middle Pennsylvanian coal swamps, lycopod trees form 60—95% of the peat biomass. It is estimated that 20—30% of their original biomass was root system and 70—80% was aerial plant parts or shoot systems. If a whole tree were preserved as peat, it would result in a shoot/root biomass of about 4/1. The amount of aerial plant material is critical for community analyses that may be based solely on that. Shoot/root ratios of peats are commonly close to 1/1 indicating enormous loss of aerial plant material, which greatly reduces the accuracy of reconstructing standing vegetation from peat deposits preserved in coal balls and may significantly alter peat-spore relationships since spores are more likely to be preserved. However, most of the community analyses are carried out for coal seams with high shoot/root ratios, such as the Springfield (No. 5) and Herrin (No. 6) Coal Members of the Illinois Basin Coal Field (Fig. 1). Shoot/root ratios reported below were derived from large random coal-ball samples or profiles of the permineralized peat.

Quantitative relationships of spore floras and peat deposits

The relative numerical abundance of palynomorphs (homospores, microspores, prepollen and pollen less than about 210 μm in diameter) from channel samples of coal is the main means of estimating regional, interregional and stratigraphic patterns of coal-swamp vegetation. Coal-ball assemblages are a base of reference for these palynological data and provide the most direct evidence of the vegetation and of the botanical constituents of the coals. Both kinds of data, which have different kinds and degrees of resolution, are amenable to making estimates of the vegetation and environments. Each data set provides a basis to evaluate the other and together they provide a much better resolution of the geologic times and kinds of botanical change. Coal-ball peat deposits from a given locality may not be generally representative of the broader composition of the vegetation. In some cases this can be explained by taking into account the paleogeography and environments of deposition, which are important in the interpretation of regional gradients in the vegetation. In other cases we have to rely on data from the spore assemblages for the regional picture. Conversely, the dispersal of spores into coal swamps from surrounding vegetation, particularly acute in those swamps with large perimeter to small areas, may drastically bias estimates of vegetation without comparative data from peat deposits. Both sources of data have preservational biases that need not be presented here, but are nevertheless important and noted elsewhere. The extensive use of coal-spore floras is predicated on the premise that there are relative, predictable relationships (including biases) between the dominant components of spore assemblages and those of peat deposits. Such quantitative relationships need to be outlined briefly in order to emphasize their particular utility and their differences among the main kinds of trees.

Reproductive biology in relation to estimates of vegetation

Quantitative estimates of biomass based on miospores and peat may vary significantly because the dominant trees had different reproductive biologies. There are sharp contrasts in resolution levels between the lower vascular plants, which dominated the coal swamps, and the gymnosperms, which were generally subdominant. Habits and habitats are also closely linked with the differences in reproduction. With the exception of calamitean (sphenopsid) trees, which are omitted here, the principal trees reproduced only sexually.

Lower vascular plants. Psaronius tree ferns and the dominant *Lycospora*-producing lycopods (*Lepidophloios*, true *Lepidodendron* and *Paralycopodites*) can be ranked as the first and second, respectively, in so-called over representation in almost any spore flora. The tree ferns were homosporous and produced small spores that were dispersed broadly by wind and water; palynology samples this output. All the lycopod trees were heterosporous; the *Lycospora* producers released large numbers of moderately small, wind and water-borne microspores. Palynomorph studies measure only the microspore fraction from the lycopods. The large reproductive outputs of the tree ferns and *Lycospora* producers are consistent with extensive geographic dominance of these trees in the Pennsylvanian coal swamps. Palynomorph floras are particularly sensitive to the mutual relative abundances of these two groups and to the regional appearance and extinction of the source plants. The level of resolution is so good that spores from these plants occur in most spore assemblages even if the source plants were growing at some distance from the sample site. It is this representation of regional floras that adds precision to miospore biostratigraphy; at the same time, it may bias an assessment of the local coal-swamp vegetation (Peppers, 1982).

Spore floras provide a clear documentation of the relative importance of *Lepidophloios harcourtii*, *L. hallii* and *Paralycopodites* to the extent that *Lycospora* species can be related to major species of trees. Many patterns determined by palynology have been confirmed from coal-ball peat sources. However, the abundance of *Lycospora granulata* in the upper Pottsville and Allegheny Formations in the Appalachian region may, in part, represent *Lepidodendron hickii*. The abundance of *Lycospora granulata* in the Desmoinesian of the Midcontinent parallels that of the source plant, which is largely *Lepidophloios hallii*. This places in doubt the interpretation of *Lycospora granulata* beyond the peat confirmation range of *Lepidophloios* *hallii*. Some very tenuous ecological evidence suggests that *Lepidodendron hickii* and *Lepidophloios* may both be important sources of *Lycospora granulata* in the Lower Pennsylvanian and in the middle and upper parts of the Middle Pennsylvanian in the Appalachians. The morphology of their spores may not be significantly distinct to allow differentiation when making spore analyses by use of standard light microscope. It is noteworthy that the two fundamentally most similar lycopods in the peat assemblages are *Lepidophloios* and *Lepidodendron hickii*. Where the significantly different leaf cushions are missing or the stelar structure is unpreserved, their tissues are generally indistinguishable.

There are two generically distinct groups currently included in *Lepidodendron*. In this paper we refer to one group as "coal-swamp" *Lepidodendron* (*L. vasculare*, *L. scleroticum*, *L. phillipsii*, *L. dicentricum*) and the other as true *Lepidodendron* (*L. hickii*, *L. serratum*) (DiMichele, 1983). Peat-based studies (Leclercq, 1930) document the importance of coal-swamp *Lepidodendron* species in lower Westphalian A coal swamps from western Europe and also from the Middle Pennsylvanian of the Midcontinent (DiMichele, 1979; Eggert and Phillips, 1982). Nevertheless, the record of *Cappasporites* in the spore flora is almost always less than the relative abundance of the parent plant in the peat. The microspore output was significantly less (based on cone size and number) than that of *Lycospora* producers; *Cappasporites* is typically twice as large in diameter and was commonly dispersed as tetrads. In Europe these microspores have been variously reported as *Granisporites* or *Apiculatisporis* (verified by R. Ravn, Amoco Production Company, pers. commun., 1983).

Gymnosperms. In contrast to the over-representation of tree ferns and *Lycospora*-bearing lycopods in palynomorph assemblages, the two groups of seed plants are possibly under represented (cordaites) or often not represented at all (*Medullosa*). The lack of true representation of *Schopfipollenites* (large prepollen of *Medullosa*) in the spore flora is not a problem in the Lower and lower Middle Pennsylvanian when *Medullosa* was not very abundant in coal swamps. However, in younger coals the absence of such data exaggerates the percentage of the other spores, especially *Lycospora* and tree-fern spores. The study of Winslow (1959) provides substantial information (see Fig. 12) on the abundance of *Schopfipollenites* from *Medullosa* in the Illinois Basin Coal Field. As long as *Medullosa* ranked third or less in the coal swamps and did not significantly change in abundance, this absence of data can be taken into account. However, the importance of *Medullosa* in coal swamps has to be determined directly from the peat. Where we lack such information on peat deposits, it leaves open the possibility that *Medullosa* did attain greater importance than we presently recognize. It was never dominant on a whole-seam basis at any of the sites we have sampled extensively.

The cordaites were the only gymnosperms to dominate any of the Pennsylvanian coal swamps that we have studied, and this occurred in both limnic

(Galtier and Phillips, in press) and paralic coal swamps (Raymond and Phillips, 1983). The disparity in abundance of *Florinites*, the most common pollen of the cordaites, and the actual importance of cordaites in some coal swamps has been noted (Neves, 1958; Peppers, 1982). Most cordaitean-rich (subdominant) coal-swamp floras register small percentages of pollen because, in part, they are usually coupled with *Lycospora*-dominated spore floras. The great abundance of cordaites in some lower Desmoinesian coal swamps may not be as widespread as inferred from coal-ball peats. Preservational factors are also very important in relating peat and spore data as are the preparation techniques for spore analysis.

RESULTS

Information from coal-ball peat and palynomorph studies is presented separately for three stratigraphic intervals, each of which includes one of the major times of vegetational change in the Pennsylvanian. The geographic scope of each interval differs because of the distribution of coal balls and relevant palynomorph data. The intent is to utilize vegetational patterns from the Illinois Basin Coal Field as a basis for interregional comparisons.

The three intervals are the following: Early and early Middle Pennsylvanian, which shows an interregional change in composition of the vegetation at the onset of the "first drier interval"; the middle part of the Middle Pennsylvanian, during which regional differences in dominance patterns become evident; and, the late Middle to Late Pennsylvanian transition, which includes the "second drier interval" — the most conspicuous change in coal-swamp vegetation.

COMPOSITION OF COAL SWAMPS AND EVIDENCE OF INTERREGIONAL CHANGE IN THE EARLY AND EARLY MIDDLE PENNSYLVANIAN

Peat deposits in western Europe — lower Westphalian A and Westphalian A/B boundary

Coal balls of early Westphalian or equivalent age have been found only in Europe. The most abundant of these occur in approximately equivalent seams of the lower Westphalian A and extend from the Lancashire Coal Fields to the Ruhr in what Schopf (1941) called the "Great Coal-ball horizon". In the Ruhr and The Netherlands, the coal is the Finefrau-Nebenbank (Kukuk, 1909; Hirmer, 1928; Koopmans, 1928); in Belgium, it is the Bouxharmont (Leclercq, 1925). In the Lancashire Coal Fields coal balls occur in the Union Seam and in its upper split, the Upper Foot Seam, and the equivalent in Yorkshire, the Halifax Hard Seam (Stopes and Watson, 1909). Studies of the coal-swamp plants from these peat deposits began over a century ago, and the floras are among the best known in the Upper Carboniferous. Quantitative peat data are presented here from the Union Seam and its upper split at Lancashire, and from the Bouxharmont Seam of Belgium.

Many occurrences of coal balls in the slightly younger Katharina Seam of the Ruhr, at the Westphalian A/B boundary, have been reported (Kukuk, 1909). However, only permanent slide collections from the earliest studies (Felix, 1886) were available for quantitative assessments. The Katharina Seam is important in providing evidence of the onset of changes in vegetation that are also indicated by palynomorph studies in the United States (Peppers, 1979).

Early coal-swamp composition and differences in the distribution of peat components

Distribution of coal balls in the Union Seam varied, but they were locally scattered throughout the seam profile, which averaged about 1.5 m in thick-

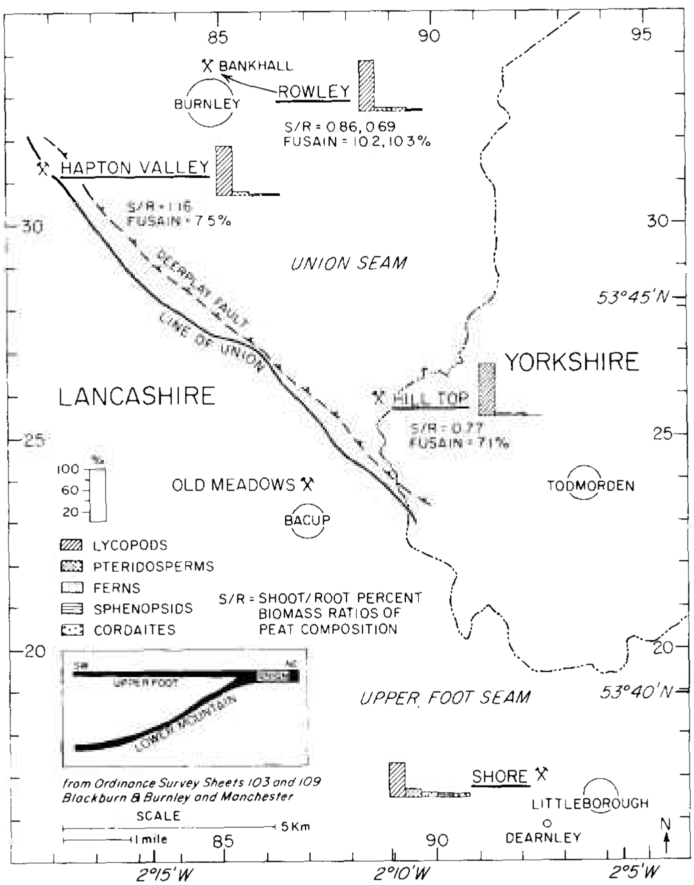


Fig. 3. Simplified map of the Lancashire coal field, England. Peat constituents in coal balls are indicated for coal-mine localities in relation to the line-of-union (split) of the 1.5-m-thick Union Seam, which is in the northeast. The Upper Foot and Lower Mountain Seams are in the southwest. Summary data are given in Tables 1 and 2.

ness. At exposures south of and near the "line of union" (the Union Seam splits into the Upper Foot and Lower Mountain in a southwestern direction) at the Old Meadows Pit (Fig. 3), Stopes and Watson (1909, p. 189) observed that coal balls were scattered throughout the thickness of the Upper Foot and the Lower Mountain where the two were separated by only about 20 cm or less of "ganister", a sandstone seat earth. At the Shore Mine near Littleborough coal-ball aggregates attained thicknesses of two meters or more; the Upper Foot Seam was otherwise only 20—30 cm thick nearby (Lomax, 1915, p. 6). The coal-ball deposits from the Union and Upper Foot are considered representative of the coal-swamp flora. However, in the case of coal-ball slide collections for the Upper Foot Seam, the vegetational content no doubt has been biased quantitatively for selection of aerial plant parts and plants of particular interest to the investigators. Nevertheless, significant floristic differences still can be recognized between the peats of the Upper Foot and the Union Seam. Furthermore, quantitative vegetational differences can be noted in the Union Seam at various distances from the line of union.

Large random samples of coal balls were collected from buried spoils of the Union Seam at three sites (Fig. 3). The most distant locality north of the line of union is at Rowley near the Bankhall Colliery, about 5 km from the Hapton Valley Colliery, which is located at the line of union. The Hill Top drift mine, almost 10 km southeast of the other two, is 1.5 km north of the line of union. The Shore Mine in the Upper Foot is about 10 km south of Hill Top. The Charbonnages de Werister Colliery in the Bouxharmont Seam (approximate equivalent of the Upper Foot Seam) near Liege, Belgium, is about 560 km east of the Shore Mine.

Vegetational and floristic differences

The peat composition at all the localities is overwhelmingly dominated by lycopod trees, and on the whole the assemblages may be characterized as mixed lycopod. However, the Union Seam lacks the gymnosperms, *Mesoxylon* and *Medullosa*, both of which occur laterally in the upper split, the Upper Foot, and in approximately equivalent coals in continental Europe (as exemplified by the Bouxharmont Seam). While both of these gymnosperm genera were relatively rare in early Westphalian A coal swamps, their presence in the Upper Foot, along with the greater general diversity of its flora suggests quite a different coal-swamp environment from that of the Union Seam. *Psaronius* was extremely rare everywhere (DiMichele and Phillips, 1977). The only report of an authentic polycyclic *Psaronius* stem specimen is from a roof nodule (not coal-swamp peat) at Dearnley (Scott, 1920, p. 276), just south of the Shore Mine (Fig. 3).

Union Seam. Lycopod dominance is approximately the same at each of the three localities in the Union Seam, 91 to 95% (Table 1), which is the highest level of dominance observed in the Upper Carboniferous. The other groups of vascular plants are represented by trees (*Calamites*), liana seed ferns (*Lyginopteris* and *Heterangium*), and small ferns. There are no reports of *Psaronius, Medullosa* or even *Mesoxylon* (except for a *Mitrospermum* ovule at Dulesgate near the line of union).

The principal differences in vegetation among sites in the Union Seam are the relative proportions of the lycopod genera, which, for the most part, appear to be monotypic. *Lepidodendron* is clearly dominant, but two generically distinct groups are involved: *L. vasculare*, which we call here "coal-swamp" *Lepidodendron; L. hickii* and *L. serratum* are true *Lepidodendron*, the common genus in clastic deposits (DiMichele, 1983). At Rowley and Hill Top *Lepidodendron vasculare* is the most abundant with smaller and approximately equivalent amounts of *Lepidodendron hickii, Lepidophloios harcourtii*, and *Paralycopodites*. In some of the lycopod assemblages it was not always possible to distinguish between *Lepidodendron hickii* and *Lepidophloios harcourtii* and there was a significant amount of lycopod aerial plant material not even identifiable to genera. At Hapton Valley, *Lepidodendron hickii* is second in abundance only to *Lepidodendron vasculare*, and much of the inseparable *L. hickii-Lepidophloios* biomass may belong to *L. hickii*. If so, *L. hickii* would be the dominant lycopod at the line of union. At the Hill Top locality, about 1.5 km from the line of union, *Paralycopodites* and *Sigillaria* reach their greatest abundance, although they do not dominate assemblages from any site.

Upper Foot and Bouxharmont Seams. The most diverse peat flora in the lower Westphalian A is from the Upper Foot Seam at the Shore Mine, which is undoubtedly the only mine ever reopened just to collect the coal balls (Scott, 1920, p. 11). Permanent slide collections from the British and Hunterian Museums were quantified with the following procedures used to avoid further biases: removal of slides prepared from the same coal ball within each collection, separate data tallies for each collection, and separate treatment of the Scott Collection into "before" and "after" his major studies of gymnosperms (Table 2).

Lycopods account for 52—64.5% of the peat biomass in the estimates and were no doubt somewhat more abundant than that. Pteridosperms were the second most important group with 18—27% of the biomass and most of that was *Lyginopteris*. While pteridosperm estimates are probably high, it is evident that *Lyginopteris* was more abundant at the Shore Mine than at any of the other sample sites. This was also the case for cordaites, but, on the whole, they were probably less abundant constituents than the reported 4.8—15.9% and perhaps were selectively included in the slide collections.

The coal-ball peats from the Bouxharmont Seam in Belgium include some specimens collected and studied by Leclercq (1930) from three layers in a 95-cm-thick part of the seam. In the Bouxharmont Seam lycopods account for 80.5% of the peat biomass; *Lepidodendron vasculare* is dominant. Small ferns and sphenopids are the secondary components of the peat assemblage

TABLE 1

Peat composition (% biomass) of lower Westphalian A coals in western Europe based on random samples of coal-ball peat

Coal	Locality	Collection	Major taxa					Shoot/root ratios	Fusain	Sample size	
			Cordaites	Ferns	Lycopods	Seed-ferns	Sphenopsids			Coal balls	cm^2
Union	Rowley RS1	B.M.N.H.	0	2.6	93.0	3.3	1.1	0.86	10.2	138	17,027
Union	Rowley RS1	U. Montpellier	0	2.6	93.3	3.0	1.1	0.69	10.3	102	9,705
Union	Hill Top	B.M.N.H.	0	2.3	95.3	2.0	0.4	0.87	7.7	58	8,164
Union	Hapton Valley	U. Montpellier	0	1.3	91.0	7.2	0.5	1.16	7.5	104	13,077
Bouxharmont	Werister RS1	U. Liege	2.9	8.1	80.5	2.5	6.0	1.01	5.2	134	7,871

Union seam localities in Lancashire, England, are shown in Fig. 4. Collections indicated are: British Museum (Natural History), London; University of Montpellier, France; and University of Liege, Belgium. Total sample size = 536 coal-ball specimens and an area of 55,844 cm^2.

TABLE 2

Peat composition (% biomass) of Upper Foot Seam at Shore Mine, Shore-Littleborough, Lancashire, England, based on coal-ball peat

Collection	Major taxa					Shoot/root ratios	Fusain	Sample size	
	Cordaites	Ferns	Lycopods	Seed-ferns	Sphenopsids			Coal balls	cm^2
Hunterian Museum-Kidston	4.8	8.8	52.1	27.4	6.9	2.66	2.9	19	462
British Museum (N.H.)									
Scott 1	15.9	3.7	52.3	23.7	4.4	2.69	3.0	84	1,555
Scott 2	7.7	5.4	64.5	18.4	4.0	1.38	3.5	168	3,592
Oliver	11.8	4.5	53.8	24.4	5.5	1.62	6.5	80	2,758[a]

[a]Sampling is based on 0.5 cm^2.
All samples are from permanent thin-section collections from the Hunterian Museum, Glasgow, and British Museum (Natural History), London.

with 8.1 and 6.0% of the biomass, respectively. Cordaites and pteridosperms, with 2.9% and 2.5% of the biomass, are relatively rare. While the diversity of the Bouxharmont rivals that of the Upper Foot, seed plants account for only 5.4% of the total biomass, and the paucity of *Lyginopteris* is an obvious quantitative difference.

Peat constituents and preservation

The shoot/root ratios from the Union and Bouxharmont Seams are 0.69 to 1.16 with a simple average of 0.96 (Table 1). Variation in shoot/root ratios is 0.69—0.86 at Rowley. The highest shoot/root ratio (1.16) occurs at the Hapton Valley site at the line of union; this is the only place where *Lepidodendron vasculare* was probably not the most abundant lycopod and also where the largest portion of peat was identifiable (unidentifiable material in the Union Seam ranges from 7.3 to 17.8%). Based on the hypothetical 4/1 shoot/root ratio of a completely preserved lycopod tree, the peat composition indicates loss of at least 71—83% of the aerial biomass.

The peat deposits from the Hapton Valley Mine, which have the highest shoot/root ratios, consist of 36.1% periderm (mostly from aerial plant parts) and 4.3% wood (about equally from stems and roots). The periderm/wood ratio is approximately 8.5/1, a ratio similar to that found in peat deposits of Westphalian age that are highly lycopod-dominated and that have small amounts of cordaites. These durable secondary tissues account for about one-half the total fusain.

Peat from the Union and Bouxharmont Seams consists of 5.2—10.3% fusinized material (Table 1). Fusain is highest in the Union Seam (Rowley: 10.2—10.3%), decreasing near or at the line of union. The lowest fusain occurs in peat from the Upper Foot (Shore-Littleborough: 2.9—6.5%) (Tables 1, 2). The amount of fusain has to be considered relative to shoot/root ratios because aerial portions of plants are thought to be the main fusinized components. Thus, 7.5 to 10.3% fusain is a relatively high amount for a peat deposit with shoot/root ratios of about one; in the Union Seam even some stigmarian root systems were partially fusinized.

Composition of peat deposits in the Katharina Seam

Coal-ball distribution in the Katharina Seam of the Ruhr varied considerably from site to site (Kukuk, 1909, 1938) but apparently was limited to scattered parts of the upper or lower benches, which were commonly separated by a zone of many thin, closely spaced shale partings. On the basis of the Felix Collection, representing 81 coal balls (2,297 cm^2), the major taxa were lycopods (64.9% biomass), with almost equal amounts of cordaites (9.7%), pteridosperms (9.8%), and sphenopsids (10.8%). Small ferns accounted for 4.8%. The lycopods are the same taxa as those in the Union Seam, but *Paralycopodites* and its cones are more abundant in the Katharina. *Lyginop-*

teris accounted for 91% of the pteridosperm peat. This genus became extinct just above the Westphalian A/B boundary; the Katharina Seam is the youngest peat source of *Lyginopteris*.

The collection is no doubt biased for aerial portions of plants, and the shoot/root ratio is 2.14. Fusain content is comparably very low at 0.8%. Lycopods and cordaites were the main sources of roots, accounting for 30.2% (total of all roots is 31.8%). Cordaitean assemblages were represented largely by roots, which exhibit eccentric growth rings in the wood as in deposits from the Upper Foot and Bouxharmont Seams and in some stratigraphically next higher peats in eastern Kentucky.

The almost equal abundance of cordaites, seed ferns and calamites (sphenopsids) represents the earliest indication, based on coal-ball peats, of a significant change in the vegetation of early Westphalian coal swamps. The concurrent rise of cordaites and calamites as well as the diminution in lycopods is consistent with the palynomorph data from coals of comparable age in Europe and the United States, but the changes in the spore floras are much more complex as will be noted in the next section.

Peat deposits and spore floras in the eastern United States — Central Appalachians and Illinois Basin Coal Field

Paleobotanical data on composition of Early to early Middle Pennsylvanian coal swamps of the United States are restricted currently to the Central Appalachians and the Illinois Basin Coal Field (Fig. 4). Peat deposits occur in eastern Kentucky and Tennessee (Fig. 1) in the upper Pottsville and equivalent coals and, hence, provide the next younger stratigraphic links with data from older coal-ball peats in western Europe. Spore floras provide the stratigraphic basis for comparisons between coals of the Illinois Basin Coal Field, the Central Appalachians and western Europe from as low as the lower Westphalian A up to the Pottsville—Allegheny (Appalachian) and Atokan—Desmoinesian (Illinois Basin) transitions dealt with in the next section.

Composition of peat deposits in the Central Appalachians

The Upper Path Fork coal bed of the lower Middle Pennsylvanian (approximately equivalent to the Lower Elkhorne) (Fig. 1) is the oldest Pennsylvanian seam to yield abundant coal balls. The dominant and subdominant plants are lycopods and cordaites, which is a recurrent pattern in those peat data that we have from the upper Pottsville (Table 3). Despite the dearth of data from coal-ball peat (Fig. 5) in the lower Middle Pennsylvanian, the following observations can be made:

(1) The increased abundance of cordaitean trees noted in the Katharina Seam continues into the lower Middle Pennsylvanian as does the rarity of *Medullosa* and *Psaronius*.

Fig. 4. Principal Pennsylvanian coal basins in the eastern half of the United States. The Western Interior Coal Region includes the Forest City, Cherokee and Arkoma Basins. The Eastern Interior Coal Region includes the Illinois and Michigan Basins. Modified from Wanless (1969).

(2) Dominance of lycopod trees continues with variability, including *Lepidophloios harcourtii* (Upper Path Fork), *Paralycopodites* (Hamlin) and *Lepidodendron hickii* ("High Splint").

(3) Shoot/root ratios are generally even lower than those in western Europe (Union and Bouxharmont Seams) and correlate with the relative abundance of cordaites (the more cordaites, the lower the shoot/root ratio) including the lowest ratio (0.47) and the most cordaites in the Upper Path Fork (Table 3).

(4) Fusain levels are high in relation to shoot/root ratios except in the Hamlin coal bed, which has significant variability in shoot/root ratios but low fusain levels.

The peat deposits in the lower Middle Pennsylvanian, which had variable depositional environments, would be largely uninterpretable without the spore floras from these and many other coals in eastern Kentucky and Tennessee. However, the peat deposits are a reference base of in situ vegetation. In terms of the average swamp moisture and the environments of peat accumulation, the key data from peats are: (1) the record low shoot/root

TABLE 3

Peat composition (% biomass) of upper Pottsville coals in northeastern Tennessee and eastern Kentucky based on random samples of coal-ball peat

Coal and Locality	Major taxa					Shoot/root ratios	Fusain	Sample size	
	Cordaites	Ferns	Lycopods	Seed-ferns	Sphenopsids			Coal balls	cm^2
"High Splint"[1]-Tennessee	33.0	4.0	50.9	2.7	9.4	0.72	9.0	32	3,340
Hamlin[2] Kentucky									
Shock Branch	1.7	0.5	91.1	0.3	6.4	1.3	0.8	85	4,462
Lewis Creek	14.3	1.1	78.4	0.6	5.6	0.87	2.6	84	6,715
Upper Path Fork[3] Kentucky									
Cranks Creek	36.7	3.1	54.5	2.1	3.6	0.47	7.4	159	7,296

[1] Reported as "Splint Coal" by McLaughlin and Reaugh (1976) and "Upper Splint or Block Seam" (Reaugh and McLaughlin, 1977).
[2] Coal originally identified as Copland (Schopf, 1961) and mapped as Hamlin by Lewis (1978).
[3] Reported by Phillips and Chesnut (1980).
Locations of coal-ball sites in eastern Kentucky are shown in Fig. 6. Total sample size = 360 coal-ball specimens and an area of 21,813 cm^2.

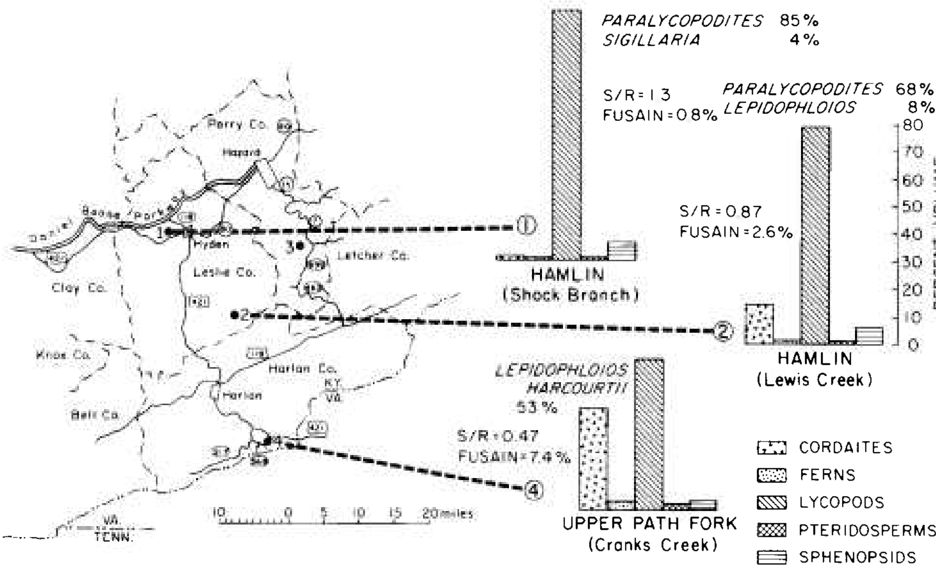


Fig. 5. Map of a portion of eastern Kentucky (Central Appalachians) with peat constituents determined from random samples of coal balls; coals and localities are indicated. Summary data are given in Table 3. The Shock Branch (1) and Lewis Creek coal-ball deposits (2) were reported as being in the Copland coal bed by Schopf (1961), but according to those who mapped the Hyden West GQ (Lewis, 1978) and Cutshin GQ (Ping, 1977) they are in the Hamlin coal zone. The coal balls from the Bear Branch coal-ball locality (3) according to Schopf (1961) are probably slightly older than the Copland coal bed (?) and may also be from the Hamlin coal zone. The Crank's Creek coal balls occur in the Upper Path Fork Coal 427 m below the Copland coal bed and about 323 m below the Smith coal zone (the equivalent of the Hamlin coal zone).

ratios (and high fusain content) for a lycopod-dominated coal swamp in the Upper Path Fork; this is consistent with Peppers' (1979) "drier interval"; (2) an interval of *Paralycopodites*-dominated coal swamps, which is rare in the Pennsylvanian; and then (3) a shift to abundance of trees that might be considered generally more indicative of clastic swamps than coal swamps — true *Lepidodendron*, a different cordaites (bearing *Cardiocarpus magnicellularis* ovules), and calamites.

The Upper Path Fork and "High Splint" coal beds are exceptional because their vegetation combined abundant wood- and periderm-producing trees (cordaites and lycopods). The peat composition of the Upper Path Fork includes 29.6% wood and 20.2% periderm for a ratio of 1.47. Cordaites contribute a total of 25.6% wood, 95% of which is derived from roots. Lycopods contribute a total of 19.1% periderm, more than 75% of which is derived from the aerial portions of the trees. The "High Splint" has one of the highest wood/bark ratios, 2.0 (32%/16%). With the exception of cordaitean-rich coals, Lower and Middle Pennsylvanian peat deposits are composed generally of about one-third or more periderm and relatively little (4—7%) wood.

The relative increase of cordaites resulted in one of the most important changes in composition of the peat in the lower Middle Pennsylvanian, if the limited sampling were generally representative of the vegetation. Spore floras are not supportive of such a generalization. Nevertheless, there is some basis to compare the prevalent wood source (cordaitean roots) with changes in climate inferred from other data. Most specimens of *Amyelon*, the roots of cordaites, in the Lower and lower Middle Pennsylvanian peat deposits exhibit eccentric growth rings except in the Upper Path Fork coal bed. This phenomenon extends stratigraphically up to and including the Hamlin coal. The only intervening coal not in Table 3 from which coal balls have been examined (Hignite coal bed of eastern Kentucky) exhibits the same pattern of growth rings and lycopod-cordaites dominance. Widespread insect burrowing is particularly evident in woods of the Upper Path Fork, Hignite, and Hamlin coal beds (Taylor and Scott, 1983).

Comparison between miospore floras in the Illinois Basin Coal Field and the Central Appalachians

The correlation of miospore floras in coals in the lower Middle Pennsylvanian of the Illinois Basin Coal Field and eastern Tennessee have been reported by Phillips and Peppers (1984), and data from eastern Kentucky coals have been added herein to the comparison for the obvious reason that most of the peat data are derived from that area. Despite the potential biases that are involved in using essentially random coal samples (and only one channel sample per coal), there are a number of parallel interregional trends in the abundance patterns of dominant *Lycospora* (Fig. 6), the intercalated rises in spores of herbaceous lycopods (Fig. 7) and the general increase in abundance and diversity of tree-fern spores (Figs. 7, 8). There are also a number of quantitative interregional differences in the lycopods, sphenopsids and cordaites.

The patterns of change in abundance of lycopod spores are the most diagnostic of the changes in vegetation. There is a stratigraphic decline in dominance of *Lycospora pellucida* (*Lepidophloios harcourtii*) at about the time of the Alma and Upper Elkhorn coals in the Appalachians. *Lycospora pellucida* remains subdominant in the Central Appalachians longer than in the Illinois Basin Coal Field (Fig. 6), and *L. granulata* is much more abundant from the outset in the Illinois Basin Coal Field than in the Appalachians. The maximum abundance of *Lycospora micropapillata* (*Paralycopodites*) occurs between the Lower Whitesburg and Copland coals beds of eastern Kentucky; peat deposits in the Hamlin coal bed, which is within this interval, contain abundant *Paralycopodites*. While the major stratigraphic pattern of change is the shift in dominance of *Lycospora pellucida* (*Lepidophloios harcourtii*) to *Lycospora granulata* (*Lepidophloios hallii* and/or *Lepidodendron hickii*) across the *Lycospora micropapillata* zone, we are uncertain of the relative importance of the tree species (*Lepidophloios* or *Lepidodendron hickii*) high in the Pottsville and on into the Allegheny of the Appalachians. Although at relative low levels, *Cappasporites* (coal-swamp *Lepidoden-*

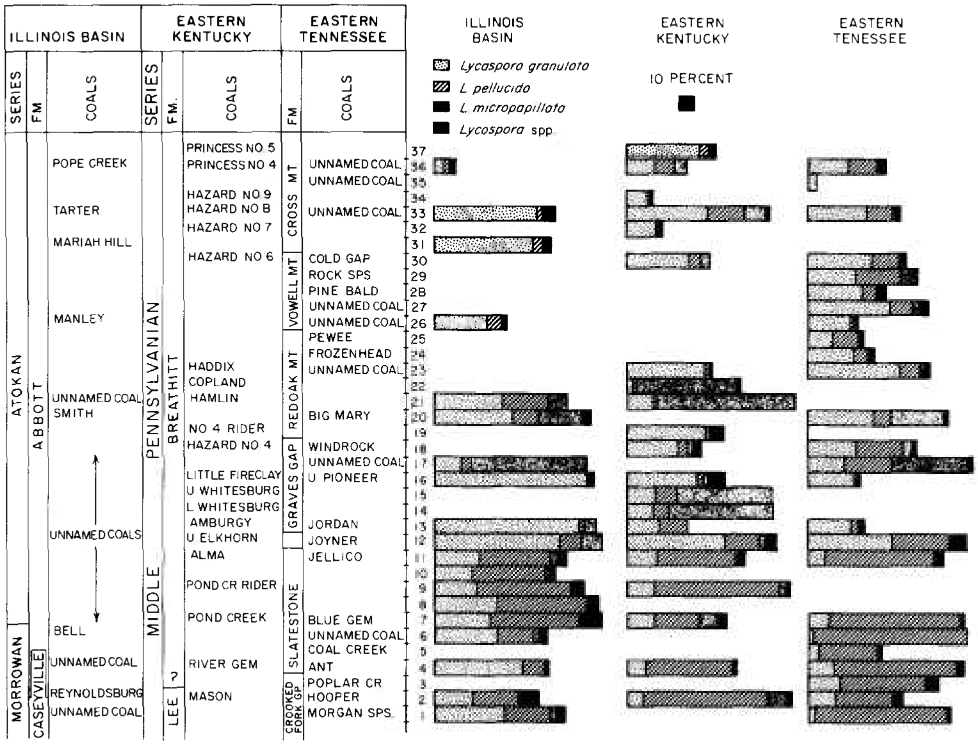


Fig. 6. Interregional stratigraphic comparison of the relative abundance of *Lycospora* species (percent number of miospores in channel samples) in lower Middle Pennsylvanian coals of the Illinois Basin Coal Field, eastern Kentucky and northeastern Tennessee (Central Appalachians). Data derived, in part, from Phillips and Peppers (1984) with additions from the following coals and sources in eastern Kentucky: *2* = Mason Coal (MAC. 2783), 838 m S. line, 701 m E. line, Varilla Quad., 25-C-72, Bell Co.; *4* = River Gem Coal (MAC. 991 A-B), Saxton Mine, 4.8 km N. of Jellico, just N. of Kentucky—Tennessee line, Whitley Co.; *7* = Pond Creek Coal (MAC. 2700), 1524 m S. line, 152 m E. line, Nangatuck Quad., 13-P-86, Martin Co.; *8* = Pond Creek Rider (MAC.2699), 1005 m S. line, 1387 m E. line, 2-L-86, Lick Creek Quad., Pike Co.; *9* = Alma Coal (MAC. 2678 A-D), W. side Tug Fork, directly across from Borderland (West Virginia), Pike Co.; *10* = Upper Elkhorn Coal (MAC. 2712), 37°40′15″N, 82°44′32″W, at junction of Lewis Fork and Brandykeg Creek at Lancer, Lancer Quad., Floyd Co.; *11* = Amburgy Coal (MAC. 2760), 805 m E. of Hyden, Leslie Co.; *21* = Hamlin Coal (MAC. 2669), E. side Hwy. 15, SE corner, Hyden 7.5′ Quad., Perry Co.; *16* = Little Fireclay Coal (MAC. 2675a) and 22 Copland Coal (MAC. 2675b), Greater Branch along U.S. 460 (Geol. Soc. Ky., 1953, stop 2); *23* = Haddix Coal (MAC. 2711), 823 m S. line, 1.4 km E. line, 11-G-71, Creekville Quad., Clay Co.; *14* = Lower Whitesburg (MAC. 2666 A-B), *15* = Upper Whitesburg (MAC. 2666 C-D), *18* = Hazard No. 4 (MAC. 2666 E-G), *19* = No. 4 Rider (MAC. 2666H), *30* = Hazard No. 6 (MAC. 2666 J-M), and *32* = Hazard No. 7 (MAC. 2666 N-P), Messer Branch Section, 1.6 km SW Hazard, 2-I-76, 3-I-76, Hazard South Quad., Perry Co.; 33 = Hazard No. 8 (MAC. 2671 A-D), Four Seam Coal Company at head of Buffalo Creek, Perry Co.; 34 = Hazard No. 9 (MAC. 2671 A-C), along Buffalo Creek, below Four Seam Coal Company, Perry Co.; 36 = Princess No. 4 (MAC. 2737 A-C), 1.5 km S. line, 884 m E. line, 25-X-80, Oldtown Quad., Greenup Co.; and 37 = Princess No. 5 (MAC. 1987 A-E), NW corner intersection Hwy. 60 and 64,8 km SW Ashland, Boyd Co.

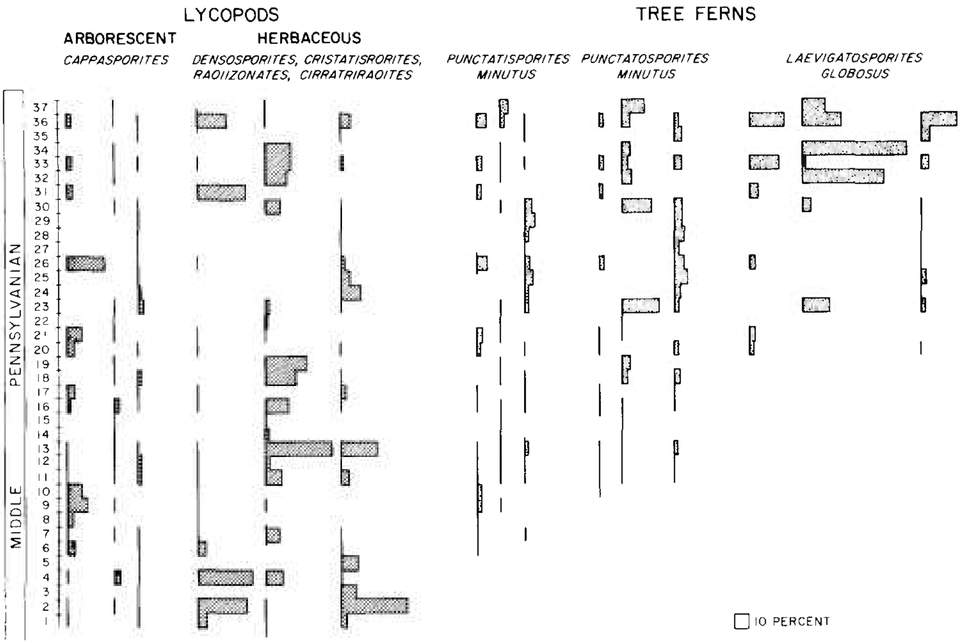


Fig. 7. Interregional stratigraphic comparison of the relative abundance of lycopod miospores other than *Lycospora* and tree-fern spores (based on channel samples) in lower Middle Pennsylvanian coals of the Illinois Basin Coal Field, eastern Kentucky and northeastern Tennessee (Central Appalachians). Numbered plots of data refer to those coals listed in Fig. 6.

dron) is generally more abundant in the Illinois Basin Coal Field than in the Appalachians. This may provide a clue to the differences in abundant lycopods of the two regions since *Lepidophloios* tends to occur in assemblages with either coal-swamp *Lepidodendron* or *Lepidodendron hickii* but not both. The herbaceous lycopods sporadically exhibited marked increases in abundance, namely near the transition between Lower and Middle Pennsylvanian (near the Westphalian A/B boundary), in the *Lycospora micropapillata* zone and high in the Breathitt (upper Pottsville) Formation and equivalent strata. Miospore floras indicate that northeastern Tennessee usually has a greater abundance of cordaites and sphenopsids than the other sampled areas (Fig. 8); this is consistent with the peat of the "High Splint" coal bed.

The upward increasing abundance and diversity of tree-fern spore floras does not agree with any peat data we have. Near the top of the Breathitt (uppermost Pottsville) tree-fern spores dominate in several of the Hazard Coals of eastern Kentucky.

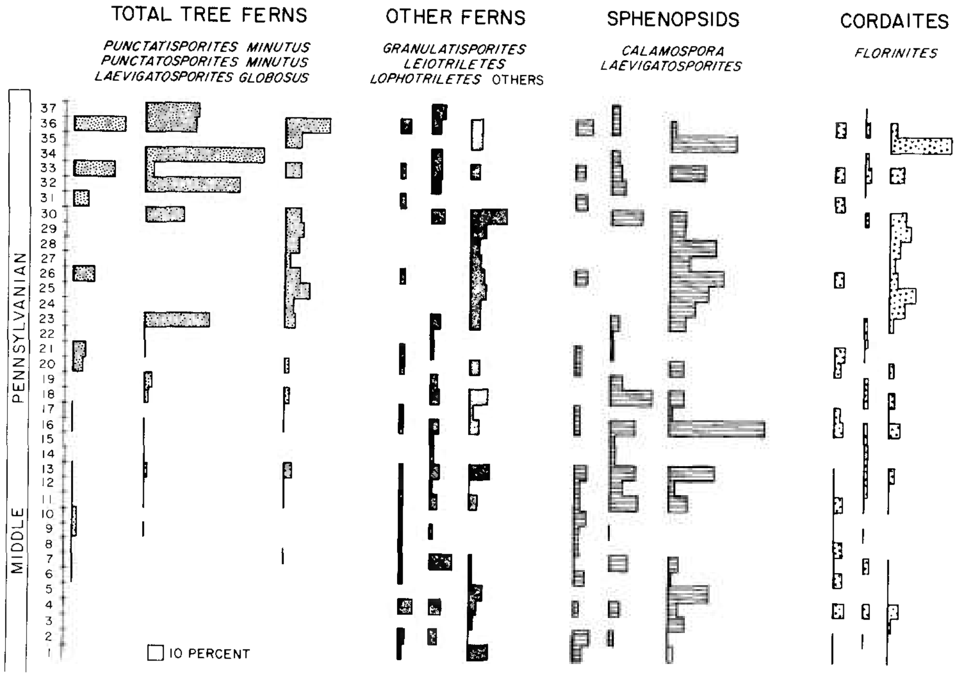


Fig. 8. Interregional stratigraphic comparison of the relative abundance of miospores of total *Psaronius*, other ferns, sphenopsids and cordaites (based on channel samples) in lower Middle Pennsylvanian coals of the Illinois Basin Coal Field, eastern Kentucky and northeastern Tennessee (Central Appalachians). Numbered plots of data refer to those coals listed in Fig. 6.

COMPOSITION OF COAL SWAMPS AND EVIDENCE OF INTERREGIONAL CHANGE IN THE LATE MIDDLE PENNSYLVANIAN

Lower Desmoinesian spore floras of selected coals in the Western Interior Coal Region

The relative distribution of major sporomorphs in 17 Desmoinesian coal seams in Oklahoma were summarized by Wilson (1976). We macerated samples from several of the coals in the Western Interior Coal Region, principally in order to compare their spore content with the vegetational composition of the peat. The results obtained from our study (Fig. 9) are difficult to compare with Wilson's (1976) summary for the following reasons: (1) only some of the coals he included were studied for the present report; (2) some of our coal samples are from Kansas and Missouri, rather than from Oklahoma; and (3) only a few samples were analyzed from each of the individual coals that contain coal balls. Differences in reporting the data are also a problem since Wilson reported relative abundances of major genera, whereas we have divided some genera into species and have combined others according to the major plant groups that produced the spores. For example, Wilson showed that *Laevigatosporites* is the most abundant genus in many of the coals, but we have divided the genus into the tree-fern spores, *L. globosus* and *Punctatosporites* (*Laevigatosporites*) *minutus*, and the sphenopsid spores, *L. desmoinesensis* and *L. vulgaris*.

The stratigraphic change in lower Desmoinesian vegetation, based on the sporomorphs of selected coals (Fig. 9), is most extensive near the basalmost coal (approximately equivalent to the Rock Island (No. 1) Coal Member of Illinois). The unnamed coal of Iowa (lower Desmoinesian) is the oldest coal that contains a dominance of *Florinites* (cordaites). This is associated with a

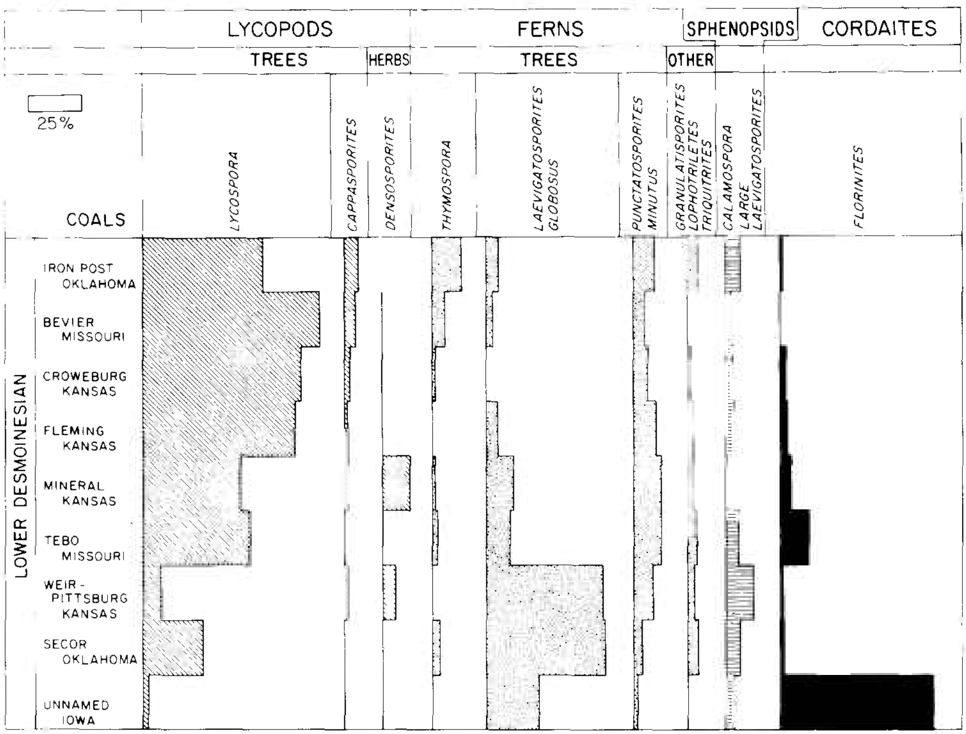


Fig. 9. Stratigraphic pattern of percent abundance of major miospore taxa from channel samples of selected coals in the lower to middle Desmoinesian of the Western Interior Coal Region (see Fig. 4 for coal basins). Sources of coal samples with ISGS maceration numbers are stratigraphically the following: Unnamed Iowa coal from Urbandale Mine (MAC. 823) with location in Raymond and Phillips (1983); Secor Coal (MAC. 2713), Blevins, Burdette and Vogt Mine No. 1. SE of Checotal, Oklahoma; Weir-Pittsburgh Coal (MAC. 2691), NE SE NE Sec. 30, 30S, 25E, Crawford Co., Kansas; Tebo Coal (MAC. 635), Hudson-Frazer Mine, Sec. 36, T. 44 N., R. 25 W., Henry Co., Missouri; Mineral Coal (MAC. 2687), Bill's Coal Company, Chetopa Mine, Sec. 28, 34S, 21E, Kansas; Fleming Coal (MAC. 2690), Pittsburg and Midway Hole No. 4, NW SE SE, Sec. 29, 32S, 21E, Cherokee, Kansas; Croweburg Coal (MAC. 2686), Mackie-Clemens Mine No. 22, Sec. 4, 28S, 25E, Kansas; Bevier Coal (MAC. 1171-B), strip mine, 11 miles S of Bevier, NE NW Sec. 31, 56N, 14W, Macon Co., Missouri; and Iron Post Coal (MAC. 2684), Peabody Rogers County Mine No. 2, W of Vinita, Rogers Co., Oklahoma.

decline in the abundance of *Lycospora* to the lowest sustained level observed until the Middle-Upper Pennsylvanian transition. The main miospore pattern in the lower Desmoinesian sequence of coal swamps is the concomitant rise and return to dominance of *Lycospora*-producing lycopods and a decline in cordaites. The tree ferns are quite abundant in the lowermost coals, decline somewhat in the middle part, and begin increasing again toward the Bevier and Iron Post coals, associated with a shift from *Laevigatosporites globosus* to *Thymospora.*

Lower Desmoinesian peat composition in the Western Interior Coal Region

Coal-ball data from seven of the coals in Oklahoma, Kansas, and Iowa suggest stratigraphic trends in peat composition that are generally consistent with those in sporomorph floras. Differences in vegetation from the Arkoma Basin and northeastern Oklahoma shelf to the northern part of the Forest City Basin are also apparent from the peat and spore data (Fig. 10), but it should be noted that the oldest coals with coal balls from each of the basins are not stratigraphically equivalent (Fig. 1). Those available data indicate an increasing amount of cordaites from Oklahoma to Iowa and a decreasing amount of lycopods. The coal-ball peats in the oldest Desmoinesian coals of Iowa (Table 4) indicate greater abundance and diversity of cordaites than in Kansas where cordaites were also quite significant. The time-transgressive

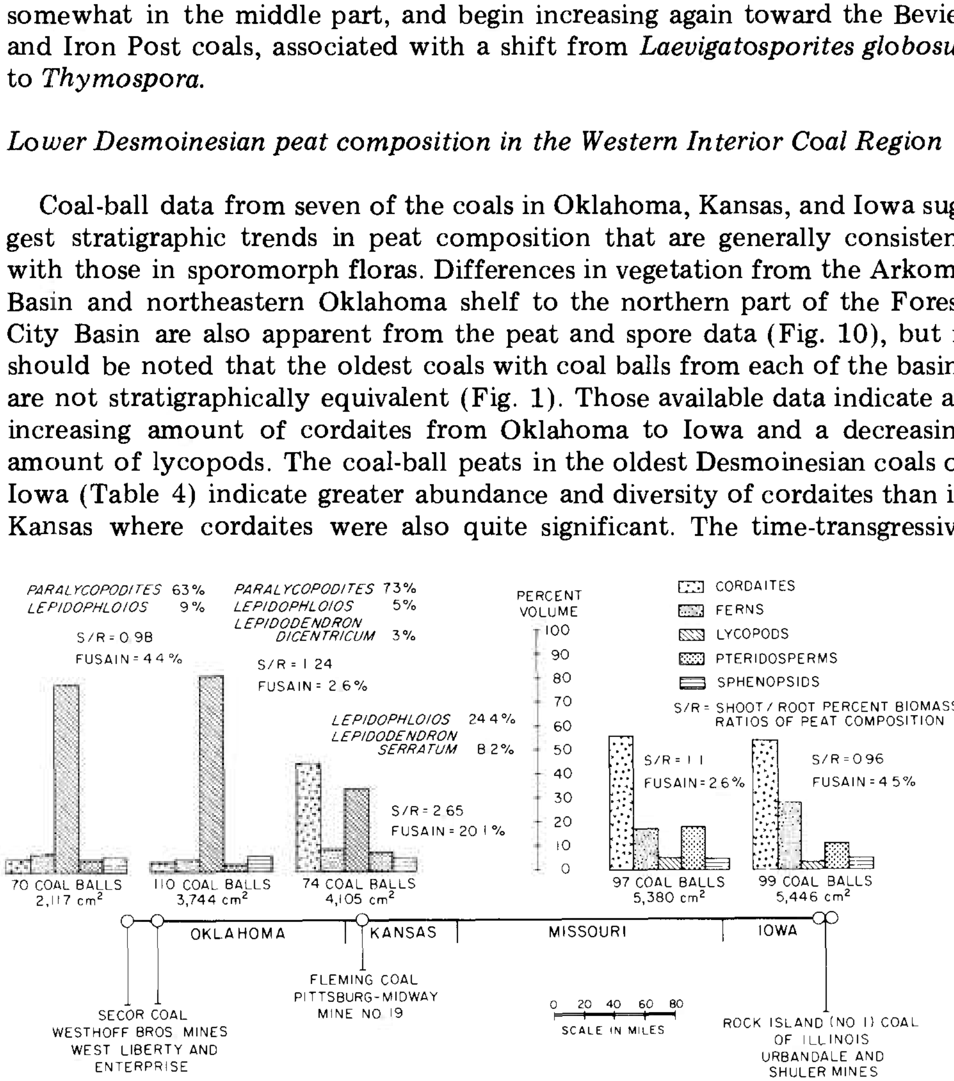


Fig. 10. Comparative transect of coal-swamp vegetation in the lower Desmoinesian of the Western Interior Coal Region showing percent volume (biomass) of plants in peat. The Secor Coal sites are in the Arkoma Basin, the Fleming Coal in the Cherokee Basin and the sites of the Iowa coal, approximately equivalent to the Rock Island (No. 1) Coal Member of Illinois, in the northern part of the Forest City Basin (see Fig. 4). This transect does not represent equivalent coals (see Fig. 1 for stratigraphic positions of each). Summaries of peat constituents are given in Table 4.

TABLE 4

Peat composition (% biomass) of lower Desmoinesian (lower Westphalian D) coals of Western Interior Coal Region of United States based on random samples (RS) and profiles (VS) of coal-ball peat

Coal and Locality			Major taxa					Shoot/root ratios	Fusain	Sample size	
			Cordaites	Ferns	Lycopods	Seed-ferns	Sphenopsids			Coal balls	cm²
Iron Post	Oklahoma	VS1	3.3	37.0	42.9	7.1	9.7	1.2	3.5	99	5,304
		RS1	7.5	26.2	32.9	21.9	11.5	1.9	5.1	160	4,984
Bevier	Kansas	RS1	29.6	10.2	49.1	7.5	3.6	1.77	9.5	26	1,482
		RS2	30.2	12.1	50.4	2.9	4.4	1.09	5.8	26	1,883
Fleming	Kansas	RS1	44.8	8.9	34.1	7.4	4.8	2.65	20.1	74	4,104
Secor	Oklahoma	VS1	4.7	6.6	77.8	5.0	5.9	0.98	4.4	70	2,117
		VS2	3.9	5.1	81.8	2.7	6.5	1.24	2.6	110	3,744
Coal at Weldon Mine, Iowa		RS1	20.4	10.1	55.3	10.1	4.1	1.29	4.8	42	2,293
(Approx. = to Buffaloville of Illinois Basin)		RS2	28.5	10.0	43.4	14.4	3.7	1.56	3.9	65	3,985
Star Mine, Iowa		RS1	72.7	2.9	19.0	4.8	0.6	0.96	5.1	47	6,907
Atlas Mine, Iowa		RS1	81.0	1.5	17.2	0.2	0.1	1.07	2.7	16	1,090
Coal at Urbandale Mine, Iowa		RS1	55.6	16.7	5.2	18.1	4.4	1.1	2.6	97	5,380
(Approx. = to Rock Island (No. 1) of Illinois) Shuler Mine, Iowa		RS1	53.7	27.7	2.9	10.6	5.1	0.96	4.5	99	5,446

Total sample size = 931 coal-ball specimens and an area of 48,719 cm^2.

transect from the Secor coal of Oklahoma to the unnamed coal at the Urbandale and Shuler Mines in Iowa also shows differences in the major lycopods. *Paralycopodites* dominated in Oklahoma, *Lepidophloios* was subdominant in the Fleming coal of Kansas, and very minor amounts of coal-swamp *Lepidodendron* occurred in Iowa swamps. The earliest documentation of the subdominance of *Psaronius* and *Medullosa* by in situ peat is in the cordaitean-dominated coal swamps of Iowa. The overall stratigraphic trend in composition of vegetation in the peats from the Western Interior Coal Region coincides with that noted in the sporomorph floras. Cordaites decreased in abundance and lycopods returned to dominance. *Psaronius* and *Medullosa* again became major components of the swamps by Iron Post coal time.

With the exception of the Fleming coal of Kansas, the shoot/root ratios of the lower Desmoinesian coals range from 0.96 to 1.9. The fusain content is relatively low, 2.6—5.1%, except in the Fleming and Bevier coals, which contain 5.8—20.1% fusain. The fusain in the two Bevier samples is 5.8% and 9.5%. Coal balls from the Fleming coal exhibit the highest fusain content found thus far in the Pennsylvanian; major categories of botanical constituents in this coal are 22.1% wood and 19.2% periderm, with these two categories accounting for 14% fusain. The unnamed coal from the Urbandale and Shuler Mines is also rich in wood (26.5—34.3% of the biomass) and contains only 0.6—3.9% periderm. While wood is usually a minor constituent of tropical Pennsylvanian peat deposits, those coals mentioned above, the Upper Path Fork coal bed of eastern Kentucky (Fig. 5), and the "High Splint" coal of Tennessee (McLaughlin and Reaugh, 1976; Reaugh and McLaughlin, 1977) are significant exceptions mostly because of the abundance of the woody cordaitean trees.

Comparison of lower to middle Desmoinesian vegetational composition between the Western Interior Coal Region and the Illinois Basin Coal Field

Comparisons among Desmoinesian peats of Iowa, Kansas and Oklahoma provide a preliminary basis for considering environmental differences that existed within the Interior Coal Province. The same basic stratigraphic changes in coal-swamp vegetation occurred in both the Western Interior Coal Region and the Illinois Basin Coal Field, but the abundance of cordaites was consistently less in the Illinois Basin (Fig. 11). In drawing these comparisons it is recognized that the coals being compared are not stratigraphically equivalent, although some are very close. However, the repetition of similar kinds of coal swamps in the intervals sampled allows comparisons of trends and indicates approximate synchroneity of similar kinds of change.

In contrast to the extreme dominance of cordaites in Iowa at about the time of the Rock Island (No. 1) Coal swamp of Illinois, the Indiana coal approximately equivalent to the Murphysboro of Illinois, contains peat dominated (71.5—74.4% biomass) by *Lepidodendron vasculare* with *Pennsylvanioxylon birame* (cordaites) contributing 11.5—14.5% of the biomass

(Fig. 11). In Iowa *P. birame* is the most abundant cordaitean tree and *L. vasculare* is the most common of the rare lycopod trees.

In the Bevier coal of Kansas and the Summum (No. 4) Coal Member of Illinois (see Fig. 1) lycopod trees dominated the vegetation with more cordaites in the western region than in the eastern. However, the genus of dominant lycopod and the species of subdominant cordaites are different in the two areas. We suspect, from sporomorph floras, that the dominance of *Lepidodendron phillipsii* in the Summum Coal at Peabody Northern Illinois Mine may not be representative of most of the Summum coal swamp, which is dominated by *Lycospora granulata* (*Lepidophloios*) (Peppers, 1970).

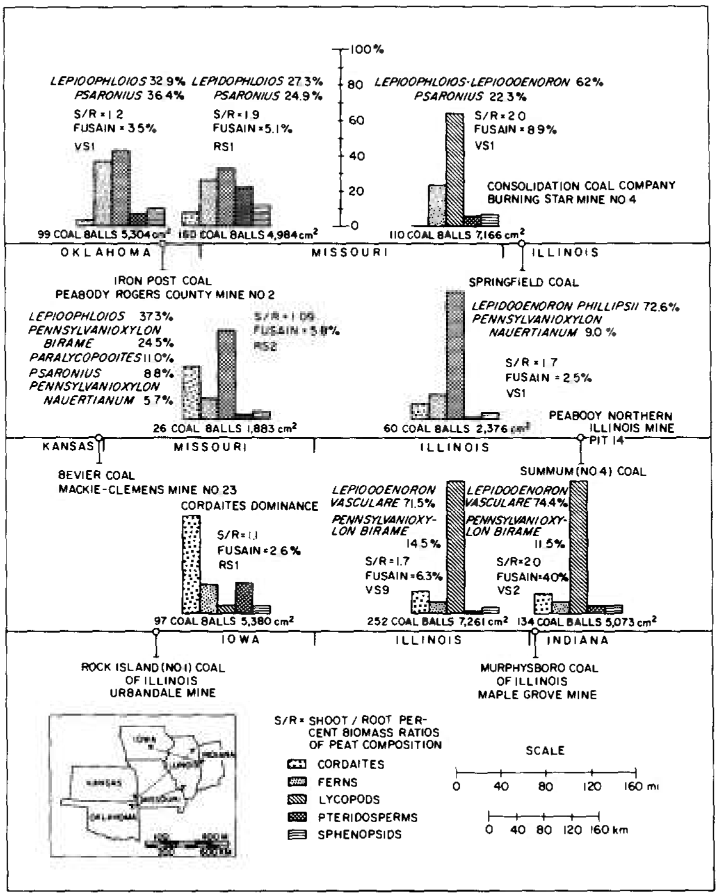


Fig. 11. Comparative interregional transects of coal-swamp vegetation in lower to middle Desmoinesian between coals of similar stratigraphic intervals of the Western Interior Coal Region and the Illinois Basin Coal Field showing percent volume (biomass) of structural peat constituents. Histograms for random samples (RS) and profile samples (VS) are given for the coals. Geographic locations of comparative sites are shown in lower left inset. For stratigraphic positions of each coal see Fig. 1. Summaries of peat constituents are given in Tables 4 and 5.

Nevertheless, the regional differences in species of cordaites are most informative. *Pennsylvanioxylon nauertianum* is subdominant in the Summum Coal (9.0% of the biomass), whereas *P. birame* (24.5%), the brackish water indicator, and *P. nauertianum* (5.7%) have been recorded from the Bevier Coal. This assemblage represents the first occurrence of *P. nauertianum*, the last occurrence of *P. birame*, and the end of brackish-water cordaites in paralic coal basins as major elements of the vegetation. The last minor phase of cordaitean abundance in the Desmoinesian is seen in the next higher Iron Post Coal and these cordaites have not been identified adequately. With the later exception of local occurrences within coals such as the Friendsville (Upper Pennsylvanian), cordaites do not contribute a significant biomass (> 1%) to paralic coal swamps in any younger Pennsylvanian coals in Illinois.

The change in coal-swamp vegetation at the time of the Springfield Coal may represent a zenith in available freshwater in the Interior Coal Province. It also represents the further development of some of the largest deltaic coal swamps of all geologic time from the Colchester to the Herrin Coal. However, the prevalent trend to larger coal swamps should not overshadow the actual time of the most significant change in the vegetation. This was near the beginning of the Desmoinesian and relates, in part, to marine transgressions and regressions and brackish influences in some areas of the swamps. While brackish conditions had an influence on expanding cordaites, we suspect that there were other significant environmental changes that allowed tree ferns to actually radiate into coal swamps. These are discussed later.

Coal-swamp vegetation and peat constituents in the Illinois Basin Coal Field

The Illinois Basin Coal Field has served as a comparative section for assessing patterns of change in the vegetations of Pennsylvanian-age coal swamps (Kosanke, 1947, 1950; Peppers and Phillips, 1973; Phillips et al., 1974). The sporomorph plots of average relative abundance are shown for the major plant groups in Fig. 12. The general pattern of lycopod domination through two-thirds of the Pennsylvanian, followed by that of tree ferns is the most basic pattern. There are interruptions of these generalized patterns on a coal-by-coal basis.

Diversity in miospore floras and relations to environmental changes

Studies of average diversity and turnover of spore species in Illinois Basin coals provided a basis for inference of the "first drier interval" by Peppers (1979). This work has been expanded into an interpretative plot of average species diversity, intended to serve as an indirect measure of the relative magnitude of environmental change. Coal-swamp diversity, as measured by miospores, is significantly greater than measures based on extensive floristic lists from coal-balls because of the nature of sampling (dispersed spores versus in situ peat and greater number of sampling sites for palynology) and because of biases in coals which may receive large spore rains from plants

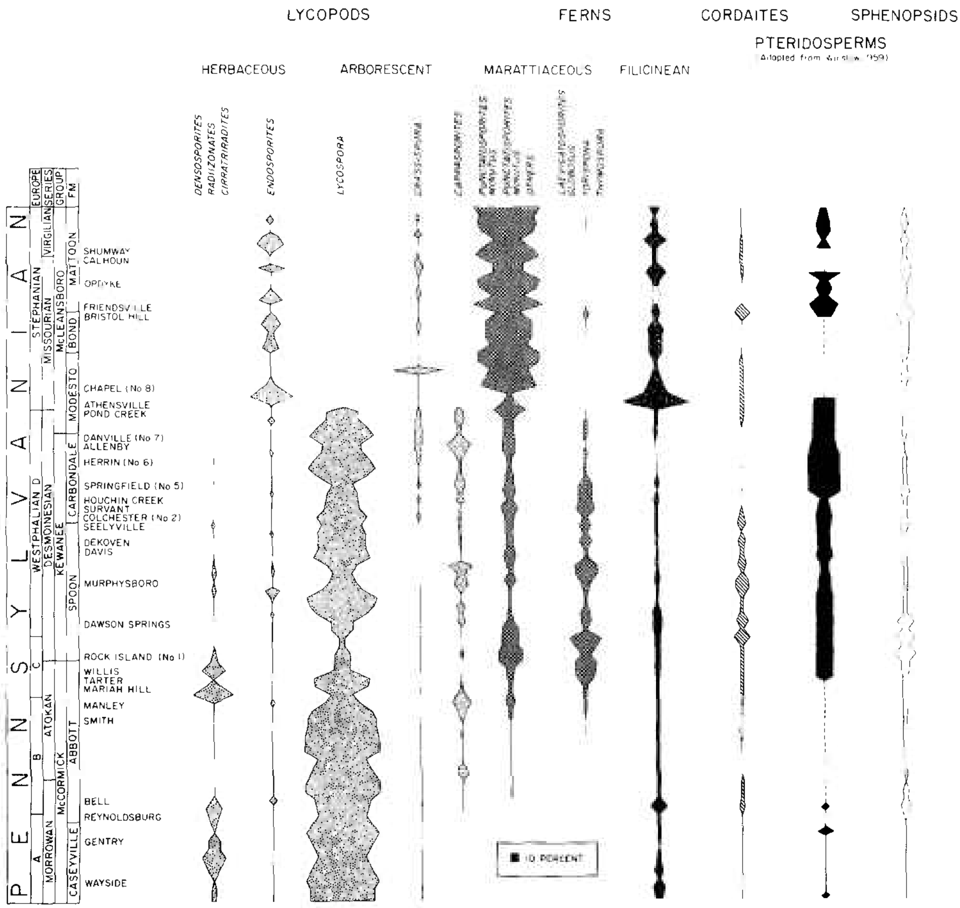


Fig. 12. Average relative abundance of major Pennsylvanian-age coal-swamp plants based on spore floras from channel samples in the Illinois Basin Coal Field. Modified and expanded from Phillips et al. (1974) with additions from Winslow (1959).

outside of the coal swamps — particularly in small coal swamps. Regardless of potential sampling of non-coal-swamp plants, coal palynology samples indicate regional changes in diversity and can suggest with precision when major environmental changes occurred.

Beginning low in the Pennsylvanian, the species diversity is extremely low near the position of the Gentry Coal Member (Fig. 13) and, with the exception of the large diversity in the upper Caseyville, the first rise in diversity occurs just below the Smith Coal of western Kentucky and does not drop significantly until the decline between the Murphysboro and Colchester (No. 2). The large diversity of spores in several upper Caseyville coals may be due to contributions from plants surrounding the local coal swamps (Ravn, 1979; Ravn and Fitzgerald, 1982). The net rise below the Smith Coal apparently represents the collective result of the "first drier interval" with some introductions of plant species from outside the coal swamps, some evolution from within, minor extinctions, and continued rain of exotic spores from non-swamp plants.

Maximum turnover rate for the Pennsylvanian occurs at about the Rock Island (No. 1) Coal with little net loss of species diversity (Peppers, 1979). Peaks of high species diversity occur just below the Dawson Springs (No. 4) coal bed of western Kentucky and between the Colchester (No. 2) and Springfield (No. 5). Between these high levels in a significant drop in diversity between the Murphysboro and Colchester. In terms of loss (extinction and/or paleogeographic migration out of the area) this marks the last evidence from coal balls of *Pennsylvanioxylon birame* and *Lepidodendron vasculare* in the Illinois Basin — the producers of 86% of the biomass.

The maximum species diversity was reached in the interval between some of the largest coal swamps (Colchester and Springfield) with declines prior to the Herrin and Danville. The Herrin, which constitutes the largest coal resource in the Illinois Basin Coal Field, had one of the most homogeneous floras that we have observed.

The maximum loss of species occurred prior to deposition of peat for the Lake Creek Coal (Fig. 13). This low species diversity is comparable to that occurring below the Smith Coal. The low density in the Lake Creek Coal represents a time of considerable variation in coal-swamp and marsh vegeta-

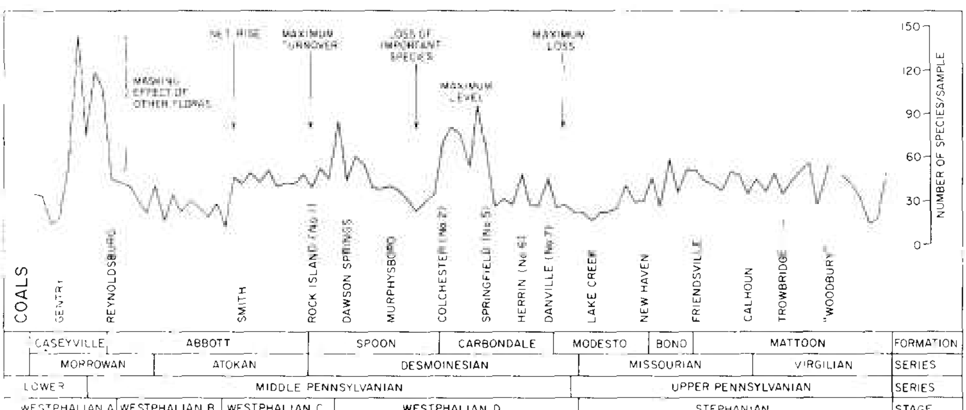


Fig. 13. Graph of species diversity of miospore floras in channel samples of Pennsylvanian-age coals in the Illinois Basin Coal Field with selected coals indicated. Adapted from Peppers (1979) and expanded with additional data. There is apparently a marked masking effect due to the incursion of spores from extra coal-swamp floras in the Morrowan, as in Iowa (Ravn, 1979). The first significant rise in species diversity occurred midway in the lower Middle Pennsylvanian; the maximum turnover rate (Peppers, 1979) occurred at Rock Island Coal time; there was a loss of important (dominant and subdominant) species between the Dawson Springs and Colchester Coals; the maximum level of endemic species is in the lower Carbondale and the maximum loss of species between the Danville and Lake Creek Coals.

tion following the extinction of all the previously important lycopod genera and several of the tree-fern species. This interval represents a transition during which coal-swamp communities were restructured from lycopod-dominated to tree-fern dominated ones.

While the subsequent Upper Pennsylvanian coal-swamp floras increased again in average species diversity, they never again attained the levels of diversity that existed in the Desmoinesian. Furthermore, the Upper Pennsylvanian diversity may be largely a function of the presence of many amphibious plants that had population centers in both coal-swamp and clastic-substrate areas. The coal-swamp flora was not as distinct from adjacent floras as it had been in the Desmoinesian.

Peat constituents of the coals

The shoot/root ratios of coals in the Spoon and Carbondale Formations overlap with but are generally higher than those from older coals (Table 5). While ratios of less than one are found at some sample sites in most of the coals, the shoot/root ratios generally increased stratigraphically with 1.6 as the average for the Murphysboro equivalent, 2.13 for the Summum, 2.29 for the Springfield and then 1.8 for the Herrin. The lowest and highest ratios (0.89 and 3.67) are from the Springfield Coal with the highest from lycopod-tree fern swamps within 0.5 km of the Galatia Channel. Most of the samples of the Springfield were taken from near paleochannels. Variations in ratios in three channel samples along a 10 m face in the Herrin Coal at AMAX Delta Mine of southern Illinois are 1.95, 2.72 and 2.46. A random sample of coal balls from the Herrin Coal at Sahara No. 6 Mine of southern Illinois was intermediate (1.48) between the two profiles (1.17 and 1.93) in the same area. Most of the botanical constituents of the Springfield and Herrin peat deposits are aerial plant material with periderm generally accounting for 33.1—38.7% of the biomass and wood 5.8 to 6.4%; periderm/wood ratios are in the general range of 5/1 to 6.7/1 (see also Phillips et al., 1977).

Despite the high shoot/root ratios the fusain content of the coals at most sites is relatively low, being usually in the range of 2.4—6.9%. The exceptions of 8.6—8.9% in the Springfield and 8.1—10.4% in the Herrin (see Harvey and Dillon, 1985) are in close proximity to major paleochannels except for the site in Burning Star Mine No. 4 in Illinois.

Regional variation in the vegetation of the Springfield and Herrin Coals

Some studies of the Springfield (Eggert et al., 1983) and Herrin Coals (Phillips et al., 1977; Phillips and DiMichele, 1981; Mahaffy, in press; DiMichele and Phillips, 1985) have emphasized both successional and lateral changes in coal-swamp vegetation, particularly in relation to the major paleochannel system contemporary with each of these major coal swamps. In the Springfield coal swamp, *Lycospora* (mostly from *Lepidophloios*) was greater in abundance near the Galatia paleochannel than elsewhere (Fig. 14). The area north of the plotted paleochannel system that has 40 to 60% *Lycospora*

TABLE 5

Peat composition (% biomass) of Desmoinesian (Westphalian D) coals in the Illinois Basin Coal Field based on profiles (VS) and random samples (RS) of coal-ball peat

Coal and Locality		Major taxa					Shoot/root ratios	Fusain	Sample size	
		Cordaites	Ferns	Lycopods	Seed-ferns	Sphenopsids			Coal balls	cm^2
Herrin										
Peabody Ken (KY)	VS2[a]	0.0	13.0	75.0	10.7	1.3	2.66	5.3	183	7,271
Peabody Eagle Surface (IL)	VS1	0.0	22.2	64.6	9.0	4.2	0.98	4.3	33	6,073
Sahara Mine 6 (IL)	VS2[a]	0.5	16.8	72.2	6.0	4.5	0.98	6.0	186	23,013
Sahara Mine 6	VS4[b]	<0.1	14.9	64.9	16.1	4.1	1.93	6.5	259	13,574
Sahara Mine 6	VS5[b]	0.2	16.6	63.4	15.4	4.4	1.17	6.6	201	12,635
Sahara Mine 6	RS2	0.6	14.9	61.3	16.3	6.9	1.48	6.4	53	4,675
AMAX Delta (IL)	VS1[a]	<0.1	11.1	72.1	14.2	2.6	1.95	6.5	96	2,695
AMAX Delta	VS2[a]	0.5	11.0	76.6	8.8	3.1	2.72	4.0	411	14,504
AMAX Delta	VS3[a]	1.8	13.7	63.2	19.7	1.6	2.46	5.8	67	4,960
Old Ben Mine 24 (IL)	VS3+5	0.1	12.0	77.8	7.4	2.7	1.67	10.4	325	16,238
Old Ben Mine 24	VS4	0.5	10.1	68.9	16.3	4.1	1.89	8.1	101	4,790
Springfield										
Consolidation Burning Star 4 (IL)	VS1[c]	0.0	23.6	63.8	5.9	6.7	2.0	8.9	110	7,166
AMAX Wabash (IL, IN)	VS1[c]+RS1	0.1	18.4	69.5	9.9	2.1	3.61	8.6	152	9,084
Lemmon Bros. (IN)	VS5	0.0	12.5	72.8	10.5	4.2	2.0	4.0	186	9,824
Peabody Lynnville (IN)	VS1-7	0.1	8.9	43.9	43.0	4.1	2.97	1.4	184	13,127
Houston Shaft (IN)	RS1[c]	0.4	18.1	55.8	24.4	1.3	0.89	0.8	60	2,727
Summum										
Peabody Northern Illinois, Pit 14	VS1	9.0	13.8	72.7	0.8	3.7	1.72	2.5	60	2,376
Peabody Northern Illinois, Pit 14	RS1+2	7.1	10.8	71.7	5.0	5.4	2.53	2.4	106	5,129
Unnamed coal at Maple Grove Mine (IN)	VSC2[d]	11.5	6.1	74.9	3.7	3.8	1.98	4.0	134	5,073
(Approx. = to Murphysboro Coal of	VS5[d]	8.1	1.9	85.3	0.6	4.1	0.96	6.9	51	2,192
Illinois)	VS7	17.2	5.1	70.9	0.9	5.9	1.82	4.3	79	2,402
	VS9	14.5	6.5	75.0	1.0	3.0	1.69	6.3	252	7,261

[a] Data published by Phillips et al. (1977).
[b] From Phillips and DiMichele (1981).
[c] Modified from Eggert et al. (1983).
[d] From Eggert and Phillips (1982).

Coal-ball samples represent only upper half of seam in Murphysboro and Summum Coal Members. Springfield coal-ball samples are derived from close proximities to paleochannels except for the Burning Star Mine site; profiles from the Lynnville Mine are traverses only in the upper split at Eby Pit. Total sample size = 3,289 coal-ball specimens with an area of 176,789 cm^2.

is also near portions of the Galatia system not shown in Figure 14 (see Eggert et al., 1983). The greater abundance of *Lycospora* in proximity to the paleochannels is consistent with these as the most continuously wet areas (perhaps long periods of standing water), strong dominance of *Lepidophloios*, high shoot/root ratios and the thickest coal deposits (Smith and Bengal, 1975). A similar pattern for the Herrin Coal was shown by Phillips and Peppers (1984) where the maximum abundance of *Lycospora* paralleled the Walshville paleochannel except in the vicinity of a lake or flood basin (Fig. 15) where the maximum abundance shifted to the lacustrine area.

There is a significant difference in the levels of abundance of *Lycospora* in miospore floras in proximity to the paleochannel systems of the Springfield (35—60%) and Herrin (65—85%) Coals. Spores of tree ferns are very abundant in proximity to the Galatia paleochannel system and despite the

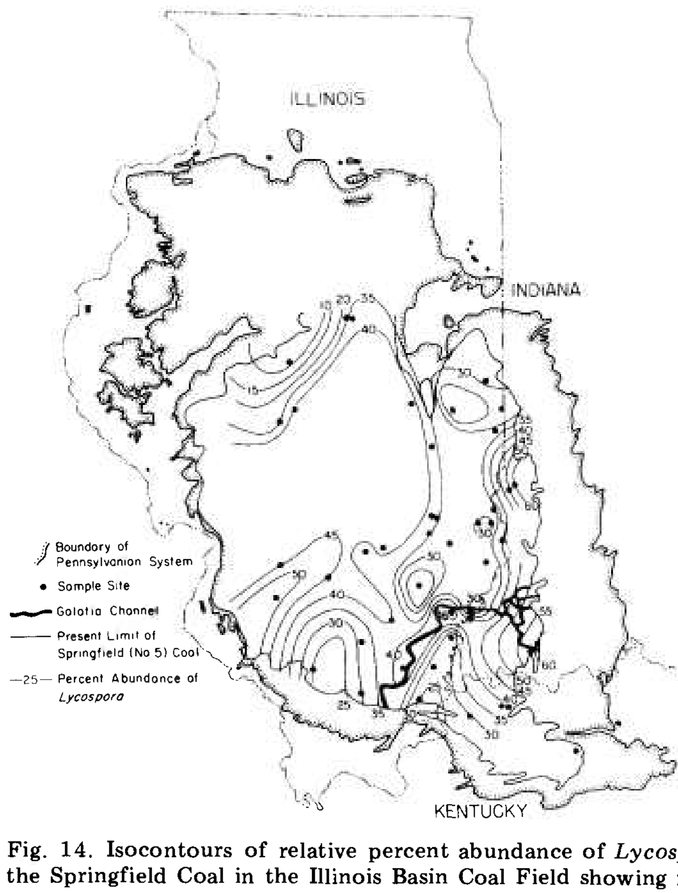


Fig. 14. Isocontours of relative percent abundance of *Lycospora* in channel samples of the Springfield Coal in the Illinois Basin Coal Field showing maximum abundance levels in proximity to the Galatia channel, especially the Indiana portions. High percentages shown north of the plotted paleochannel system also agree with data compiled by Eggert et al. (1983) that indicate a paleochannel is in that area. For further explanation see text and for comparison of similar patterns in the Herrin Coal Member see Phillips and Peppers (1984, fig. 11).

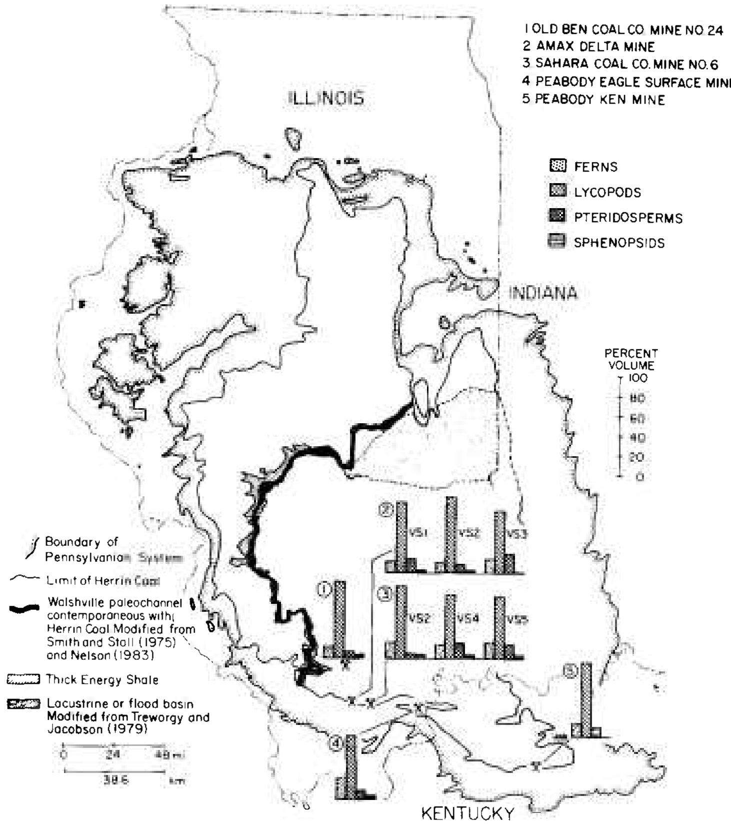


Fig. 15. West—east traverse across the Herrin Coal in selected mines in the southern part of the Illinois Basin Coal Field showing similar structural peat composition based on percent volume (biomass) of major taxa. The Herrin Coal is exceptional in the relative uniformity of abundance of major taxa across the heavily mined southern portion, but significant differences in the peat constituents are observed in the sites nearest the Walshvill paleochannel and in the extreme eastern portion (see Table 5 for summary data). Plotted data are derived from Phillips et al. (1977), Phillips and DiMichele (1981), and DiMichele and Phillips (1985).

significant fern biomass contribution of 8.9—18.9% to the peat, they are markedly over-represented in the miospore flora. This suggests that the vegetation growing along the levees could have been an important additional spore source (Eggert et al., 1983). Also, *Medullosa* occurs in greatest abundance at some of the sites (Table 5) and hence biases the estimates based on miospores. In the Springfield Coal there is a broad north—south area of low abundance of *Lycospora* in eastern Illinois along the north, northwestward trending La Salle Anticlinal Belt. The low of about 30% *Lycospora* along the Illinois—Indiana border is a sample from the AMAX Wabash Mine that is within 0.5 km of the Galatia channel, also the closest site to the channel sampled by a peat profile from coal balls. In this case the dominant lycopods were *Sigillaria* in the lower part of the profile and *Lepidophloios* in the upper part. There were abundances of other plants, such as *Sutcliffia* (medullosan seed fern), suggesting representation of what may have been some levee-type vegetation within the profile.

In general, estimates of vegetation based on peat and spores are in much closer agreement in the Herrin than in the Springfield. One can encounter almost as much variation in the peat composition along the coal face in a given mine (compare Sahara No. 6 with AMAX Delta, Table 5) as across most of the Herrin coal swamp (Fig. 15). The Springfield shows much more local variability with tree-fern spores most abundant to the east of the La Salle Anticlinal Belt.

Lepidophloios is most abundant in the Herrin Coal at the Old Ben Mine No. 24 (VS3+5 in Table 5) near the Walshville channel (Fig. 15) and the Peabody Ken Mine at the eastern margin of our sampling in western Kentucky. These two sites are also among the highest in lycopod biomass, 77.8% and 75%, respectively. The Ken Mine peat deposits were quite high in periderm, 38.9%, and lower than usual in wood, 2.0%, with a periderm/wood ratio of almost 20/1. These may have formed in a lacustrine or oxbow deposit; recent studies (Williamson and Williams, 1984) indicate a paleochannel system existed in that area, but it is not clear whether it was contemporary with the Herrin (Kentucky No. 11) Coal.

Coal-swamp vegetation and peat constituents of selected coals in the upper Pottsville and Allegheny Formations in the Appalachians

Miospore floras

Palynology of coals in the Appalachian Coal Region in the upper part of the Pottsville Formation and in the Allegheny Formation up to the Lower Kittanning Coal (Fig. 16) indicates that lycopods, ferns, and sphenopsids were rather evenly represented in the floras. The two oldest coals shown in Fig. 16, the High Splint (Pennsylvania and eastern Kentucky) and Lower Mercer (West Virginia), contain a relatively small percentage of *Lycospora*. The large percentage of sphenopsids (*Laevigatosporites desmoinesensis* and *L. vulgaris*), ferns (*Punctatosporites minutus*, and *Speciososporites minutus*), and herbaceous lycopods (*Densosporites*) in the High Splint coal suggests more open swamp vegetation possibly with periodic dryness or exposure of the substrate and consequently with higher nutrient levels.

Kosanke (1973) correlated the interval from the Princess No. 5B coal to the Princess (No. 9) coal with the interval from the Davis Coal Member to the Chapel (No. 8) Coal Member of Illinois. Palynology of the coals in this interval in the Appalachians is similar to that in the upper part of the Spoon Formation and the Carbondale Formation in Illinois (Peppers, 1970). The sphenopsid *Laevigatosporites* is greatly reduced in abundance above the Princess 5B coal, and fern spores increase significantly in the Middle and Upper Kittanning coals, the Rider coal, and Lower Freeport coal.

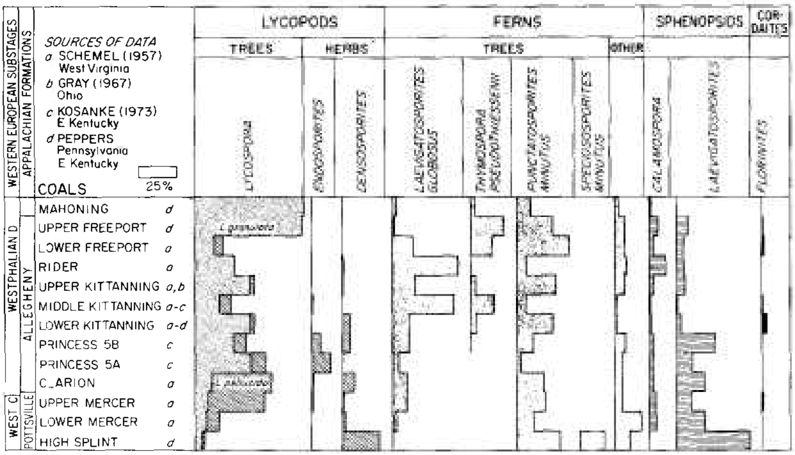


Fig. 16. Percent abundance of major miospore taxa from channel samples of selected coals in the uppermost Pottsville, Allegheny and lowermost Conemaugh of the Central and Northern Appalachians, based on sources indicated in the figure and the following: High Splint Coal (MAC. 2696 A-C), U.S. Steel Mine 32, 2.4 km W. of Kentucky-Virginia state line on side of Black Mountain, Harlan Co., Kentucky; Upper Freeport Coal (MAC. 2816), Pittsburg Plate Glass Company, Creighton Mine, Allegheny Co., Pennsylvania; and Mahoning Coal (MAC. 2789), W. side of Route 164, NE 1/2, SW 1/4 Sec. 29, Washington Township, Columbiana Co., Ohio. Princess 5A and 5B are names applied in the Princess Reserve District of eastern Kentucky; High Splint is a coal name applied in the Upper Cumberland Reserve District of eastern Kentucky.

The two youngest coals, the Upper Freeport and Mahoning coals, are dominated by *Lycospora* and probably formed in a very wet swamp populated by essentially the lycopod trees *Lepidophloios* and *Lepidodendron*. *Florinites* (cordaites pollen) is quite rare in all the coals represented in Figure 16. The paucity of cordaites in the lower part of the section contrasts sharply with the lower Desmoinesian patterns of the Interior Coal Province. The abundance of tree-fern spores is generally greater in the Allegheny Formation than that in the Spoon and Carbondale of Illinois and exhibits a sustained increase up to the two youngest *Lycospora*-dominated coals, Upper Freeport and Mahoning, the last of which is in the Conemaugh Formation.

Composition of peat

With the exception of the Tennessee coal referred to as the "High Splint" there are only two coal-ball sources known from the uppermost Pottsville to the top of the Allegheny Formation. Coal balls were reported from a coal referred to as above the Middle Kittanning Coal (Cross, 1967) or the Upper Kittanning (Ferm and Cavaroc, 1969) from western Pennsylvania. A collection of 35 coal balls (1,937 cm^2) from the site indicates that the biomass is composed of 45.5% lycopods, 34% seed ferns (mostly *Medullosa*), 12.5% ferns (mostly *Psaronius*), and 8% sphenopsids. As in coal of comparable age in the Illinois Basin Coal Field cordaites are rare or absent. The abundance of ferns is comparable to that of Illinois Basin coals, but such an abundance of seed ferns is found only in Illinois Basin coals in patchy sites close to the paleochannel system in the Springfield Coal (see Eggert et al., 1983). The shoot/root ratio is 1.38, and the fusain content of 2.6% is low. The amount of wood present is higher than usual, 10% (mostly calamitean), and periderm composes only 7% of the biomass.

The second occurrence of coal balls was reported from the Lower Freeport Coal of eastern Ohio by McCullough (1977, p. 128) who reported: "Lycopod periderm was the only identifiable floral constituent in 36% of the concretions. Twenty percent of the coal balls contained some amount of fusain-like material..." He also provides a table showing percent occurrences in 100 peels with lycopod periderm in 84, stigmarian roots in 48, *Myeloxylon* (*Medullosa* assemblage) in 44 and *Psaronius* in 24.

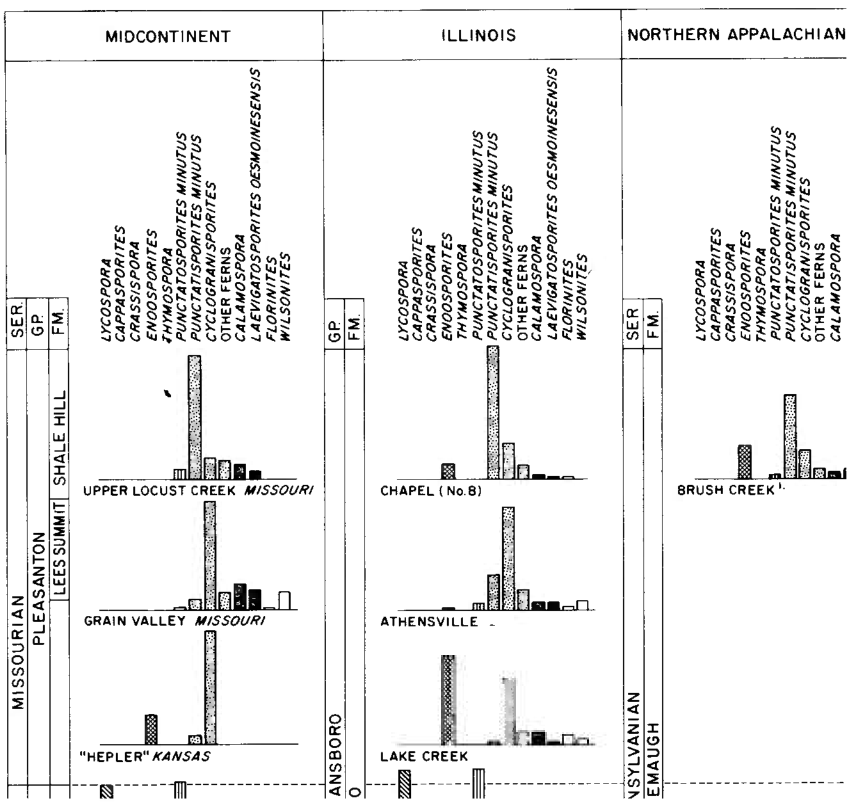
COMPOSITION OF COAL SWAMPS AND VEGETATIONAL CHANGES IN THE TRANSITION TO LATE PENNSYLVANIAN

Coal-swamp vegetation and peat constituents in the Illinois Basin Coal Field

Peat deposits occur in six Upper Pennsylvanian coals in the Illinois Basin Coal Field, extending across the Missourian into the base of the Virgilian (Fig. 1, also see Scheihing, 1978). In the Missourian the vegetation was strongly dominated by *Psaronius* in all the known peat deposits (Table 6, and the Parker Coal Member which is not included in the table), constituting 64.3 to 83.5% biomass (Willard, 1984; Galtier and Phillips, in press). Seed ferns, principally *Medullosa*, were subdominant accounting for 11.7—24.2% of the biomass. Lycopods, sphenopsids, and cordaites were generally minor contributors to the peat (up to 3.9%) except in particular coals and areas of the swamps.

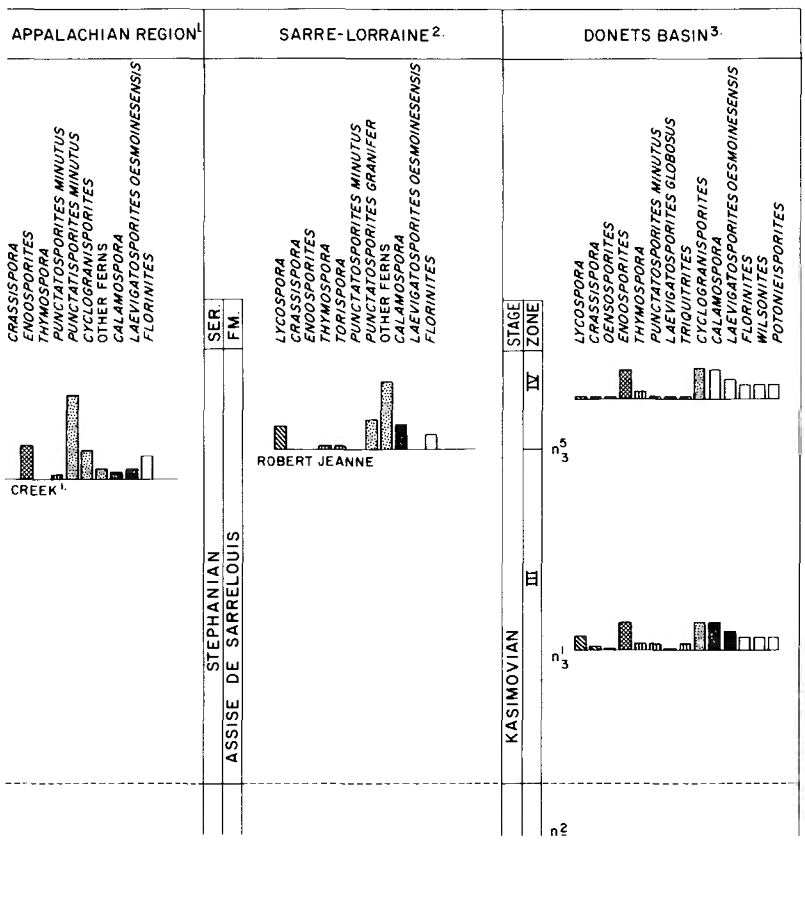
The distribution of other plant groups may well have been patchy in most Missourian coal swamps in south central Illinois; sampling is usually inadequate to document this. *Sigillaria* (lycopod trees) accounts for about 10% of the peat in the Bristol Hill Coal Member and in one random sample from the Calhoun Coal Member. In another sample of the Calhoun Coal calamites contributed almost 10% and seed ferns were twice as abundant as in the other Calhoun estimate. In the Friendsville Coal cordaites account for almost 10% of the peat, a record high for a paralic coal basin in the Upper Pennsylvanian. The Friendsville Coal was sampled in a grid system (Willard, 1984), and almost all the cordaitean peat was localized in one small part of the sample area.

All shoot/root ratios of Upper Pennsylvanian peats are near 0.5 (range 0.42 to 0.6) and must be interpreted differently than those of the Lower and Middle Pennsylvanian. The bulk of peat is composed of *Psaronius* roots, which largely formed the buttressing mantle of the trunks as well as the root systems in the substrate. Conservative estimates that treat 50% of the root material as aerial (Phillips and DiMichele, 1981) would reverse the "shoot"/



MIDCONTINENT
ILLINOIS
NORTHERN APPALACHIAN
SER.
GP.
FM.
MISSOURIAN
PLEASANTON
SHALE HILL
LEES SUMMIT
LYCOSPORA
CAPPASPORITES
CRASSISPORA
ENOOSPORITES
THYMOSPORA
PUNCTATOSPORITES MINUTUS
PUNCTATISPORITES MINUTUS
CYCLOGRANISPORITES
OTHER FERNS
CALAMOSPORA
LAEVIGATOSPORITES OESMOINESENSIS
FLORINITES
WILSONITES
UPPER LOCUST CREEK MISSOURI
GRAIN VALLEY MISSOURI
"HEPLER" KANSAS
ANSBORO
CHAPEL (No.8)
ATHENSVILLE
LAKE CREEK
NSYLVANIAN
EMAUGH
BRUSH CREEK

pp. 83–86


APPALACHIAN REGION[1]
SARRE-LORRAINE[2].
DONETS BASIN[3].
CRASSISPORA
ENOOSPORITES
THYMOSPORA
PUNCTATOSPORITES MINUTUS
PUNCTATISPORITES MINUTUS
CYCLOGRANISPORITES
OTHER FERNS
CALAMOSPORA
LAEVIGATOSPORITES OESMOINESENSIS
FLORINITES
CREEK[1].
SER.
FM.
STEPHANIAN
ASSISE DE SARRELOUIS
LYCOSPORA
CRASSISPORA
ENOOSPORITES
THYMOSPORA
TORISPORA
PUNCTATOSPORITES MINUTUS
PUNCTATOSPORITES GRANIFER
OTHER FERNS
CALAMOSPORA
LAEVIGATOSPORITES OESMOINESENSIS
FLORINITES
ROBERT JEANNE
STAGE
ZONE
KASIMOVIAN
IV
III
LYCOSPORA
CRASSISPORA
OENSOSPORITES
ENOOSPORITES
THYMOSPORA
PUNCTATOSPORITES MINUTUS
LAEVIGATOSPORITES GLOBOSUS
TRIQUITRITES
CYCLOGRANISPORITES
CALAMOSPORA
LAEVIGATOSPORITES OESMOINESENSIS
FLORINITES
WILSONITES
POTONIEISPORITES
n_3^5
n_3^1
n^2

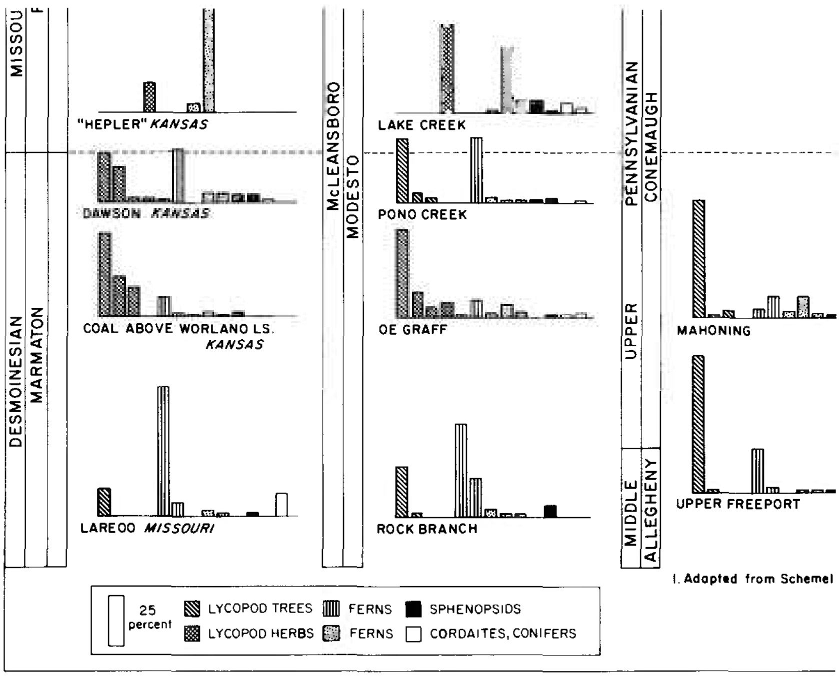
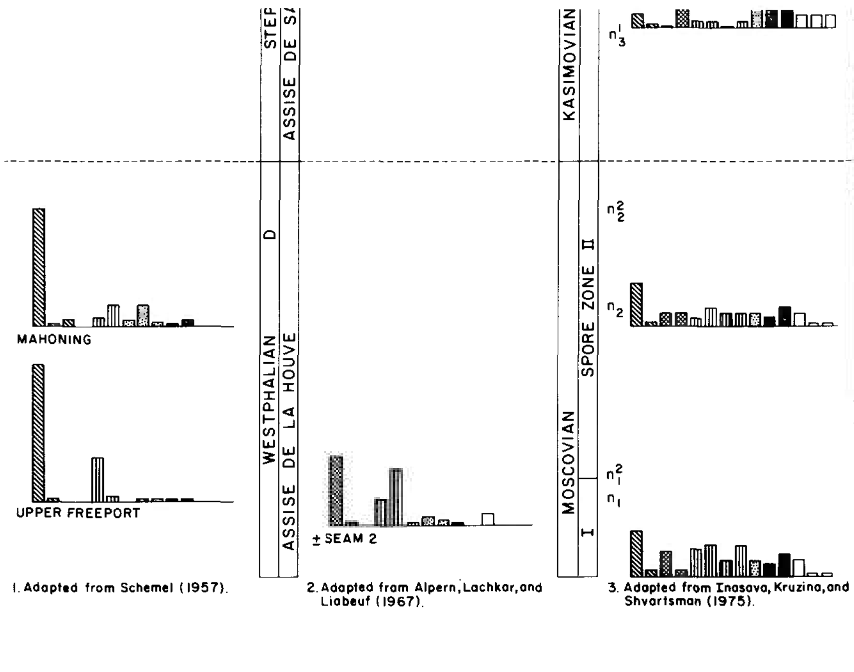


Fig. 17. Comparative histograms of percent of major spores in coals near the and equivalent assemblages. Data for those coals in the Interior Coal Province Data on the Appalachians are from Schemel (1957) with additions of the M published data are indicated in the figure.



n coals near the Desmoinesian—Missourian, Westphalian—Stephanian boundaries, or Coal Province (Midcontinent and Illinois) are derived from studies by Peppers. ditions of the Mahoning Coal (Philips and Peppers, 1984). European sources of

TABLE 6

Peat composition (% biomass) of Missourian (lower Stephanian) coals in Illinois based on random samples (RS) and profiles (VS) of coal-ball peat

Coal and Locality		Major taxa					Shoot/root ratios	Fusain	Sample size	
		Cordaites	Ferns	Lycopods	Seed-ferns	Sphenopsids			Coal balls	cm^2
Calhoun										
Berryville (outcrop)	RS1[a]	0.0	74.3	10.5	12.5	2.7	0.56	4.1	29	1,864
Berryville (outcrop)	RS2	0.3	64.3	1.9	24.2	9.3	0.6	3.6	100	5,933
Opdyke										
Dix (outcrop)	RS1[a]	0.0	83.5	0.0	15.7	0.8	0.43	1.4	38	1,460
Friendsville										
Allendale Coal Co. Mine	VS[b]+RS[a]	9.5	70.8	0.5	15.3	3.9	0.42	2.3	389	13,257
Bristol Hill										
Alpha Mining	RS1[a]+2[b]	0.2	76.5	9.7	11.7	1.9	0.44	14.9	105	3,190

[a] Data from these samples are given by Galtier and Phillips (in press).
[b] Data from these samples are from Willard (1984).
Total sample size = 661 coal-ball specimens and an area of 25,704 cm^2.

root ratios to about 2.0, but we have no anatomical means of distinguishing consistently between subterranean and aerial roots. The principal botanical components change in the transition to typical Upper Pennsylvanian peat deposits, from abundant bark and associated cortical tissues to mostly air-chambered (aerenchyma) roots, which were not only less resistant to decay, but also much more compactible. Peat to coal ratios would be much higher than in the Lower and Middle Pennsylvanian. Resin-rodlet abundance is noted in the coals (Lyons et al., 1982) because of the importance of medullosan seed ferns in the vegetation. The fusain in Upper Pennsylvanian peat is generally low (1.4—4.1%). The highest fusain level recorded, 14.9%, is in the Bristol Hill Coal (see comparable inertinite percentage in Harvey and Dillon, 1985).

Spore assemblages near Desmoinesian—Missourian and Westphalian—Stephanian boundaries

The major floral changes that took place at the Desmoinesian—Missourian and equivalent boundaries are illustrated by histograms of spore assemblages from coals adjacent to the boundaries (Fig. 17). Most of the coal samples from the Midcontinent Region were collected by Heckel and his colleagues (see Schutter and Heckel, 1985) as part of studies on the stratigraphic relationships and paleontology of different lithofacies in the cyclothems adjacent to the boundary. The histograms for the Sarre-Lorraine Basin were constructed from range charts showing the relative abundance of major spores in the Westphalian and Stephanian coals (Alpern et al., 1967). Histograms for the Donets Basin represent the spore populations of several coals that were diagrammed together within spore zones by Inosova et al. (1975).

The general patterns noted in spore assemblages from below to above the Desmoinesian—Missourian and the equivalent Westphalian—Stephanian boundary are the following:

(1) Lycopod trees, represented by *Lycospora*, dominate or nearly dominate the spore floras of coals immediately below the boundary. Above the boundary *Lycospora* is generally insignificant or absent.

(2) Coal-swamp *Lepidodendron*, represented by *Cappasporites* (except as reported in Europe), also disappears at the boundary.

(3) Marattiaceous tree ferns, represented by *Thymospora*, decrease progressively in abundance toward the Westphalian—Stephanian boundary, while those represented by *Punctatosporites minutus* increase in abundance.

(4) However, across the boundary into the Stephanian both *Thymospora pseudothiessenii* and *Punctatosporites minutus* nearly disappear.

(5) Marattiaceous spores dominated most of the paralic coal-swamp floras in North America and Europe above the boundary, but there is a distinct change in the taxa that predominate on each side of the boundary; *Punctatisporites minutus*, *Punctatosporites granifer*, and *Cyclogranisporites* rise to predominance in the Stephanian.

(6) *Chaloneria*, an herbaceous lycopod, represented by *Endosporites*, became abundant in coal swamps and marshlands of the Stephanian.

PERSPECTIVES AND INTERPRETATIONS OF INTERREGIONAL CHANGES IN VEGETATION

Perspectives

Impact of fluctuating environments

Pennsylvanian (Late Carboniferous) tropical coal-swamp environments reflect regional paleogeography. The fluctuating distribution of epicontinental seas, freshwater wetlands, lowlands of slight relief and the Allegheny (Hercynian) orogeny created the milieu for coal-swamp development. The extensive water cover along the southern half of the paleocontinent of Laurussia markedly influenced atmospheric moisture levels at a time when the paleoclimate also was being altered by the pole to pole formation of Pangaea, by a long-term net emergence of land, and by the orographic belts of Laurussia and Gondwana (Rowley et al., 1985). Oscillations in Pennsylvanian climate and tectonics created a dynamic mosaic of emergent land and wetlands that expanded and contracted. This caused the extinctions of many plant species and allowed establishment in swamps of many others.

"Holding capacity" between coal-swamp expansions

Swamplands, lakes, rivers and other wet habitats had "holding capacities" that affected the nature of sequential contraction and expansion phases of coal and clastic swamps. The nature of "holding environments" in which shrinking coal-swamp populations may have survived between times of major coal-swamp occurrences reflects both paleoclimate and basinal geology. It is from such areas, should coal swamps have become temporally or regionally discontinuous, that the competitive colonization of new coal-swamp areas would have occurred. Thus, vegetational analysis of a sequence of coals in a region indicate some of the selective environmental factors of the "holding areas" — namely "holding capacity". One extreme example is the "holding capacity" between coal swamps at the Middle—Late Pennsylvanian transition in the United States, which was negligible and marked by mass extinction. At the other extreme are the coal swamps represented by seams in the Carbondale Formation in the Illinois Basin Coal Field and equivalent coals in the Western Interior Coal Region. In this case, a potentially large "holding capacity" (including perhaps the overlapping of coal swamps through time) was part of the ecological fabric that allowed swamp floras to reach their maximum diversity.

The quantitative composition of coal-swamp vegetation changed significantly in some "holding areas" that existed between regional expansions of coal swamps. The fluctuations in the ecology of a single coal swamp during peat accumulation also have a bearing on the colonization and composition of subsequent coal-swamps.

Edaphic control and high threshold responses

Coal swamps were buffered against all but the most severe climatic (mostly moisture) changes because of the water-holding capacity of a peat substrate. The low pH, low availability of mineral nutrients, flooded conditions, and low oxygen levels of peat substrates, at least during part of a season, created edaphic conditions which excluded all but highly specialized plant species. As major environmental changes occurred, differential effects on coal-swamp species followed, suggesting distinct and different thresholds to ecological disruption.

Coal swamps were not only environments with unusual edaphic conditions, but they were affected by repeated fluctuations in water availability and significant disturbances, such as incursions of brackish water, fires and clastic influx. The dominant trees, such as lycopods or ferns, were highly adapted to disturbances. They grew quickly, required minimal nutrients, were composed mostly of non-woody tissues, had determinant growth or relatively small stature, generally large reproductive allocations, and reproductive bodies that were dispersed rapidly and extensively by wind and water.

On a peat substrate the dominant trees exhibit relatively high threshold responses to regional environmental changes and consequently provide an average guide to the most severe changes in climatic factors. When major floristic changes occurred they are found between successive expansions of coal-swamp sequences from one seam to the next, and these are the exception rather than the rule.

Interregional differences in coal-swamp vegetation

There are differences as well as similarities in coal-swamp vegetation among regions within the United States and between the United States and Europe. These differences are even greater between the Euramerican coal belt and its Cathaysian extension in the Stephanian and Permian. However, within the conterminous Euramerican area the timing of vegetational change is approximately synchronous in the major coal regions. Regional differences in tectonic setting, historical aspects of the vegetation, and local environmental differences may make the patterns of vegetational change somewhat different in each coal region, but these do not mask the synchroneity of the timing of change, which appears to be truly interregional.

Midcontinent and Appalachian regions

Rather subtle differences are detectable in spore floras of the Illinois Basin Coal Field and the Central Appalachians. New spore species appear at the beginning of the "first drier interval" in several coals lower in the Illinois Basin Coal Field than in the Appalachians (Phillips and Peppers, 1984, p. 213). At higher stratigraphic levels (near the *Paralycopodites* zone), new species appear in the Appalachian region several coals lower than in the

Illinois Basin. This shift in timing is consistent with an initial west to east drying trend (or increased seasonability) followed by a return to more moist conditions (or reduced seasonability) from the opposite direction.

Euramerican coal regions

The drastic changes in coal-swamp vegetation are transitional across the Middle—Upper Pennsylvanian boundary and are very similar in each of the major coal regions of the United States and Europe. However, an important difference between the vegetation on either side of the Appalachians is the continued presence of some *Lycospora*-bearing lycopods in Europe. This is possibly the result of a more asymmetrical change in the drying of the climate there (Hedeman and Teichmüller, 1971). There were apparently gradual transitions between Westphalian and Stephanian floras in the southern parts of Europe (the so-called Cantabrian Stage as in Spain; Wagner, 1966).

In both the Sarre-Lorraine (Alpern et al., 1967) and the Donets Basins (Inosova et al., 1975) the spore genus *Lycospora* continues to be found in coals of the Stephanian and Kasimovian but at markedly reduced abundance. In the Massif Central of France *Lycospora*-producing lycopods survived throughout the Stephanian in the limnic basins, detected as small percentages of the spore floras (Liabeuf et al., 1967). Occasional specimens of *Lycospora* have been observed in Virgilian coals in the Illinois Basin Coal Field (Peppers, 1985) and in the Appalachian Basin (Clendening, 1974).

Lepidodendron is reported from compression floras of the Stephanian of Spain (Lorenzo, 1979) and *Ulodendron* occurs in compression floras from the Kasimovian of the Donets Basin (Stschegolev, 1975). These provide megafossil evidence of the survival of lycopods in Europe that are missing in the Upper Pennsylvanian rocks of the United States. The particular kind of lepidodendroid lycopods that survived are not known with certainty, although that described by Lorenzo (1979) appears to be most like a coal-swamp *Lepidodendron*, the kind lacking infra-foliar parichnos. So far as we can ascertain the lepidodendrons did not extend into the Permian of Europe.

Cathaysian paleofloristic province

Based on compression floras vegetational changes that occurred in the Euramerican floristic province at the Westphalian—Stephanian boundary coincided with differentiation of the paleotropical belt into western Euramerican and eastern Cathaysian floristic provinces (Li and Yao, 1982). However, in contrast to the patterns in the United States and Europe, lycopod trees thrived in coal swamps and clastic environments of deposition (particularly seat earths and some roof shales but not in mineral-rich partings of coals) in the Stephanian and Early Permian of North China and in those of the Late Permian of South China. The lycopods include species of *Lepidodendron* as well as *Sigillaria*. Instead of a diminution in *Lycospora* at the Westphalian—Stephanian (Middle—Upper Carboniferous) boundary in North China (Shanxi Province), *Lycospora* attained its zenith in the coal swamps of the Stephanian, along with abundant Marattialean spores (Ouyang and Li, 1980). Other Euramerican trees found in Chinese coal-swamps include calamites and cordaites. Although quantitative peat data are not yet available from the Upper Carboniferous coal balls in the Xi Shan coal field of Shanxi Province, those from the uppermost Permian of southwestern China (Guizhou Province) are composed of *Lepidodendron*-like trees, *Psaronius* and cordaites in that order of importance. Much of the same kind of tropical coal-swamp vegetation that characterized the Euramerican coal belt of Westphalian time continued to flourish to the end of the Permian in Cathaysia.

Stratigraphic patterns and environmental inferences — major plant groups

Most of the paralic coal swamps of the Early and Middle Pennsylvanian of the eastern half of the United States were dominated on a "whole seam basis" by lycopod trees (Fig. 18). The dominant genera were *Lepidophloios*, coal-swamp *Lepidodendron*, true *Lepidodendron*, and *Paralycopodites*, all of which became extinct during the Middle–Late Pennsylvanian transition in the United States. Other important tree genera were *Mesoxylon*, *Pennsylvanioxylon*, *Psaronius* and *Medullosa*. These genera formed most of the peat biomass in the only coal swamps of the Midcontinent not dominated by lycopods during the Desmoinesian (in Iowa). All were subdominant to lyco-

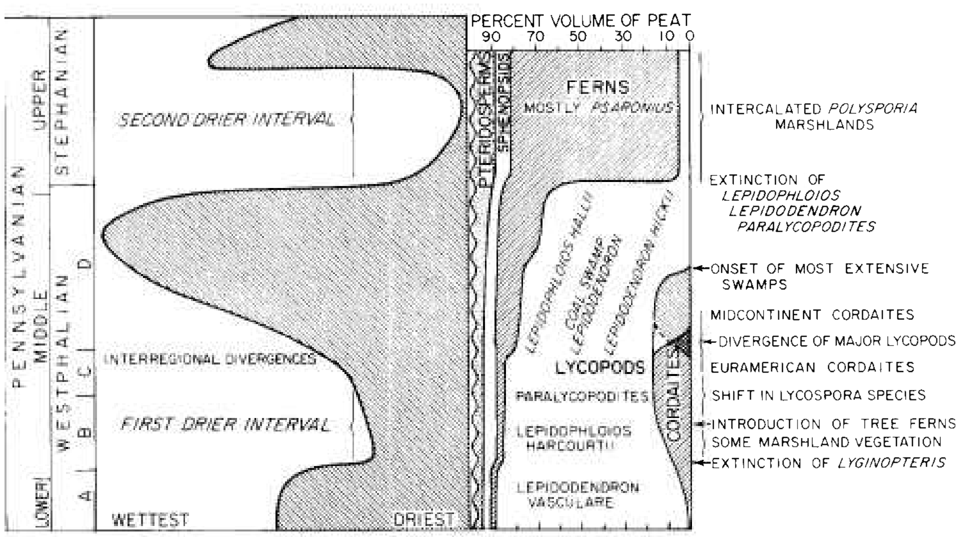


Fig. 18. Generalized stratigraphic patterns of abundance of Pennsylvanian coal-swamp vegetation in the United States with a relative wetness curve indicating the three most important times and kinds of changes. The vegetational diagram is based on distribution of spores and plants as well as other data available before 1980; the relative wetness curve is based on abundance of identified bituminous coal resources compiled by Phillips et al. (1980) plotted on a semi-log scale. Adopted and modified from Phillips and Peppers (1984, fig. 8).

pods in varied coal swamps during the Middle Pennsylvanian, and all the genera continued into the Late Pennsylvanian.

Lycopods

All of the lycopod tree genera were present in the earliest Westphalian coal swamps of Europe and the United States, but only *Sigillaria* and herbaceous lycopods such as *Selaginella*, *Sporangiostrobus* and *Chaloneria* survived into the Late Pennsylvanian in the United States. Despite the grossly similar architecture of lycopod trees, they exhibited significant differences in growth and ecological adaptations, especially as related to reproductive biology (Phillips, 1979; DiMichele and Phillips, 1985), resulting in segregation within coal swamps. Hence, they indicate different intraswamp conditions.

Factors controlling lycopod distribution appear to be complex, but one of the major elements was the water regime of the swamp. On a relatively wet to drier scale within the swamps, *Lepidophloios* probably dominated in the wettest areas with standing water. The next wettest habitats were occupied by lepidodendrons but appear to have been modified by disturbances to a considerable extent. Some species of coal-swamp *Lepidodendron* were tolerant of slightly brackish influences. True *Lepidodendron* trees also inhabited moderately wet but variable habitats and were dominant in some wet environments where the nutrient level was perhaps higher than usual for coal-swamps. True *Lepidodendron* and *Sigillaria* were common in wet-clastic environments of deposition during the Early and Middle Pennsylvanian; this is in marked contrast to the coal-swamp centered *Lepidophloios* and coal-swamp *Lepidodendron*. Species of *Paralycopodites* occurred in transitional environments from clastic to coal-swamp conditions or within coal-swamp sequences following disruptions and degradation of peat (lower water tables). Consequently, *Paralycopodites* was seldom dominant on a "whole-seam basis". *Sigillaria* was usually the least important lycopod tree in coal swamps except in the Upper Pennsylvanian.

Early and Middle Pennsylvanian coal swamps were developed mostly in the *Lepidodendron-Lepidophloios* habitat ranges. In some swamps, especially those of massive peat accumulation, the greatest overlaps occurred among lycopods. However, *Lepidophloios* seems mostly to co-occur, on a whole-seam basis, with either coal-swamp *Lepidodendron* or with true *Lepidodendron*, but not with both. The relative importance of lycopod-tree genera changed at the Lower—Middle Pennsylvanian and during several intervals within the Middle Pennsylvanian. With each of these changes there were accompanying increases in the importance of one or more of the other major groups of trees.

Lycopod communities of the Lower Pennsylvanian were mixed; *Lepidodendron vasculare* was generally most abundant, followed by *Lepidophloios harcourtii* and *Lepidodendron hickii*, with *Paralycopodites* and *Sigillaria* still less abundant. In the vegetational transition spanning the Lower—Middle Pennsylvanian boundary (near the Westphalian A—B boundary) *Lepidophloi-*

os harcourtii, cordaites, calamites, and herbaceous lycopods increased in abundance. A transitional stage, consisting of several coals in the lower Middle Pennsylvanian in which *Paralycopodites* was dominant, might be regarded as indicative of the end of the "first drier interval". Other plant groups increased in abundance more steadily, and dominance shifted from *Lepidophloios harcourtii* to trees that produced *Lycospora granulata* microspores.

During these changes in lycopod dominance the first major marine transgression occurred in the Illinois Basin Coal Field; this is represented by the Lead Creek Limestone Member in the upper Atokan of Indiana and western Kentucky. Subsequently, other marine transgressions occurred from the west into the Midcontinent during the early Desmoinesian. The abundance of lycopods dropped to the lowest level in the Middle Pennsylvanian in the Western Interior Coal Region. There was an influence of brackish conditions mostly in the Western Interior Coal Region but extending across the Illinois Basin Coal Field. As trees generally intolerant of brackish influence, most of the lycopods were displaced to freshwater habitats, with major exceptions among the coal-swamp lepidodendrons, especially *Lepidodendron vasculare*, which is inferred to be somewhat tolerant of such conditions. It was during and after this disruptive change in Midcontinent coal swamps that other species of coal-swamp *Lepidodendron* appear in abundance; *L. vasculare* subsequently disappears from the coal swamps.

In the upper Pottsville-Allegheny transition in the Appalachian Region, at about the same interval as the onset of brackish influence in the Midcontinent, *Lepidodendron hickii* appeared as a major element in those coal-swamp floras we have studied. The data are based on few peat deposits. Coal-ball deposits from the "High Splint" coal in Tennessee are dominated by *Lepidodendron hickii*. The only Allegheny coal balls that are quantified are from the coal above the Middle Kittanning coal of western Pennsylvania. They also exhibit a dominance of *L. hickii*. *Lepidophloios* also occurs in these peat deposits from Tennessee and Pennsylvania. We have insufficient coal-ball data to make comparisons with changes in vegetation indicated by spore floras. The spore floras indicate an increased abundance of *Lycospora pellucida* (*L. harcourtii*) from the Lower Mercer to the Clarion coal interval followed by a rise in abundance of *Lycospora granulata*.

Cordaites

The cordaites were the only gymnosperms known to achieve dominance or sole subdominance in any coal swamps (whole seam basis) in the Middle Pennsylvanian of the eastern half of the United States. In paralic coal basins the rise and decline of cordaites was entirely within the Middle Pennsylvanian. The two main kinds of assemblage are *Mesoxylon* with *Mitrospermum* ovules and *Pennsylvanioxylon* with *Cardiocarpus* ovules (Costanza, 1983). In the lower Middle Pennsylvanian *Mesoxylon* rose in importance from the beginning of the "first drier" interval until the middle Middle Pennsylvanian.

The abundance of roots of *Mesoxylon*, penetrating peats dominated by *Lepidophloios harcourtii*, a wet indicator, suggest that the two kinds of trees did not grow together and were adapted to different intra-swamp environments. The *Mesoxylon* organ assemblage (one natural species) existed from the earliest Westphalian. There is no evidence of aerating tissues in the root systems (Cridland, 1964) as in all the other coal-swamp trees. Instead, the larger roots (*Amyelon*) usually exhibit eccentric growth rings, apparently disruptions of root growth not evident in the trunk and branches. Such "growth rings" may be responses to seasonal or sporadic flooding for prolonged periods, a phenomenon somewhat similar to the formation of eccentric growth in modern cypress knees. The abundance of *Mesoxylon* without aerating systems apparently indicates tolerance of periodic flooding in coal-swamp environments at a time when the other main group of gymnosperms (seed ferns) and amphibious tree ferns were not yet important in coal swamps. It is interesting to note, in general, that cordaites and, to a lesser extent, calamites filled significant habitat gaps in the early Middle Pennsylvanian until *Psaronius* and *Medullosa* expanded as subdominant plants.

Only in what we infer to be brackish-influenced coal swamps of the early Desmoinesian did cordaites co-occur in peat deposits with abundant seed ferns and tree ferns. *Pennsylvanioxylon* was the most important genus, particularly *P. birame* with *Cardiocarpus spinatus* ovules (Costanza, 1983). The extreme cordaitean dominance and diversity occurred in the northern part of the Forest City Basin at the onset of the Desmoinesian. Cordaites were less abundant in younger coals of the Illinois Basin Coal Field and the Arkoma Basin than in the Forest City Basin. The stratigraphic importance of cordaites, as a whole, ended almost synchronously across the Midcontinent at about Iron Post and Springfield Coal time. In contrast to the lack of aerating tissues in the older *Mesoxylon* assemblages, the roots of cordaites in brackish-influenced coal swamps exhibited aerenchyma (Costanza, 1983).

The brackish tolerance of early Desmoinesian cordaites is founded on several lines of deduction. However, the mangrove-like habitat inferred for one particular species, *Pennsylvanioxylon birame*, should not be applied to all early Desmoinesian cordaites. The distribution of forest types in such swamps is thought to be fundamentally different from other coal swamps, but is not, as yet, resolved (Raymond, 1983; Raymond and Phillips, 1983; Raymond et al., 1984).

Psaronius tree ferns

The patterns of change suggested by the various estimates of relative abundance of *Psaronius* are the most dramatic and puzzling of any of the tropical trees. The sensitivity of miospore floras provides an interesting record of *Psaronius* in the Euramerican coal belt long before these plants can be documented by other means as an actually significant component of clastic-substrate or coal-swamp communities during the middle Middle Pennsylvanian. There appears to be some disparity between the earlier tree-fern spore record and the peat deposits up to near the beginning of Desmoinesian time; however, peat and spore data are in general agreement in the Hamlin Coal, which exhibited relatively few tree ferns. While such a spore record could be dismissed as extra-swamp in origin, there is also an apparent disparity with the generalized stratigraphic pattern of compression floras — the logical extra-swamp source for over-representation of tree-fern spores. Pfefferkorn and Thomson (1982) report an increase in tree-fern foliage in compression floras that could parallel that of tree-fern expansion in coal swamps; however, they lump their assemblages into such major stratigraphic intervals that comparisons are uncertain. Such extra-swamp abundance could add to the over-representation of tree-fern spores in some Desmoinesian and equivalent coal swamps.

The only modern analogs for the environmental tolerances of *Psaronius* are the living Marattiales, which hardly compare with the tree sizes of *Psaronius*. The Marattiales occur in the moist tropics as understory plants along the lower slopes of mountains up to about 2000 m in tropical and montane rainforests, especially on islands (Troll, 1970). Only one species (*Marattia fraxinea*) is not entirely tropical, occurring in the temperate but highly maritime parts of eastern Australia and on the North Island of New Zealand. Other modern tree ferns of the Filicales overlap the Marattiales environmentally and are much more widespread. They occur in mild temperate lowlands and wet tropical mountains; these tree ferns seem to be more tolerant of cool temperatures than the Marattiales. Moisture and altitude seem to be the limiting factors in their tropical or near tropical distribution (Troll, 1970).

The possibility exists that *Psaronius* might have been tolerant of slightly cooler temperatures, as exhibited by modern Filicalean tree ferns, and could have inhabited lower altitudes of mountains in the tropical belt; if not, then an alternative may be more temperate latitudes of Euramerica or other land masses. Such speculative considerations are perhaps appropriate in the case of *Psaronius* considering the conflict between miospore data and those from the peat and the compression-fossil records of the lowlands. Spore abundance that started to rise during the "first drier interval" may reflect "spore rain" from remote regions prior to actual expansion across the paleotropical lowland belt. Tree ferns did not dominate any of the compression floras prior to the upper Westphalian D (upper Desmoinesian). However, such ferns dominated 11 of 14 floras, being first or second in abundance in upper Westphalian D and younger floras (Pfefferkorn and Thomson, 1982).

We agree with the general interpretation of Pfefferkorn and Thomson (1982) that the response of the floras preserved in clastic rocks may be more rapid than those of the coal swamps. However, the change in tree-fern abundance in both clastic and peat-accumulating environments is one of rising importance during the wettest interval, the time of the largest coal swamps, and evidently, the most extensive shifts in habitable space. Once *Psaronius* became established in paleotropical habitats, its enormous capability for swift dispersal and fast growth led to rapid integration into existing vegetation especially in disturbed habitats.

The shift to tree-fern dominance just above the Middle—Upper Pennsylvanian boundary is the most drastic permanent change in coal-swamp vegetation following the lycopod extinctions. This change is much more complex than the generalized data plots indicate. Several major species of *Psaronius* also suffered extinction or near extinction. Lycopods and several other kinds of plants dominated the intervening coal-forming environments between the abrupt decline in *Lepidophloios*, *Lepidodendron* and *Paralycopodites* and the clear establishment of *Psaronius* dominance. *Psaronius* generally dominated coal swamps thereafter and extended into the Permian as a major tree in peat-accumulating environments of limnic (Galtier and Phillips, in press) and paralic coal basins of the paleotropical belt.

Lyginopteris and Medullosa seed ferns

The stratigraphic patterns of change in distribution of seed ferns consists of two parts, one for the liana-like to shrubby *Lyginopteris* and one of *Medullosa* trees. In the Early Pennsylvanian the larger seed ferns were mainly represented by a robust vine, *Lyginopteris*. It was cosmopolitan like many other seed ferns in clastic and peat-accumulating environments. *Lyginopteris* became extinct just above the Lower—Middle Pennsylvanian boundary in the United States and just above the Westphalian A—B boundary in Europe (Patteisky, 1957; Gillespie and Pfefferkorn, 1979). This extinction at the onset of the "first drier interval" is most conspicuous and coincides with the extinction of the spore *Schulzospora*.

Medullosa was larger than *Lyginopteris* but still small in relation to lycopod trees. *Medullosa* was uncommon in early Westphalian peat deposits, and there is a decided lag between its rise in importance and the earlier extinction of *Lyginopteris* (Phillips, 1980). *Medullosa* did not substantially increase in abundance until near the middle of the Middle Pennsylvanian at about the same time that *Psaronius* became abundant. While medullosans were generally diverse and dominant kinds of trees in moist lowlands of the Pennsylvanian (Pfefferkorn and Thomson, 1982; Peppers and Pfefferkorn, 1970), species of *Medullosa* apparently did not expand into coal swamps during the "first drier" interval, as did cordaitean gymnosperms. *Medullosa's* most characteristic distributional pattern is one of fluctuating and increasing abundance upward to the upper Middle Pennsylvanian, followed by a more sustained level of abundance thereafter. *Medullosa* exhibited more of a patchy distribution than the other main types of trees. In general, *Medullosa* parallels the abundance patterns of *Psaronius* usually at lower and more inconsistent levels. Abundance of *Medullosa* suggests higher nutrient levels in the peat; it occurs near mineral-rich bands within the coal, and is associated often with high fusain levels to which *Medullosa* was a major contributor.

Interregional vegetational patterns in relation to environment

While this study deals principally with one suite of environmental conditions, those of coal swamps, the Pennsylvanian Period was an age of wetlands in which the patterns of vegetational changes in coal-swamps were hardly separable from those of other vegetation of the tropical belt. With the onset of the Pennsylvanian, the changing paleogeography of drylands and freshwater wetlands seems to have reinforced the evolutionary differences in reproductive biology and growth of trees that originated in the Mississippian or earlier. Gymnosperms were the best adapted to dispersal and slow growth in the dryland habitats, while lower vascular plants, especially the heterosporous lycopods and the calamitean trees, dominated wetlands. The greatest overlap of habitats was in the clastic-rich wetlands.

The combination of a dynamic tropical climate in concert with markedly changing habitats greatly influenced the adaptive patterns that emerged among the five basic kinds of trees. Trees were the most important elements of most plant communities and every major group exhibited arborescent forms. The limits imposed by growth-rate and habit, physiology, and reproductive biology were such that at the beginning of Pennsylvanian time: (1) lycopods totally dominated the coal swamps and represented most of the arborescent diversity; (2) other lycopods and calamites dominated the clastic swamps; (3) pteridosperms characterized the moist lowlands; and, (4) cordaites were apparently most abundant in the drier lowlands where conifers evolved during the Early Pennsylvanian (Peppers and Pfefferkorn, 1970; Oshurkova, 1977; Scott and Chaloner, 1983). The transitional environments that changed between drylands, clastic-rich wetlands and coal swamps apparently constituted recurring habitat space that any of the main kinds of trees could occupy, depending on migration rates and duration of the habitat. Preemption of habitat space was important, but we have no compelling evidence that communities were largely structured by competition between major kinds of trees (lycopods, sphenopsids, cordaites), which had markedly different adaptations.

"First drier interval"

The beginning of vegetational change near the Early—Middle Pennsylvanian transition (Peppers, 1979) was detected by changes in relative abundances of many kinds of spores and plants. The principal coal-swamp changes included:

(1) the rapid expansion of *Lepidophloios harcourtii* (a wet indicator) and a significant decrease in the importance of *Lepidodendron vasculare*;

(2) concurrent fluctuating abundance of herbaceous lycopods (Densospore marshlands) within coal swamps, and the appearance of *Chaloneria* (marshlands);

(3) increase in abundance of small cordaitean trees to subdominant levels, and increase in calamites;

(4) extinction of *Lyginopteris*; and

(5) the "rain" of tree-fern spores, increasing stratigraphically in diversity and quantity but lacking confirmation in peat deposits.

The overall pattern of vegetational change suggests a fluctuation in freshwater regime that resulted in oscillating wet and drier conditions within individual coal swamps and between sequential coal swamps (seams). This pattern is consistent with erratic monsoonal circulation and varied seasonal availability of freshwater. If the "first drier interval" can be explained as marked fluctuation of wetness due to monsoonal circulation, then the most likely paleogeographic change is the rise of a transequatorial orographic barrier, the ancestral Appalachian highlands (Rowley et al., 1985).

Floristic patterns of change that can be interpreted as migration outside the coal swamps are provided by the compression-floral zonation of Read and Mamay (1964), which recognizes Zone 7 (Zone of common occurrence of *Megalopteris* spp.) as occurring concurrently with the beginning of the "first drier interval". The *Megalopteris* flora, which includes cordaites and apparently some of the earliest *Pecopteris* foliage from tree ferns, is considered a drier-type flora. The observations of Read and Mamay (1964), Cross (1977), Leary (1981), Leary and Pfefferkorn (1977) suggest the possibility of a "*Megalopteris* flora" migration eastward to, but not beyond the transequatorial Appalachians, while the *Lonchopteris* flora existed on the European side (Read and Mamay, 1964; Dix, 1934). This would be consistent with a reduction in moisture from the east. Cross (1977) provides another explanation of *Megalopteris* distribution.

End of the "first drier interval" and onset of wetter environments

The paleobotany of coal swamps between the waning of the "first drier interval" and the middle Middle Pennsylvanian is beset with the incongruities of marine transgressions from the east prior to those from the west. Changes in the paleogeography that took place during this time are the initial shift of major coal swamps from the southern half of the central Appalachians to the northern half and expansion of major coal-forming areas in the Midcontinent. If the interregional stratigraphic correlations (Fig. 1) are approximately correct in the middle part of the Middle Pennsylvanian, the differences in patterns of coal-swamp vegetation in the Appalachians and Midcontinent are at least slightly asynchronous. The lack of close synchrony is perhaps compatible with the key environmental controls, which differed from east to west.

If a modest mountain range, the transequatorial Appalachians, were a paleoclimatic factor in the tendency for monsoonal circulation in the "first drier interval", the gradual return of wetter conditions toward the middle of the Middle Pennsylvanian and progressively into the Desmoinesian of the Midcontinent would require either a lowering of such a barrier or the further elevation of such mountains to form what Rowley et al. (1985) term a "high-altitude heat source". The latter model would be compatible with increased rainfall in the Appalachians as a developing interior mountain range within

Pangaea. As Rowley et al. (1985) pointed out, such a high-altitude heat source could theoretically offset some easterly flow (as an orographic barrier) and also the tendency for north—south monsoonal circulation by shifting some flow from the west (Rowley et al., 1985). If substantial moisture from transgressive epicontinental seas existed in the west, during Desmoinesian time, abundant rainfall could have been delivered by westerly flow into the Appalachians. Rainfall would have been augmented by the Michigan River System in the Midcontinent.

The "high altitude heat-source" model of Rowley et al. (1985), although highly speculative, would be consistent with a major Appalachian orogeny and barrier, increased erosion and sedimentation rates, and sustained water supply to the largest coal swamps. In the Midcontinent the beginning of major marine transgressions no doubt played an important role in the amelioration of a more moist paleoclimate as did the freshwater damming effect on large deltaic plains resulting in extensive coal-swamp development. It also is plausible that, given an adequate freshwater regime, subsidence patterns would effect the stratigraphic pattern of coal abundance — thus, making it an environmental variable independent of paleoclimate. Such subsidence-tectonic factors could create stratigraphic patterns difficult to separate from paleoclimatic wetness.

Most of the Midcontinent was topographically unsuitable for significant coal deposits before the Desmoinesian; exceptions are noted in the Hartshorne coal beds of the Arkoma Basin and the Bell coal bed of western Kentucky and Lower and Upper Block Coal Members of western Indiana in the Illinois Basin Coal Field. As sedimentary infilling and deltaic platforms increased in size there was a concomitant change in coal-swamp vegetation suggesting an increase in freshwater availability in the Midcontinent. This offset the earlier brackish influences that began with the Mariah Hill Coal bed in Indiana and western Kentucky and, a little later, the Rock Island Coal and equivalent coals. "Wetter" swamps probably reflect a combination of more water influx and markedly changed paleogeography due to basin infilling. This progressively wetter regime is well documented regardless of its proximate cause, by the rising importance of *Lepidophloios*, which is indicative of the wettest conditions, in both the Western Interior Coal Region and the Illinois Basin Coal Field. The level of wetness, possibly the least seasonal climate, seems to have peaked in the Midcontinent at about the time of the Springfield and Herrin Coals and equivalents, which are characterized by *Lepidophloios*, coal-swamp lepidodendrons and *Psaronius* generally in that order of importance.

Onset of the driest interval

The threshold level of late Middle Pennsylvanian coal-swamp trees was not significantly affected until conditions reached a catastrophic level near the Middle—Late Pennsylvanian boundary. It is the mass extinction of coal-swamp vegetation, particularly some lycopod genera, that originally recalled the attention of paleobotanists to the paleoclimatic importance of the Desmoinesian—Missourian (Westphalian—Stephanian) boundary (Phillips et al., 1974). This does not constitute the lowest moisture level for the early Late Pennsylvanian, but it does suggest that at some point the "holding capacity" of wetlands reached the lowest for the Pennsylvanian up to that time. This low "holding capacity" was of sufficient duration as to cause the interregional extinction of many coal-swamp centered trees. The truncation of stratigraphic ranges is so apparently geologically abrupt as to elicit concern over unconformities or disconformities in which the actual stratigraphic succession of change has been lost (Tschudy, 1969). While this is a possibility, the subsequent pattern of coal-swamp vegetational change, a series of coal by coal changes in dominance by trees or herbs other than the typical Middle Pennsylvanian lycopods or the Upper Pennsylvanian tree ferns, strongly suggests a mosaic transition rather than a major break in the stratigraphic succession.

As with compression floras in the "first drier interval", there is a marked west to east migrational shift in drier adapted gymnosperm floras during the "second drier interval". In the far west conifers begin appearing in the late Desmoinesian (Read and Mamay, 1964) while cordaites and conifers appear in the middle to late Missourian deposits of Kansas (Elias, 1936; Winston, 1983: Mapes, 1984) and subsequently migrate into the major coal regions of the United States. The floral migrations of the late part of the "second drier interval" resemble some Early Permian distributional patterns when the paleotropical belt underwent further drying.

While the return of conditions more favorable for peat preservation did occur at the beginning of Monongahela and equivalent time, there is little information on the actual coal-swamp vegetation except that *Psaronius* continued to be dominant, probably with subdominant *Medullosa*. There may have been increased provinciality (Phillips, 1980). In the United States, for example, *Medullosa*, *Arthropitys* (calamites) and *Psaronius* were locally abundant in that order in small random samples of peat from the Newcastle coal of Texas (Phillips, 1980) near the Pennsylvanian-Permian boundary. In the Autunian of France *Psaronius* and *Arthropitys* were the main biomass contributors to the peat (Galtier and Phillips, in press).

The occurrence of a few significant coal deposits from the Midcontinent to the Dunkard Basin, beginning with the Pittsburgh coal is evident in the occurrence of the Nodaway and Elmo coals of Iowa and Kansas and coals in a borehole in western Kentucky, which are stratigraphically higher than any previously known from the Illinois Basin Coal Field (Hower et al., 1983; Phillips and Peppers, 1984). It should be noted that Hower et al. (1983 p. 1477) have reported abundant *Thymospora thiessenii* (a species abundant in the Pittsburgh coal) from the two upper coals (Virgilian) as well as a few percent of *T. pseudothiessenі*, which was not previously considered to extend into the Virgilian in the Illinois Basin Coal Field.

Pennsylvanian bituminous coal resources and coal-swamp vegetation

The stratigraphic distribution of identified bituminous coal resources of the Appalachian Coal Region and the Interior Coal Province were suggested (Phillips et al., 1980; Phillips and Peppers, 1984) as an approximate guide to relative wetness during the Pennsylvanian Period in the eastern United States; this implies that other environmental conditions were also conducive to peat accumulation and burial. The data were compiled in order to test relative wetness as suggested by the dominant trees (Fig. 19). The stratigraphic basis for comparison began at approximately the middle of the Lower Pennsylvanian (lower Westphalian A equivalent) and extended into the basal Virgilian of the Interior Coal Province.

Paleoclimatic factors, perhaps most importantly the availability of freshwater or the balance from rainfall, runoff and evapotranspiration, probably had a major impact on the structure of coal-swamp communities. What we infer as relative wetness may, in fact, be increased or decreased seasonality

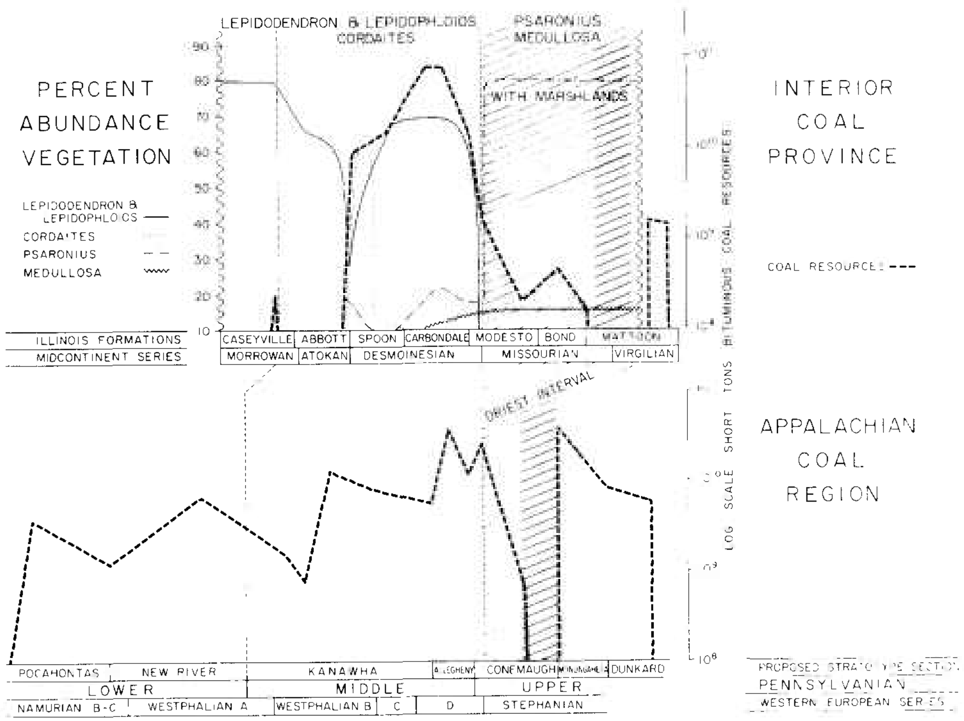


Fig. 19. Comparative stratigraphic distribution of groups of Pennsylvanian plants and bituminous coal resources in the Interior Coal Province and the Appalachian Coal Region. Plots of identified bituminous coal resources (Phillips et al., 1980) are overlain with generalized patterns of the percent abundance of major groups of coal-swamp plants for the Interior Coal Province to show relative changes in relation to paleoclimate. The percent abundance of vegetation begins at the 10 percent level.

of moisture availability. Our data do not allow this level of resolution. Other factors also may have been as important as climate. Thus our perception of relative or seasonal wetness has to be considered cautiously as a rough guide. While it is consistent with numerous other lines of reasoning, such data are not exclusively a measure of paleoclimate. They reflect the interaction of paleoclimate and the causal and modifying factors of paleotectonics and its effect on eustatic changes of sea levels, paleogeography, basinal geologies and, hence, rates of subsidence and sediment accumulation. Thus, the abundance of coal resources provides a basis for determining approximately when major changes ensued in the paleoenvironment defined by these interacting factors.

In general, the coal resource patterns suggest the following (Fig. 19):

(1) A "first drier interval", perhaps due to increased fluctuation or seasonality of available moisture, and a stratigraphic decline in coal resources in the lower Middle Pennsylvanian in the Appalachian Region;

(2) An increasingly wetter (less seasonal) interval of maximum coal resources in the upper Middle Pennsylvanian possibly modified by rates of subsidence that allowed thick coals to accumulate;

(3) A second and more severe drier interval and a marked decline in coal resources to a minimum in the lower Upper Pennsylvanian.

The most compelling evidence for a major paleoclimatic role in these patterns is the synchronous (or nearly so) times of change and the similar resulting vegetational patterns despite the interregional difference in floras and basinal tectonics.

The general decline in lycopod dominance during the beginning of the "first drier interval" occurs at the same time as the decline in the coal resources of the Appalachians. Shoot/root ratios also decline to a minimum at this time in the Upper Path Fork coal, and fusain content rises, becoming relatively high for such a low shoot/root ratio. The decline of lycopods and concomitant rise of cordaites in the Interior Coal Province is significantly different from the pattern seen in the Appalachians. The ensuing vegetational change back to lycopod dominance with rising abundance of tree ferns and seed ferns is accompanied by progressively higher shoot/root ratios and moderate fusain levels. These changes suggest wetter coal swamps more favorable for peat accumulation and preservation.

The beginning of the "second drier interval" brings together pronounced changes in vegetation, particularly extinction, and a shift to a tree-fern dominance. These clearly are tied to loss of "holding capacity". The actual set of factors causing such a severe vegetational change is probably much more complex than simply a "drier climate" although that is the net result. A major regression (see Schutter and Heckel, 1985) near the Middle—Upper Pennsylvanian transition, a subsequent major marine transgression (Ames Limestone and equivalents) (Vail et al., 1977; Crowell, 1978; Busch and Rollins, 1984), decreased rainfall and runoff, and changes in erosion, sedimentation and subsidence rates may have combined to the point of causing a minimum of coal resources in the upper Conemaugh and equivalents.

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