Quantitative Analysis and Paleoecology of the Secor Coal and Roof-Shale Floras (Middle Pennsylvanian, Oklahoma)

WILLIAM A. DIMICHELE

Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560

TOM L. PHILLIPS

Department of Plant Biology, University of Illinois, Urbana, IL 61801

GERALDINE E. MCBRINN

Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560

PALAIOS, 1991, V. 6, p. 390–409

The Secor Coal of Oklahoma (Boggy Formation, lower Desmoinesian/Westphalian D equivalent) is one of the few coals discovered, to date, in which Anabathra pulcherrima (=Paralycopodites brevifolius) *was a dominant element.* Anabathra *and* Lepidophloios *define the major assemblages in the coal, which also contains elements of medullosan pteridosperms and* Cardiocarpus spinatus *producing cordaites. The* Lepidophloios *to* Medullosa *gradient is not obscured by the numerous* Anabathra*-dominated zones, and a disturbance element is suggested in association with* Anabathra *abundance. Comparison of the coal-ball flora with a clastic-compression flora from the roof of the coal reveals widely divergent patterns of dominance and diversity. The compression flora is strongly dominated by medullosan pteridosperms with subdominant marattialean tree ferns. As in most instances, the compression flora from the immediate roof of the coal is not an accurate representation of the peat-forming vegetation, at either the level of species composition or the relative abundance of major groups of plants. The swamp and surrounding clastic deltaic environments were edaphically distinct and supported separate floras between which there was limited species exchange.*

INTRODUCTION

The lowland tropics of the Pennsylvanian Period were characterized by a diverse, complex vegetation (Gastaldo, 1987; Phillips et al., 1985; Scott, 1978). The most characteristic floras of the lowlands were those of peat-forming environments, dominated by lycopsid trees for most of the Early and Middle Pennsylvanian, with areas and times of increased cordaitean abundance (Phillips and Peppers, 1984; Phillips et al., 1985). The plant communities of these wetlands, and the swamps in particular, are often visualized as heavily forested and fairly monotonous vegetation, an image of sameness over vast areas and long periods of time. However, quantitative studies of megafossils and microfossils from coals (Peppers, 1970, 1979; Phillips and Peppers, 1984; Phillips et al., 1985) and from compression floras (Pfefferkorn and Thomson, 1982) demonstrate definitively that there were significant changes in lowland, wetland floras through time. These changes follow a stratigraphic pattern that correlates with changes in coal resource abundance (Phillips and Peppers, 1984) and with geochemistry of coal and associated rocks (Cecil et al., 1985; Cecil, 1990), which implicate climate as a major factor influencing floristic change.

Detailed studies of Pennsylvanian peat swamps have revealed considerable vegetational heterogeneity within any one swamp (DiMichele and Phillips, 1988; Feng, 1989; Phillips and DiMichele, 1981; Pryor, 1988; Raymond, 1988). Such community level studies have identified a great variety of vegetation types, from nearly monospecific forests to shrubby, scrub-like vegetation, to marsh-like assemblages of plants.

The occurrence of coal balls in the Secor Coal of Oklahoma allows examination of the source peat-swamp flora of this coal over an area of several square miles. Associated compression fossils occur in a gray-shale split between the

0883-1351/91/0006-0390/$3.00

Secor Coal and the overlying Secor Rider Coal, and provide the opportunity to contrast the peat-forming flora with a contemporaneous flora growing outside the swamp in surrounding wetlands. The vegetation of this coal is unusual in its extreme dominance by *Anabathra pulcherimma* (=*Paralycopodites brevifolius*; Pearson, 1986) a small lycopsid tree that appears to have been a colonizer with preference for parts of peat-swamps disturbed by irregular flooding and some clastic influx (DiMichele and Phillips, 1985, 1988; Eble and Grady, 1990; Calder, in press). Localized *Anabathra* dominance is known from thicker coals (e.g., the Herrin Coal of Illinois; DiMichele and Phillips, 1988), but dominance at a landscape level in peat swamps is rare.

MATERIALS AND METHODS

Stratigraphy

The Secor Coal Member is in the Boggy Formation of the Krebs Group in Oklahoma. It is of Desmoinesian age (Friedman, 1978), approximately equivalent to the early Westphalian D of western Europe (Phillips et al., 1985). The coal is present in the southern part of northeast Oklahoma shelf and in the adjacent Arkoma Basin. In northeastern McIntosh County, the Secor Coal is a single bed. To the south, southwest and northwest of this area, the seam splits into a thick lower bench, the Secor Coal by convention, and a thin upper bench, the Secor Rider, separated by terrestrial shales and sandstones, with uncommon, locally developed marine rocks (Hemish, 1988). The Secor Rider Coal is thin and high in ash (>20%) and sulfur with a marine shale roof throughout its extent. Coal balls and compression fossils occur in areas of split coal. The split and characteristics of these two benches are described by Hemish (1988).

Compression Fossils

Carbonized compression fossils were collected from light to medium gray, silty mudstones between the Secor and Secor Rider coals. Two collections were made, one in 1979, the other in 1981, at the Capital Construction Company of Oklahoma, Alpine Mine No. 2, N ½, SE ¼, NE ¼, Section 22, T. 12N, R. 17E, 7½′ Oktaha Quadrangle, McIntosh County, Oklahoma (Fig. 1). Specimens are housed in the Smithsonian Institution, National Museum of Natural History, under USNM Locality Number 38362, and in the Paleobotanical Collections, Department of Plant Biology, University of Illinois. All illustrated materials are housed at the NMNH.

Coal Balls

Coal balls were collected from spoils at three locations (Fig. 1). A total of 487 coal balls was analyzed, comprising 19,147 cm^2 of quantified surface area.

McAlester: Small random samples were made at an abandoned slope mine belonging to Joe Lemont near McAlester, in Pittsburg County, Oklahoma by Charles B. Read in the 1930's and by Sergius Mamay and Ellis Yochelson in the 1950s. Mamay and Yochelson (1962) located the site at the common corner of Sections 26, 27, 34, and 35, T. 5N, R. 14E, 7½′ Savana Quadrangle. The random sample analyzed in this study is housed in the Paleobotanical Collections, University of Illinois; coal balls bear the following accession numbers: 2022, 2039, 2050, 2052, 2059, 9165, 9864, 9865, 9872, 9873, 9891–9896, 9928, 9929, 9930–9932, 10471, 10473, 10475. Additional collections are housed in the National Museum of Natural History under USGS locality number 8764.

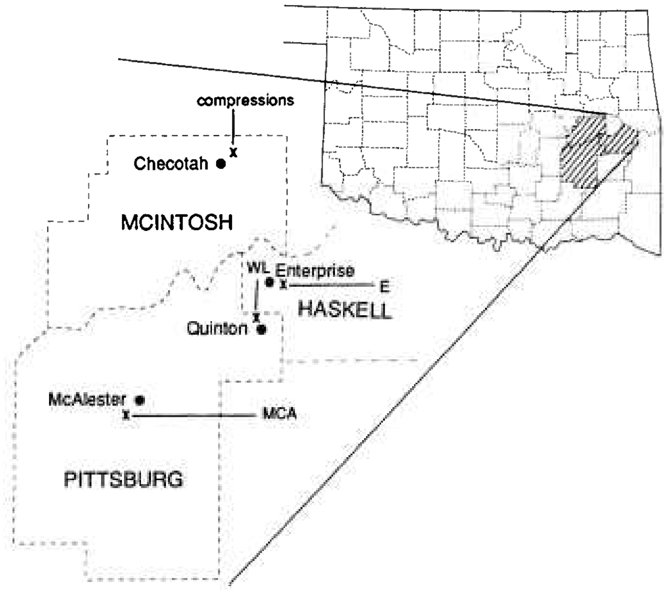


FIGURE 1—Map of Oklahoma, showing sampling locations in McIntosh, Pittsburg and Haskell Counties. Compressions were sampled northeast of Checotah. Coal ball localities are discussed in the text: McA (McAlester), WL (West Liberty), E (Enterprise).

West Liberty: A profile of coal balls was collected in 1979 at the Westhoff Brothers Mine, near West Liberty Church, in Pittsburg County, Oklahoma, SE ¼, Section 1, T. 8N, R. 17E, 7½′ Enterprise Quadrangle. The coal-ball mass occurred in a gob pile, but had attached remnants of a dark gray to black roof shale bearing linguloids and other invertebrate fossils, suggesting brackish to marine conditions. The entire thickness of the coal-ball aggregate, including coal, was 65 cm, which the operator informed us represented the full seam thickness. In this area the Secor Coal is of minable thickness and is the probable source of the coal balls (Hemish, pers. comm., 1989). Specimens are housed in the Paleobotanical Collections, University of Illinois, under the following acquisition numbers: 23310-23382.

Enterprise: Two profiles and a random sample of coal balls were collected in 1981 at the tipple of the Westhoff Brothers Enterprise Mine No. 1, near the town of Enterprise in Haskell County, Oklahoma. The mine tipple was located in the NW ¼, Section 24, T. 9N, R. 18E, 7½′

Quinton North Quadrangle. Profiles were collected from two aggregates, each approximately 60 cm thick, however, no roof shale or underclay was attached to the aggregates, so orientation could not be established. The operator informed us that coal balls, where they occurred, occupied the full thickness of the seam; the aggregates from which we collected had little coal intercalated between zones. The random sample consists of isolated coal balls collected at the tipple. It was divided in the laboratory into four subsamples to provide replicates for comparison. The Secor Coal is the probable source of the fossils (Hemish, pers. comm., 1989). Specimens are housed in the Paleobotanical Collections, University of Illinois and bear the following acquisition numbers: Enterprise VS 1—26598–26652; Enterprise VS 2—26410–26518; Enterprise RS 1—22955–23003; Enterprise RS 2—23004–23052; Enterprise RS 3—23053–23101; Enterprise RS 4—23102–23150.

Methods of Analysis

Coal Balls

Profiles and random samples of coal balls were quantified according to the techniques of Phillips et al. (1977). The resulting abundance data, reported as percentage abundances, are considered in three categories. 1) *Raw data* includes taxonomically identified plants and all unidentified materials, invertebrates and clastics. 2) *Normalized data* has all the unidentified materials, invertebrates and clastics deleted; remaining abundances are normalized to 100% identified materials. 3) *Root free* abundances are calculated by deletion of all roots from the normalized data set, which is then renormalized to 100% identified/root free abundances; because *Psaronius* trees were supported by a mantle of aerial roots (Ehret and Phillips, 1977), 50% of the roots from the outer root mantle and all of the roots from the inner root mantle are treated as aerial.

Computations of fusain abundances and percentages of unidentified material are based on raw data. Shoot-root ratios, abundances of organs, and proportions of major taxonomic groups in the peat are based on the normalized data. Root-free data are the basis for all assemblage-level comparisons and community-level interpretations, including dominance-diversity curves, calculations of species richness, diversity and equability, and ordinations. Ordination was performed with non-metric multidimensional scaling in three dimensions (Kenkel and Orloci, 1986; Prentice, 1980), using the statistical program SYSTAT (Wilkinson, 1988). Detrended correspondence analyses (Hill and Gauch, 1980) were carried out for comparative purposes using the program DECORANA; results of DCA and NMDS were similar and only NMDS results are presented. The Shannon-Wiener Information Index (H′) was calculated according to the formula in Whittaker (1975).

Profiles consisted of zones identified in the field on the basis of coal breaks between coal-ball layers. We considered these zones to be litter horizons of temporally distinct forest stands, based on their relatively uniform internal composition; palynological analyses of coal and associated coal balls (Willard, 1990) suggest that coal-ball zones are equivalent to very small increments of coal, a consequence of peat compaction. Zones are treated as independent vegetational samples in all analyses of profiles or in combined analyses of profiles and random samples.

Coal balls from the four Enterprise random collections were ordinated, treating each coal ball as a separate sample. These exploratory ordinations were used as a basis to identify recurrent assemblages of taxa in the random collections. Coal balls from identified assemblages were combined to create composite 'zones' that could be analyzed further in combination with empirically identified zones from profile collections. Composite zones were created from separate analyses combining random samples 1 and 2, and random samples 3 and 4. The McAlester random collection was treated as a single composite zone in combined analyses due to its small size and uniform taxonomic composition and matrix qualities.

Compression Fossils

Compression fossils were identified to species. Counts were then made of all discrete, identifiable plant fragments in those collections housed at the Museum of Natural History. This was contrasted with the method of Pfefferkorn et al. (1975) in which each rock specimen is treated as a 'quadrat'; any species occurring in that quadrat are tabulated once, regardless of the number of individual fragments, and abundances are reported as the number of quadrats in which a species occurs. There were 205 specimens in our sample. Results of the count and quadrat methods are compared in Table 7. Because subenvironments could not be identified a priori, the entire collection is treated as a single sample.

It is difficult to prefer one of these quantitative sampling methods over the other. The quadrat method is more difficult to manipulate statistically, and percent-occurrences of species are not additive in the absence of details on cooccurrence. In defense of the quadrat method (Pfefferkorn et al., 1975), it is rapid, it circumvents the difficulties of differential fragmentation and the question of "what to count", which is encountered in the count method. Quadrat and count methods provide very similar estimates of rank-order abundance (Table 7). Taphonomic studies of angiosperm leaves (Burnham et al., in press), suggest that count data provide the best estimate of the basal stem diameter and crown biomass of a forest. Pennsylvanian forests were dominated by plants with compound leaves, up to several meters in length, that most frequently dismembered into isolated pinnules or pinnae; consequently counts may be difficult to interpret and quadrate data may be an acceptable estimate of biomass.

DEPOSITIONAL ENVIRONMENT

The Secor Coal-Secor rider complex was deposited on the Cherokee Platform, a shelf bordering the deeper part of the Arkoma Basin (Branson, 1962). The shelf appears

TABLE 1—Composition and sample size of profiles and random samples. All percentages are based on normalized data except % fusain and % unidentified, which were calculated from raw data. Total surface area is calculated from raw data. Percentages for profiles are an average of abundances per zone within that profile.

Profile/random sample		% Lycopods	% Ferns	% Pteridosperms	% Sphenopsids	% Cordaites	% Roots	% Stems	% Leaves	% Fructifications	% Fusain	% Unidentified	Total surface area of sample (in cm^2)
West Liberty	VS1*	77.9	6.7	4.5	5.8	5.1	50.9	39.0	7.7	2.4	4.4	3.6	2117
Enterprise	VS1	87.3	2.6	2.8	5.7	1.3	55.6	37.9	4.5	1.8	2.5	13.3	3577
Enterprise	VS2	79.2	5.2	3.0	8.8	3.8	45.3	44.0	7.9	2.9	2.6	8.8	3744
Enterprise	RS1	77.5	5.3	2.5	6.2	8.4	51.4	35.1	9.9	3.6	3.5	4.1	3311
Enterprise	RS2	65.6	8.5	4.5	7.7	13.6	52.6	30.4	13.6	3.2	4.0	3.8	1790
Enterprise	RS3	80.1	3.3	3.4	5.7	7.3	38.3	48.7	11.2	1.7	3.4	2.0	1255
Enterprise	RS4	75.0	5.9	2.3	6.8	9.3	43.9	42.2	12.4	2.5	3.8	5.1	2010
McAlester	RS1	52.8	9.5	7.4	12.7	17.3	61.6	8.2	24.4	5.7	2.5	24.7	1343
Average		74.4	5.9	3.9	7.4	8.3	50.0	35.7	11.4	3.0	3.3	8.2	

to have remained relatively stable during basinal subsidence, and may have been an area of longer peat-swamp duration than in the more relatively and irregularly subsiding deeper basin. This is suggested by fewer, thinner coals, and a generally thinner section on the shelf.

The Bluejacket Sandstone lies immediately below the Secor Coal. The Bluejacket is a heterogeneous complex of rocks interpreted as coastal plain in origin, ranging from lower alluvial valley to prodeltaic (Visher, 1968). The Secor-Secor rider complex was interpreted by Hemish (1988) as a lower deltaic plain deposit. He attributed the splitting of the seam to basinal subsidence contemporaneous with peat formation, permitting rapid influx of terrestrial sediments onto the Secor peat-swamp surface. The sediments probably represent a rapidly prograding delta lobe; plants growing on the prograding deltaic silts and muds were preserved as compression fossils in crevasse-splay sediments. The Secor rider extended over the clastics as subsidence slowed and base-level stabilized along the entire coastline.

The Secor Coal can be >1 m in thickness, and is generally low in ash and sulfur throughout much of its distribution in the shelf area, particularly where it forms the lower of two splits and is capped by terrestrial gray shales (Hemish, 1988). In the Arkoma Basin the Secor Coal is high in ash and sulfur (Friedman, 1974). The coal contains partings that vary in thickness and extent (Hendricks, 1937; Dane et al., 1938; Friedman, 1978), suggesting occasional influxes of mineral-rich waters into the peat swamp and a probable planar, or rheotrophic, geometry (Calder, in press). The Secor rider and unsplit Secor Coal are considerably higher in ash, possibly due to greater transport

TABLE 2—Fusain abundance in profiles and random samples broken down by major taxonomic group. Numbers indicate the percent of total fusain in a profile or random sample contributed by a particular higher plant group. Percentages calculated from raw data. Profile abundances are an average of zone abundances. WL1 = West Liberty VS 1; E1 = Enterprise VS 1; E2 = Enterprise VS 2; ERS1 = Enterprise RS (random sample) 1; ERS2 = Enterprise RS 2; ERS3 = Enterprise RS 3; ERS4 = Enterprise RS 4; McA = McAlester RS 1.

	WL1	E1	E2	ERS1	ERS2	ERS3	ERS4	McA
Lycopods	2.82	0.68	0.62	1.29	0.06	1.00	0.12	0.07
Ferns	0.05	0.06	0.22	0.17	0.45	0.00	0.24	0.14
Pteridosperms	0.95	0.15	0.15	0.31	0.33	0.32	0.17	0.29
Sphenopsids	0.00	0.17	0.46	0.35	0.77	0.31	0.53	0.15
Cordaites	0.00	0.06	0.19	0.37	0.58	0.39	0.34	0.21
Unidentified	0.54	1.34	0.95	1.05	1.78	1.41	2.36	1.64
Total	4.36	2.46	2.59	3.54	3.97	3.43	3.76	2.50

TABLE 3—Percentage of each major taxonomic group preserved as fusain (fusinized biomass of taxon x/total biomass of taxon x) by profile or random sample. Calculated from raw data. Profile abundances are an average of zone abundances. (Abbreviations for profiles and random samples are the same as in Table 1).

	WL1	E1	E2	ERS1	ERS2	ERS3	ERS4	McA	Average
Lycopods	3.8	0.9	0.8	1.7	0.1	1.3	0.2	0.2	1.1
Ferns	0.8	4.9	4.7	3.3	5.5	0.0	4.3	1.9	3.2
Pteridosperms	19.9	7.6	6.1	12.9	7.6	9.8	6.3	5.1	9.4
Sphenopsids	0.0	4.5	7.8	5.8	10.3	5.5	8.1	1.6	5.4
Cordaites	0.0	4.5	5.3	4.6	4.4	5.4	3.8	1.6	3.7
Unidentified	15.0	10.1	10.7	25.9	46.1	68.4	46.2	45.6	33.5

of fine sediment into the swamp, and in sulfur, reflecting the marine origin of roof sediments (Hemish, 1988).

RESULTS OF COAL-BALL ANALYSIS

Peat Composition

In Table 1, the percent volume of the major plant groups, plant organs, fusain (mineral charcoal), unidentified material (including invertebrates, mud and calcite), and the total sample size are tabulated for all profiles and random samples. The taxonomic and organ composition of the peat are determined from the normalized data set; abundances of fusain and unidentified, and total sample size are determined from the raw data set. Profile abundances are an average of zone abundances within the profile. Most plant tissues are derived from arborescent lycopsids (normalized-data average, 74.4%), in particular their rooting organs and periderm (bark). Unidentified material averages 8.2% (raw data) per profile, which is within the range observed for coal-ball samples from other coals (Phillips et al., 1977; Phillips and DiMichele, 1981; Phillips et al., 1985; DiMichele and Phillips, 1988).

Fusain abundances are relatively low in the Secor coal-ball samples (raw-data average 3.3%), which may reflect relatively infrequent fires. Total fusain is listed in Table 2, by taxonomic groups within profiles and random samples. Table 3 lists the proportion of each taxonomic group preserved as fusain in each profile (% taxon preserved as fusain/% total abundance of taxon). This transformation corrects for differences in the relative abundance of each group, and reveals greatest frequency of fusinization for unidentified, pteridosperm, and sphenopsid tissues, a consistent pattern in Pennsylvanian coal-ball peats.

In general, preservation of Secor coal-ball peats is poor, which suggests that loss of organics due to decay was high. Delicate parenchymatous tissues are rarely preserved, finely macerated matrix material is abundant, and materials are often crushed or highly flattened. Indicators of decay are particularly accentuated for samples enriched in *Anabathra* periderm. There are some peats, usually those dominated by a plant other than *Anabathra*, that are better preserved; peats of this type are uncommon in profiles, but make up a larger fraction of the random sample coal balls. Marine invertebrates occur mixed irregularly within some coal balls (Mamay and Yochelson, 1962), suggesting introduction during active peat accumulation.

Plant Communities

Ecological inferences are based on root free data. The root-free counts of taxa included in these analyses are presented in Table 4; these counts represent the actual numbers of square centimeters of any particular taxon identified in a zone or random sample, excluding roots, except as noted above. We present the actual count data, rather than the percentages calculated from it (which are used in subsequent analyses), because it makes the data more accessible. Twenty-nine taxa were included in the analyses. The terminal taxa represent reconstructed whole-plants, and combine aerial organs into single taxa at as low a rank as evidence permits. Three of the taxa are categories for plant parts that could not be assigned confidently to a species, due to insufficient information: *Diaphorodendron* spp., *Pennsylvanioxylon* spp., and *Botryopteris* spp. Actual species richness was higher than the 29 terminal taxa used in the analysis: Neither *Medullosa* nor *Psaronius* were further subdivided because of difficulties in the recognition of the whole-plant species affinities of most vegetative remains. However, at least six "species" of medullosan vegetative foliage were identified, and three "species" of marattialean fertile foliage (Lesnikowska, 1989), which yields a conservative estimate of 33 whole-plant entities, if the three general categories mentioned above are not counted.

Profile Analysis

The three profiles analyzed in this study consisted of 17 total zones. Fourteen of the zones are dominated by *Anabathra pulcherrima*; in ten of the zones this plant accounts for >65% of the biomass. Figure 2 summarizes the taxonomic composition of the zones in the three profiles, based on root-free data. Results are reported as *Anabathra*, all other lycopsids, ferns, pteridosperms, sphenopsids, and cordaites. No similarities in vertical variation are detectable. *Anabathra* accounts for at least 50% of the biovolume in at least one-half of the zones of each profile. Two zones are conspicuously enriched in cordaites, zone 1 of West Liberty VS1, and zone 7 of Enterprise VS2, and demonstrate more equable abundances of the other plant groups. In each profile "other lycopsids" is a significant component of at least one zone; inspection of Table 4 reveals that in each case a different species is responsible for the biomass increase. The differences between the three profiles suggest local heterogeneity in the swamp forest, both spatially and in the local patterns of vegetational change through time.

Ordination permits simultaneous comparison of all zones and identification of major taxonomic gradients in the swamp, which presumably reflect gradients in physical conditions to a large extent. The first axis of the ordination of profile zones (Fig. 3) is almost entirely a function of *Anabathra* abundance, and so is closely correlated with measures of diversity (H′) and evenness (Table 5). When *Anabathra* abundance and H′-diversity are superimposed on the ordination, three clusters of zones emerge: those with >80% *Anabathra* and average species richness of 7.0, those with 40–60% *Anabathra* and an average species richness of 9.7, and those with <20% *Anabathra* and an average species richness of 10.3. One assemblage (E1-5), with 70% *Anabathra* and *Diaphorodendron scleroticum* as a principle subdominant, falls between the high and intermediate *Anabathra*-abundance groups.

The minor element composition of the *Anabathra*-dominated zones is highly variable. Except for those zones with >90% *Anabathra*, the most common subdominants are *Medullosa*, *Psaronius*, *Arthropitys*, and *Pennsylvanioxylon*, each occurring in four or five zones. *Diaphorodendron scleroticum* and *D. dicentricum* are second in importance, at levels >25%, in one zone each.

Three zones are not dominated by *Anabathra*. All have a notable *Lepidophloios hallii* element, which is the dominant plant in one of the zones. Of the remaining two, one is dominated by *Arthropitys*, the other by *Pennsylvanioxylon*, which is also the most diverse assemblage of the three profiles with 16 species.

Random Sample Analysis

Coal balls of the four random samples from the Enterprise Mine were combined into two sets, RS1 and RS2, and RS3 and RS4, and ordinated separately. Several iterations were run on each data set, removing groups of coal balls with similar ordination scores from consecutive analyses. Coal balls that were consistently grouped together on all three ordination axes were combined to create *composite zones* of sample sizes (number of cm^2) comparable to those of in situ profile zones. The composition of the composite zones is listed in Table 4 (composite zones are numbered within each combined random sample analysis).

Composite zones can be compared only broadly with the patterns of dominance exhibited in profiles. There is no objective means by which to determine the number of actual zones that contributed to one of the composite assemblages. Composite zones, however, are uniformly higher in species richness than profile counterparts with similar dominant taxa, suggesting that the component coal balls were drawn from multiple layers in the seam. An indication of the relative importance of any one particular composite-zone assemblage-type can be inferred from its proportion of the total random sample (in cm^2); in a profile the number of zones would provide such an estimate. The patterns of H′ diversity and evenness are very similar to those of profile zones (Table 5).

In contrast to the profiles, the *Lepidophloios hallii*-dominated composite zones account for the largest proportion of the random-sample biomass (1263 cm^2), more than twice the biomass of *Anabathra pulcherimma*-dominated composite zones (547 cm^2). Both types of assemblage are highly dominated by one species. *Anabathra* is present in 11 of 16 composite zones; *Lepidophloios* occurs in 13 of the 16 composite zones. Assemblages dominated by all other major plant groups, cordaites, *Psaronius*, medullosans, sphenopsids, and *Diaphorodendron scleroticum*, account for between 100 cm^2 and 190 cm^2 each. Cordaite (*Pennsylvanioxylon*) and sphenopsid-dominated zones were identified in the profiles, and *D. scleroticum* was significantly abundant in one *Anabathra*-dominated profile zone (E1-5; see Table 4). The similarity of composite and profile assemblages suggests that composite zones can recover patterns that, otherwise, are better defined spatially and temporally in profiles. The high abundance of *Lepidophloios hallii*, and the marked cordaite presence in the random samples is a strong indication that such assemblages were conspicuous, although perhaps patchy, components of the peat-swamp vegetation.

Combined Analysis

Combined ordination of 16 composite zones and 17 profile zones (Fig. 4) significantly amplifies the patterns detected in the analysis of profile zones alone, without altering the basic patterns detected earlier. The composite zones reinforce the pattern of *Anabathra* dominance; the entire right side of the ordination (Fig. 4), the positive portion of dimension 1, is the same as in the profile analysis (Fig. 3). Added is clear evidence of *Lepidophloios hallii*-dominance in a substantial portion of the landscape. *Lepidophloios*-dominated composite zones are very large and probably represent as great a number of actual stands as the *Anabathra* zones from the profiles. Falling between *Lepidophloios*-dominance and *Anabathra*-dominance are the largest number of composite zones. Most are dominated by or enriched in cordaites (*Pennsylvanioxylon* of two forms). *Arthropitys* is abundant in several zones and *Diaphorodendron scleroticum* is dominant in two.

A most significant pattern in the combined ordination

TABLE 4—Root-free taxonomic composition of profile and composite zones. Numbers are count data, reported as cm^2. Percentages calculated from these data were used in the ordinations and diversity calculations. WL1 = West Liberty VS 1; E1 = Enterprise VS 1; E2 = Enterprise VS 2; McA = McAlester RS 1; RS1/2 = Enterprise combined analysis of RS1 and RS2; RS3/4 = Enterprise combined analysis of RS 3 and RS 4. Numbers of zones or composite zones follow the profile or random-sample label.

	WL1-1	WL1-2	WL1-3	WL1-4	E1-1	E1-2
Anabathra pulcherrima	101	222	239	32	19	162
Lepidophloios hallii/johnsonii	3	5	—	89	2	14
Lepidodendron hickii	—	—	—	—	—	—
Lepidodendron serratum	—	—	—	—	1	23
Diaphorodendron dicentricum	—	—	—	—	—	—
Diaphorodendron scleroticum	—	—	—	—	—	—
Psaronius (*Scolecopteris gnoma*; *S. altissima*)	30	16	24	10	2	13
Medullosa (*Neuropteris rarinervis*; N. sp.; *Linopteris*; *Alethopteris lesquereuxii*; *A. sullivantii*; A. sp.)	14	8	63	14	6	18
Arthropitys	15	6	30	2	3	34
Pennsylvanioxylon sp. 1 (? *C. spinatus*)	78	18	—	—	—	20
Pennsylvanioxylon sp. 2 (? *C. magnicellularis*)	—	—	—	—	—	—
Pennsylvanioxylon sp. 3	—	—	—	—	—	—
Mesoxylon sp.	—	—	—	—	—	—
Sphenophyllum sp.	4	4	3	7	1	6
Chaloneria sp.	—	—	1	—	—	—
Heterangium sp.	—	—	1	—	—	1
Callistophyton boyssetii	—	—	—	—	—	—
Microspermopteris aphyllum	—	—	—	—	—	—
Johnhallia	—	—	—	—	—	—
Botryopteris sp.	—	—	1	—	—	—
B. mediatena	—	—	—	—	—	—
B. forensis	—	—	—	—	—	—
B. tridentata	1	—	—	—	—	—
Anachoropteris involuta	—	—	—	—	—	—
Zygopteris illinoiensis	1	—	—	—	4	—
Sermaya	—	—	—	—	—	2
Stelastellara parvula	—	—	—	—	—	—
Anachoropteris gillotii	2	—	—	—	—	—
Diaphorodendron sp.	—	—	—	1	—	—
Pennsylvanioxylon sp.	—	—	—	—	—	—
Total	249	279	362	155	35	293

	McA	RS 1/2 -1	RS 1/2 -2	RS 1/2 -3	RS 1/2 -4	RS 1/2 -5
Anabathra pulcherrima	20	—	14	9	—	10
Lepidophloios hallii/johnsonii	87	274	96	3	18	5
Lepidodendron hickii	—	1	2	—	—	—
Lepidodendron serratum	—	—	—	—	1	—
Diaphorodendron dicentricum	—	—	—	—	—	—
Diaphorodendron scleroticum	—	2	27	—	—	—
Psaronius (*Scolecopteris gnoma*; *S. altissima*)	42	25	22	5	52	15
Medullosa (*Neuropteris rarinervis*; N. sp.; *Linopteris*; *Alethopteris lesquereuxii*; *A. sullivantii*; A. sp.)	66	18	17	4	12	34
Arthropitys	—	10	10	7	14	2
Pennsylvanioxylon sp. 1 (? *C. spinatus*)	81	4	—	—	10	4
Pennsylvanioxylon sp. 2 (? *C. magnicellularis*)	—	—	—	—	—	—
Pennsylvanioxylon sp. 3	—	—	32	16	1	16
Mesoxylon sp.	—	—	—	—	—	—
Sphenophyllum sp.	16	7	12	2	—	2

TABLE 4—Continued.

E1-3	E1-4	E1-5	E2-1	E2-2	E2-3	E2-4	E2-5	E2-6	E2-7	E2-8
241	461	126	241	1	330	61	232	302	14	138
—	18	1	3	8	1	15	—	—	59	5
1	—	—	—	—	—	—	3	4	5	—
—	—	—	—	—	—	—	—	1	2	—
1	—	—	—	12	—	39	4	—	—	—
—	—	43	—	—	—	—	—	—	—	—
—	8	4	6	4	—	6	48	2	30	18
2	29	4	4	7	—	4	17	7	37	—
5	15	—	—	33	3	5	2	3	8	—
5	2	3	—	—	—	3	20	7	79	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	1	—	—	—	—	—	—
—	5	—	5	—	4	2	11	2	17	6
—	1	—	—	—	—	1	1	—	—	—
—	—	—	—	—	—	1	3	1	—	—
—	—	—	—	1	—	1	—	—	1	—
—	1	—	—	—	—	—	—	—	2	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	2	—	—	—	—	—	—	—
—	—	—	1	—	—	—	1	—	6	—
—	—	—	—	—	—	—	—	—	1	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	1	—
—	—	—	—	—	—	—	—	—	1	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	6	—	—	—	—	—	—	—	1	—
—	—	—	—	—	—	—	—	—	—	4
255	546	181	262	67	338	138	342	329	264	171

RS 1/2 -6	RS 1/2 -7	RS 1/2 -8	RS 3/4 -1	RS 3/4 -2	RS 3/4 -3	RS 3/4 -4	RS 3/4 -5	RS 3/4 -6	RS 3/4 -7	RS3/4 -8
—	11	224	4	3	11	1	—	—	2	231
3	1	3	19	9	9	—	—	—	545	5
—	—	1	1	—	—	—	—	—	—	2
—	—	5	—	2	—	—	—	—	12	—
—	—	—	—	—	—	—	—	—	14	—
—	37	1	1	21	—	—	—	—	—	1
10	3	6	13	7	2	23	1	1	19	6
2	2	16	4	2	3	7	9	—	30	5
13	12	1	9	2	37	8	—	—	15	3
—	1	11	—	6	10	3	2	1	27	8
—	—	—	—	—	—	—	—	—	—	—
—	—	3	—	9	9		—	5	—	6
—	—	—	—	—	—	—	—	—	—	—
2	7	4	6	4	3	3	1	1	9	3

TABLE 4—Continued.

	McA	RS 1/2 -1	RS 1/2 -2	RS 1/2 -3	RS 1/2 -4	RS 1/2 -5
Chaloneria sp.	3	—	1	1	2	—
Heterangium sp.	—	1	—	—	1	—
Callistophyton boyssetii	—	—	—	—	—	3
Microspermopteris aphyllum	—	—	—	—	—	—
Johnhallia	—	—	—	—	—	1
Botryopteris sp.	—	—	—	—	—	—
B. mediatena	—	—	—	—	—	—
B. forensis	3	—	—	—	—	—
B. tridentata	—	—	1	—	—	—
Anachoropteris involuta	2	1	3	—	—	—
Zygopteris illinoiensis	2	1	—	—	—	—
Sermaya	—	—	—	—	—	—
Stelastellara parvula	—	—	—	—	—	—
Anachoropteris gillotii	—	—	—	—	—	—
Diaphorodendron sp.	—	—	—	1	2	—
Pennsylvanioxylon sp.	—	—	3	—	—	—
Total	357	344	240	48	103	92

is the distinct second axis, which defines a *Lepidophloios-Medullosa* gradient. Between these end-point assemblages are *Diaphorodendron,* aligned most closely with *Lepidophloios,* and *Pennsylvanioxylon,* aligned most closely with *Medullosa*; *Psaronius* is widely distributed but in a central position. The second axis pattern is broadly the same as that found in later Middle Pennsylvanian coals (Phillips and DiMichele, 1981; DiMichele and Phillips, 1988), where *Anabathra* is a minor component, generally associated with *Medullosa* more strongly than with *Lepidophloios*. Unpublished analyses of early Middle Pennsylvanian coals show the close association of cordaites and medullosans seen in the Secor. The combined analysis demonstrates that *Anabathra* forms a distinct gradient, independent of the major gradient found most commonly in Pennsylvanian peat swamps. Furthermore, the Secor coal represents the oldest example, to date, of a swamp with significant development of the *Lepidophloios-Diaphorodendron-Psaronius-Medullosa* plexus that characterizes the major coals of the late Middle Pennsylvanian. The rare expression of *Anabathra* as a dominant element does not obscure this more typical pattern, given a large enough sample, because it is fundamentally distinct from that pattern.

The perplexing difference between the profiles and random samples is the differential abundance of *Lepidophloios* in the random samples. The three composite zones dominated by *Lepidophloios* account for 1263 cm^2, which is one-half of all random sample, root-free biomass; the remaining 15 composite zones account for a total of 1264 cm^2. Nearly one-half of the remaining biomass is in *Anabathra*-dominated coal balls, 547 cm^2, leaving 717 cm^2 approximately equally divided among composite zones dominated by the other major groups of plants. The rarity of assemblages dominated by ferns, pteridosperms, sphenopsids and cordaites in the random samples is consistent with their overall lack of importance in the peat-swamp landscape mosaic, inferred from profile analysis.

The combined profile-random sample analysis reinforces the picture of the peat swamp suggested by the profile analysis alone. The swamp appears to have consisted of a patchwork of standing pools of water of variable areal extent dominated by *Lepidophloios.* Between the wettest sites were expanses dominated by *Anabathra* in which physical conditions were heterogeneous, probably reflecting regular disturbance, including flooding, and heavy rotting of the peat. These physical conditions are deduced from the presence of clastic partings in the coal, from the very poor condition of *Anabathra*-dominated peats, and from extrapolation from *Anabathra*-dominated assemblages in other coals with additional evidence of the same kinds of physical conditions (DiMichele and Phillips, 1985, 1988; Eble and Grady, 1990; Calder, in press). Cordaites were the most conspicuous, although minor, third element, probably as scrambling or shrubby ground cover (Costanza, 1985; Rothwell and Warner, 1984). Cordaites, sphenopsids, medullosans and tree ferns appear to have been interstitial elements of the peat swamp, in closest association with *Lepidophloios,* although not as core elements of *Lepidophloios* stands. They suggest considerable microhabitat variation within the swamp.

RESULTS OF COMPRESSION FOSSIL ANALYSIS

The results of the quantitative analysis of the compression flora are presented in Tables 6a and 6b. The major plants are illustrated in Figures 5 and 6. Pteridosperms account for 59.9% of the count data and occur in 86.3% of the quadrats; ferns account for 26.2% of the count data and occur in 45.8% of the quadrats; sphenopsids account for 14% of the count data and occur in 42% of the quadrat.

TABLE 4—Continued.

RS 1/2 -6	RS 1/2 -7	RS 1/2 -8	RS 3/4 -1	RS 3/4 -2	RS 3/4 -3	RS 3/4 -4	RS 3/4 -5	RS 3/4 -6	RS 3/4 -7	RS3/4 -8
—	—	—	5	4	1	1	—	—	—	1
—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	—	—	—	—	—	—	1
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	3	—
—	—	—	1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	2	—	—	—	1	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
3	2	—	2	—	2	3	—	—	2	—
4	—	—	64	—	—	—	—	—	—	—
37	76	275	133	69	89	49	13	8	679	272

Lycopsids, represented by *Sigillaria,* were observed rarely in the mine spoils at the collecting site, but do not occur in our sample. The compression sample is distinct from the peat swamp and clearly represents a different kind of vegetation.

At a more detailed level, the count and quadrat data yield remarkably similar rank order abundances of species-level taxa (Table 7). Of the 10 most abundant taxa (excluding pteridosperm axes and calamite stems) only *Neuropteris rarinervis,* from the count-data list, and *Neuropteris macrophylla,* from the quadrat list, do not occur in the opposite list of 10 most abundant taxa.

The most abundant and widespread species in the compression flora is *Alethopteris serlii,* a xeromorphic plant that we presume to be a small tree occupying unshaded areas. Other common taxa (Table 7) include two marattialean ferns, *Pecopteris miltoni* and *Pecopteris hemitelioides,* the pteridosperm *'Mariopteris' occidentalis,* and *Annularia sphenophylloides,* a calamite. These were all trees or shrubs, with the possible exception of *'M.' occidentalis,* which may have been a vine. All of the more abundant taxa were widely distributed in the environment, judging from their occurrences in numerous quadrats.

The relative abundance and pattern of distribution of *Neuropteris* species and ground cover suggest a structurally diverse, but low canopied vegetation with considerable spatial heterogeneity in the subdominant taxa. Species of *Neuropteris* and ground cover, such as *Sphenophyllum* and *Pecopteris plumosa-dentata,* are less abundant, although still among the more common elements. The *Neuropteris* species are quite different morphologically, united collectively only by their status as conspicuous, but quantitatively minor components of the vegetation. Individual trees or shrubs may have been widely dispersed within an *Alethopteris*-dominated vegetation. In the entire flora eight species may have been vines or ground cover (*'Mariopteris' occidentalis, M. nervosa, Eusphenopteris scribani-striata, Sphenopteris macilenta, Zeilleria, Hymenophylloides, Pecopteris plumosa-dentata, Sphenophyllum emarginatum*), accounting for a total of 22.7% of the count data (13.9% if *'M.' occidentalis,* of questionable habit, is not counted), a substantial part of the total vegetation.

'Mariopteris' occidentalis is the most unusual plant in the compression flora. Described by White (1899), the plant compares more closely with *Pseudomariopteris,* particularly *P. ribyroni,* than *Mariopteris,* and may be a species of the former. It has been noted by White (1899) and Read and Mamay (1964) from the Desmoinesian of Oklahoma, and by Sellards (1908) from equivalent age rocks in Kansas, and may have been a regional endemic with a short stratigraphic range.

DISCUSSION

The lowland landscape in which the Secor Coal formed was typical of the late Middle Pennsylvanian (Westphalian D). There was a sharp distinction between the peat-forming flora, dominated by lycopsids, and the mineral-substrate flora in surrounding deltaic wetlands, dominated by pteridosperms and ferns. The distinction emphasizes the strong partitioning of ecological resources along higher taxonomic lines during the Carboniferous. Pteridosperms and ferns were minor components of Middle Pennsylvanian peat swamps, although they became increasingly important in the Desmoinesian (Westphalian D). They appeared in those parts of peat swamps least favorable to the establishment of high dominance by lycopsid trees, possibly areas with high clastic influx or peat exposure and decay.

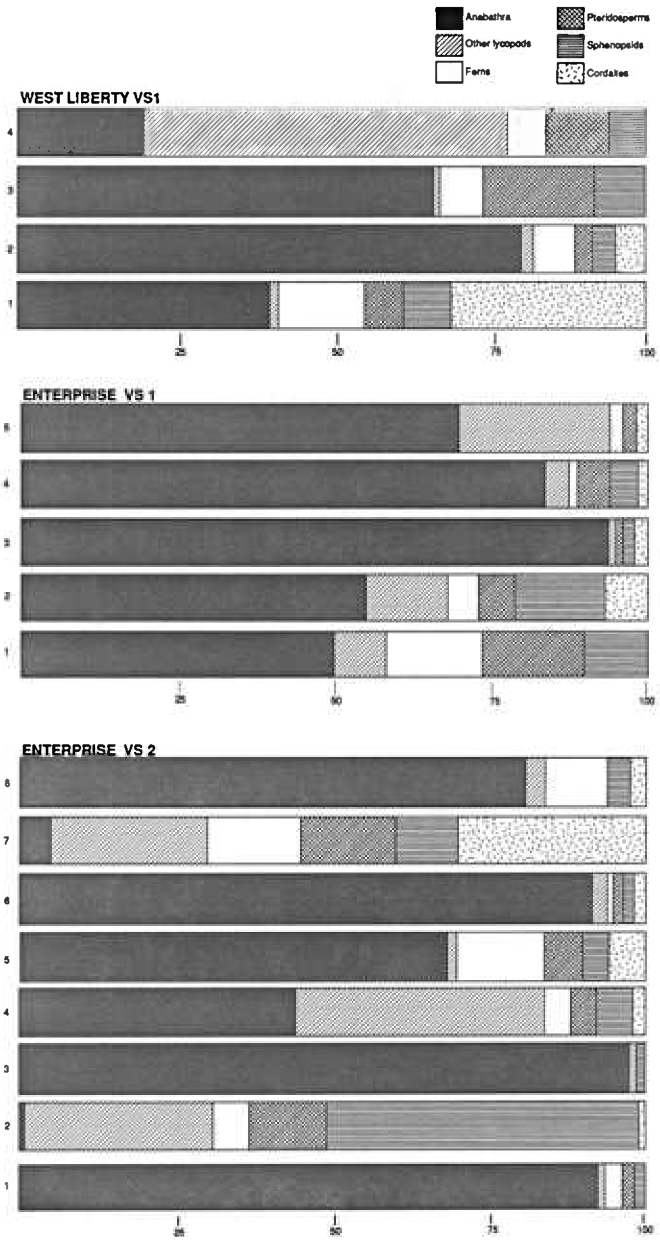


FIGURE 2—Bar diagram of major-group composition of zones in the three Secor Coal coal-ball profiles. Profiles are labelled at upper left of each set of zones; zones are numbered on the left of each bar. Total abundance is based on root-free data. Key to symbols in upper right.

The lycopsids remained, as they had for nearly 30 million years, the core dominants of standing-water habitats, in both peat-forming and clastic swamps. Differences in the ecological preferences of the major plant lineages is the cause of the clear distinction between the roof-shale flora and the flora of the coal balls. The roof shale is unrepresentative of the taxonomic composition of this coal. In only rare instances do roof shales preserve the coal-swamp vegetation. Such instances occur when the swamp is buried rapidly by flood-borne sediments, most often associated with a change in local or regional baselevel (e.g., DiMichele and DeMaris, 1987).

TABLE 5—Diversity and equability of profile and composite zones.

Locality	H′	E	Locality	H′	E
WL1-1	1.52	0.46	McA	2.08	0.60
WL1-2	0.84	0.33	E1/2-1	0.86	0.22
WL1-3	1.05	0.36	E1/2-2	1.93	0.53
WL1-4	1.27	0.51	E1/2-3	1.87	0.72
E1-1	1.58	0.61	E1/2-4	1.68	0.49
E1-2	1.55	0.47	E1/2-5	1.83	0.62
E1-3	0.29	0.22	E1/2-6	1.68	0.77
E1-4	0.71	0.20	E1/2-7	1.57	0.54
E1-5	0.86	0.39	E1/2-8	0.84	0.21
E2-1	0.41	0.21	E3/4-1	1.66	0.44
E2-2	1.50	0.56	E3/4-2	2.11	0.75
E2-3	0.14	0.29	E3/4-3	1.86	0.59
E2-4	1.57	0.44	E3/4-4	1.46	0.61
E2-5	1.16	0.29	E3/4-5	0.94	0.64
E2-6	0.44	0.17	E3/4-6	1.07	0.73
E2-7	2.00	0.46	E3/4-7	0.90	0.20
E2-8	0.72	0.41	E3/4-8	0.70	0.17

Coal-swamp Flora

The flora of the Secor peat swamp is relatively diverse, at 33 species, considering the limited paleobotanical study this coal has received. The flora contains a combination of species most typical of younger coals from the late Desmoinesian. Ecological analyses also reveal gradients more typical of those found in late Desmoinesian coals of the Illinois Basin (DiMichele and Phillips, 1988; Phillips and DiMichele, 1981). The most characteristic gradient is that from *Lepidophloios* to *Medullosa* dominance, with *Diaphorodendron* and marattialean ferns between these endpoint assemblages, and sphenopsids aligned most closely with the medullosans. The Secor coal also retains the Atokan/early Desmoinesian association of cordaites and medullosans (DiMichele and Phillips, 1990), stressing the intermediate character of this swamp flora. The gradient toward increasing *Anabathra*-dominated assemblages is only weakly developed in later Desmoinesian coals, although it has been recognized in closest association with medullosan pteridosperms.

Anabathra-dominated Assemblages

Anabathra dominance makes the Secor peat-swamp flora unexpectedly distinctive. Although Middle Pennsylvanian peat swamps were generally lycopsid dominated (Phillips et al., 1985), this generality masks the rich diversity of ecologies and life-history biologies encompassed

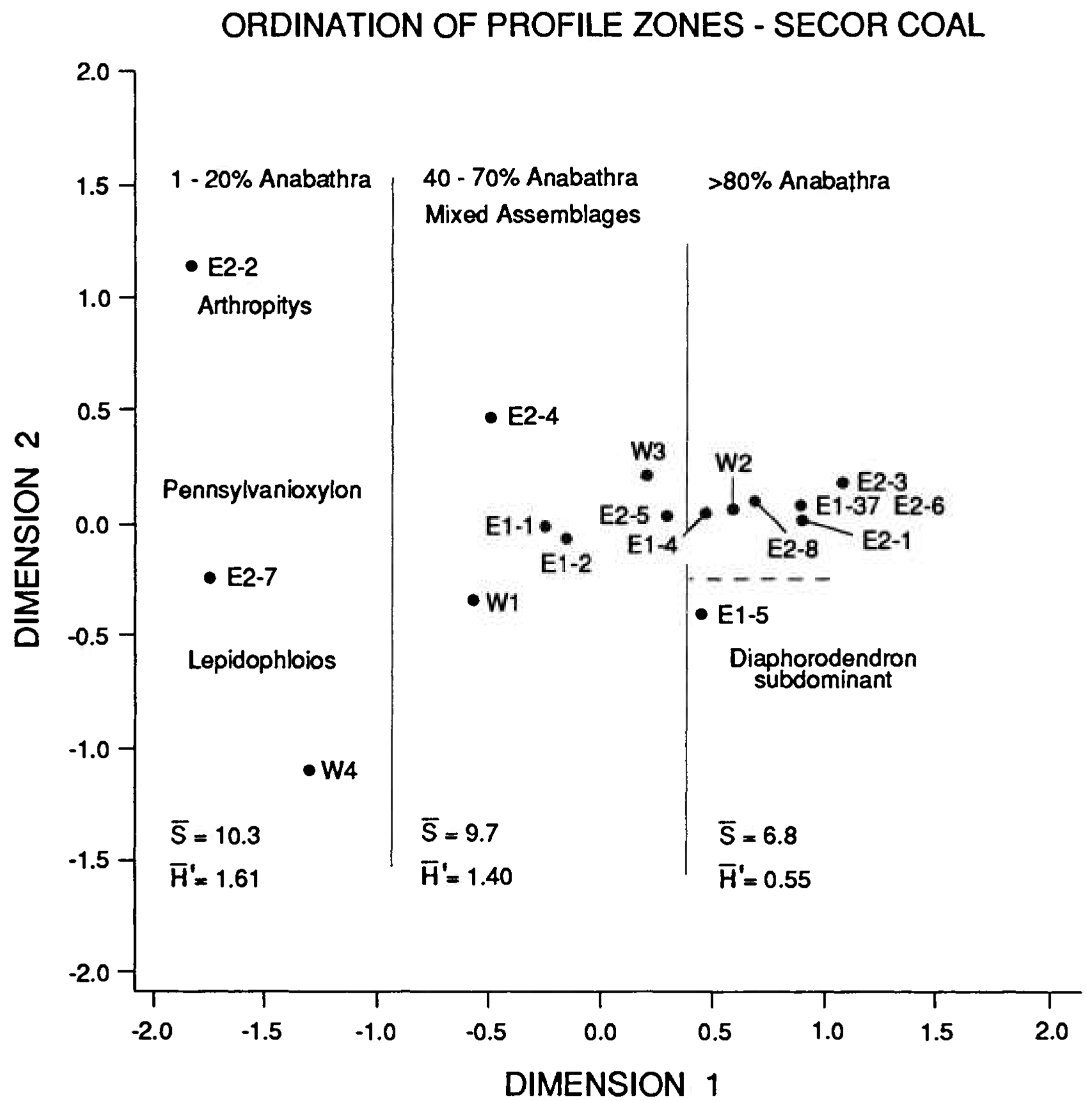


FIGURE 3—Non-metric multidimensional scaling ordination of zones from the three combined Secor coal-ball profiles. Each point represents one zone. W = zones from West Liberty VS 1; E1 = zones from Enterprise VS 1; E2 = zones from Enterprise VS 2. The zones are divided into three groups, separated by vertical lines, those with >80% *Anabathra*, those with 40–70% *Anabathra*, and those with 1–20% *Anabathra*. S = average species abundance of a group of zones; H′ = average Shannon-Wiener diversity of a group of zones.

by the lycopsids within peat-forming swamps. *Anabathra* accounts for a significant proportion of the biovolume in the Katharina Seam of Germany (Phillips and DiMichele, unpubl.), the Hamlin Coal of Kentucky (Phillips et al., 1985), and parts of the Springfield and Herrin Coals of the Illinois Basin (DiMichele and Phillips, 1985, 1988). Based on palynological analyses, the plant was important in a number of coal swamps from the eastern U.S. and Canada (Eble, 1988; Eble and Grady, 1990; Calder, in press). In the Secor Coal, the abundance of *Anabathra* does not mask the gradient from presumed-flooded *Lepidophloios*-dominated stands to more ecotonal, fire-prone medullosan-dominated habitats, which is typical of the late Middle Pennsylvanian. These patterns strongly suggest that the unusual abundance of *Anabathra* is reflective of atypical peat-swamp conditions. Detailed ecological analyses of other coals indicate that *Anabathra* favored habitats with regular disturbance, perhaps due to flooding, where its production of numerous, highly dispersible megaspores would have allowed rapid exploitation of open habitats. In coals from the Illinois Basin (DiMichele and Phillips, 1988), and the Appalachian Basin (Eble, 1988; Calder, in press), the plant was closely associated with clastic partings or the basal portion of the coal seam, suggesting an ability to tolerate, if not a preference for, areas of opportunity and limited interspecific competition.

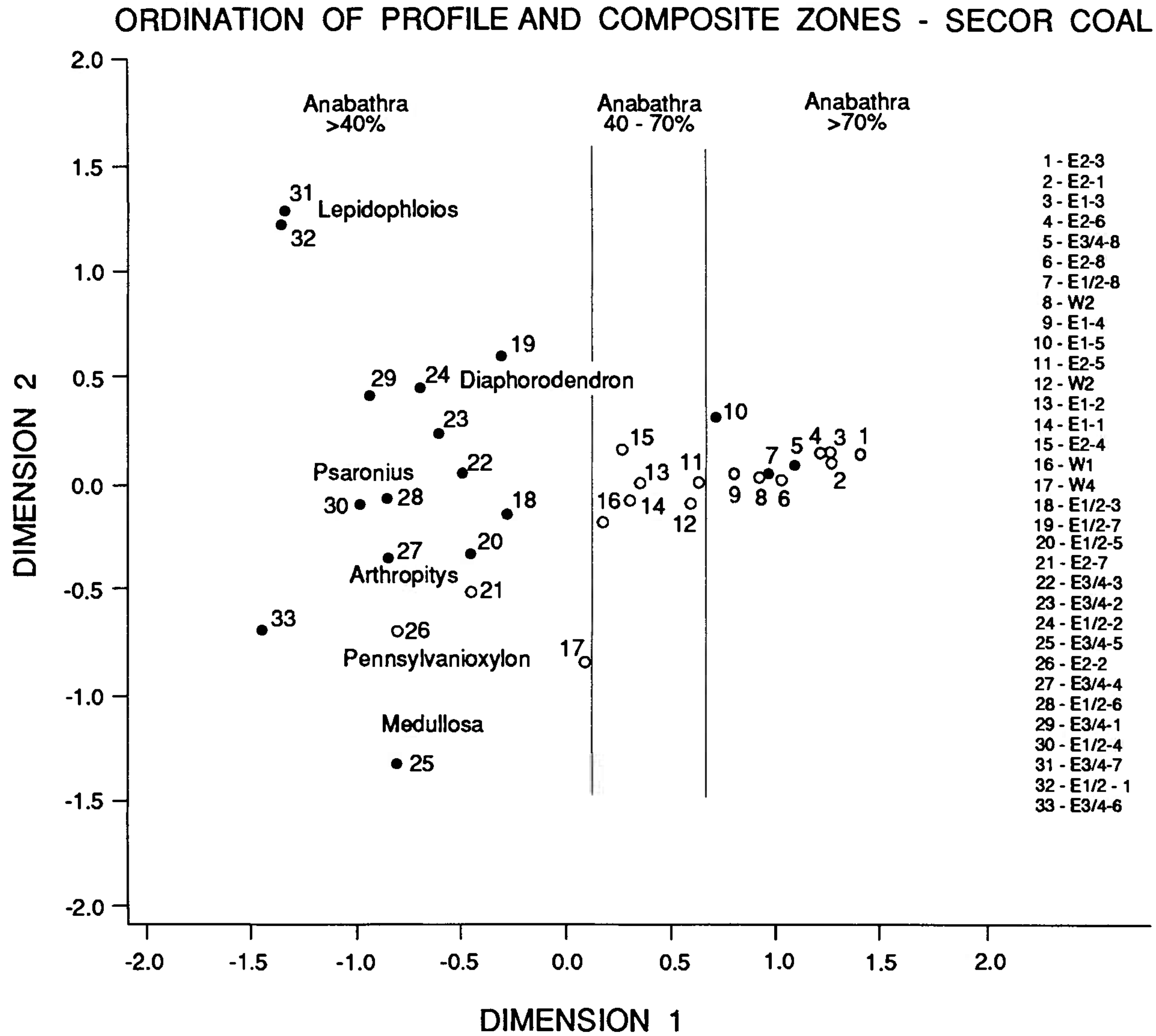


FIGURE 4—Non-metric multidimensional scaling ordination of zones from the three Secor coal-ball profiles, marked as open circles, combined with composite zones derived from random-sample analyses, marked as filled circles. The same basic groups of zones can be recognized as in Figure 3. The number of assemblages with <40% *Anabathra* is increased, and defines more clearly a second major axis, determined by *Lepidophloios* and *Medullosa* dominance. Point numbers correspond to zone labels to right of ordination. W = West Liberty VS 1; E1 = Enterprise VS 1; E2 = Enterprise VS 2; E1/2 = combined Enterprise random samples 1 and 2; E3/4 = combined Enterprise random samples 3 and 4.

Lepidophloios-dominated Assemblages

The *Lepidophloios* dominance of a significant portion of the Secor peat swamp is consistent with patterns found in numerous other Desmoinesian coals of the United States. The one *Lepidophloios*-dominated stand from the profiles (W4) is fairly typical in its low species richness, although it bears the imprint of this particular swamp in having *Anabathra* as the major subdominant. In contrast, the composite assemblages dominated by *Lepidophloios* are of relatively high species richness with 11–13 taxa each. This is in part, perhaps in large part, a reflection of the interaction of sample size and the composite nature of the assemblages. Profile zones are in general lower in species richness than all but the smallest composite zones (Table 4). Agglomeration of numerous coal balls, representing small samples drawn from a number of different stands with the same dominant taxon, compounds the likelihood of encountering different rare elements. This would be most likely in cases where stands dominated by the defining taxa were common.

TABLE 6—Taxonomic composition of compression-impression random sample.

A. Taxonomic Composition

Taxon	Count	% of total count	No. of quadrats	% of total quadrats
Alethopteris serli	651	23.79	114	55.61
Alethopteris ambigua	21	0.77	7	3.42
Neuropteris rarinervis	118	4.31	12	5.85
Neuropteris cf. *ovata*	53	1.94	19	9.27
Neuropteris macrophylla	38	1.39	15	7.32
Neuropteris cf. *osmundae*	16	0.58	8	3.90
Neuropteris cf. *obliqua*	7	0.26	3	1.46
Unidentified *Neuropteris*	39	1.42	16	7.81
Cyclopteris sp.	15	0.55	12	5.85
Reticulopteris muensteri	2	0.07	2	0.98
Dolerotheca sp.	2	0.07	2	0.98
cf. *Aulacotheca* sp.	2	0.07	1	0.49
Holcospermum sp.	1	0.04	1	0.49
Unidentified ovule	3	0.11	3	1.46
'*Mariopteris*' *occidentalis*	242	8.84	30	14.63
Mariopteris nervosa	71	2.59	16	7.81
Eusphenopteris scribani-striata	39	1.42	11	5.37
Pteridosperm axes	261	9.54	108	52.50
Sphenopteris macilenta	46	1.68	10	4.88
Unidentified *Sphenopteris*	11	0.40	5	2.44
Zeilleria/Hymenophylloides	7	0.26	1	0.49
Renaultia/Hymenophylloides	1	0.04	1	0.49
Aphlebia	26	0.95	12	5.85
Pecopteris miltonii	345	12.61	45	21.95
Pecopteris hemitelioides	205	7.49	48	23.42
Pecopteris plumosa-dentata	104	3.80	17	8.29
Pecopteris saraefolia/lamuriensis	28	1.02	4	1.95
Calamites spp.	65	2.38	35	16.59
Annularia sphenophylloides	144	5.26	28	13.66
Annularia stellata	33	1.21	13	6.34
Asterophyllities sp.	1	0.04	1	0.49
Pinnularia sp.	27	0.99	17	8.29
Sphenophyllum emarginatum	112	4.09	25	12.20
	2736 counts		205 quadrats	

B. Abundance of Major Groups

Group	Count	% of total count	No. of quadrats	% of total quadrats
Medullosans	1228	44.88		
Total Pteridosperms	1640	59.94	177	86.34
Marattialeans	604	22.08		
Total Ferns	718	26.17	94	45.85
Calamites	270	9.87		
Sphenophylls	112	4.09		
Total Sphenopsids	382	13.96	86	41.95
Lycopods Present				

TABLE 7—Top 12 taxa rank ordered: count vs. quadrat data.

Count data	Quadrat data
1. *Alethopteris serli* 23.79%	1. *Alethopteris serli* 55.61%
2. *Pecopteris miltoni* 12.61%	2. Pteridosperm axes 52.20%
3. Pteridosperm axes 9.54%	3. *Pecopteris hemitelioides* 23.42%
4. *'Mariopteris' occidentalis* 8.84%	4. *Pecopteris miltoni* 21.95%
5. *Pecopteris hemilelioides* 7.49%	5. Calamites 16.58%
6. *Annularia sphenophylloides* 5.26%	6. *'Mariopteris' occidentalis* 14.63%
7. *Neuropteris rarinervis* 4.31%	7. *Annularia sphenophylloides* 13.66%
8. *Sphenophyllum emarginatum* 4.09%	8. *Sphenophyllum emarginatum* 12.20%
9. *Pecopteris plumosa-dentata* 3.80%	9. *Neuropteris* cf. *ovata* 9.27%
10. *Mariopteris nervosa* 2.59%	10. *Pecopteris plumosa-dentata* 8.29%
11. Calamites 2.38%	11. *Mariopteris nervosa* 7.81%
12. *Neuropteris* cf. *ovata* 1.94%	12. *Neuropteris macrophylla* 7.32%

Cordaitean-dominated Assemblages

The Secor Coal is within the upper Cordaitean interval of Phillips and Peppers (1984). Coals of the western interior coal mining areas also are enriched conspicuously in cordaites relative to contemporaneous coals of the Illinois Basin (Phillips et al., 1985). Cordaites are a minor component in the Secor Coal, more important than in late Desmoinesian (Westphalian D) coals, but less abundant than we expected them to be for this stratigraphic interval and region. The dominant cordaite, which produced *Cardiocarpus spinatus* ovules, is the typical cordaite of the middle Desmoinesian (early Westphalian D). It has been reconstructed as a scrambling shrub of low stature (Costanza, 1985), perhaps an invasive opportunist, suggested by its relatively high reproductive output. It appears to have been an interstitial component of the general swamp vegetation. In profiles it occurs in low abundance in most zones. It dominates the most diverse zone, in which *Lepidophloios* is a subdominant, and nine of the 16 total species are ground cover or shrubs. The most diverse of the composite zones similarly is dominated by a cordaite, although which of the two Secor species is unclear; *Lepidophloios* is the primary subdominant in this zone, and of 13 total taxa, five are ground cover or shrubs. A second cordaite, the parent of *Cardiocarpus magnicellularis*, is less common, although it did appear as a dominant of two small composite zones.

Cordaitean abundance and distribution patterns suggest dominance of localized patches within the coal swamp. These areas supported a highly complex vegetation, which included a diverse ground cover. The cordaites evidently could tolerate a wider range of conditions than many of the smaller plants, and could grow in scattered parts of the areas populated by *Lepidophloios* and *Anabathra* trees. No cordaites were identified in the compression flora.

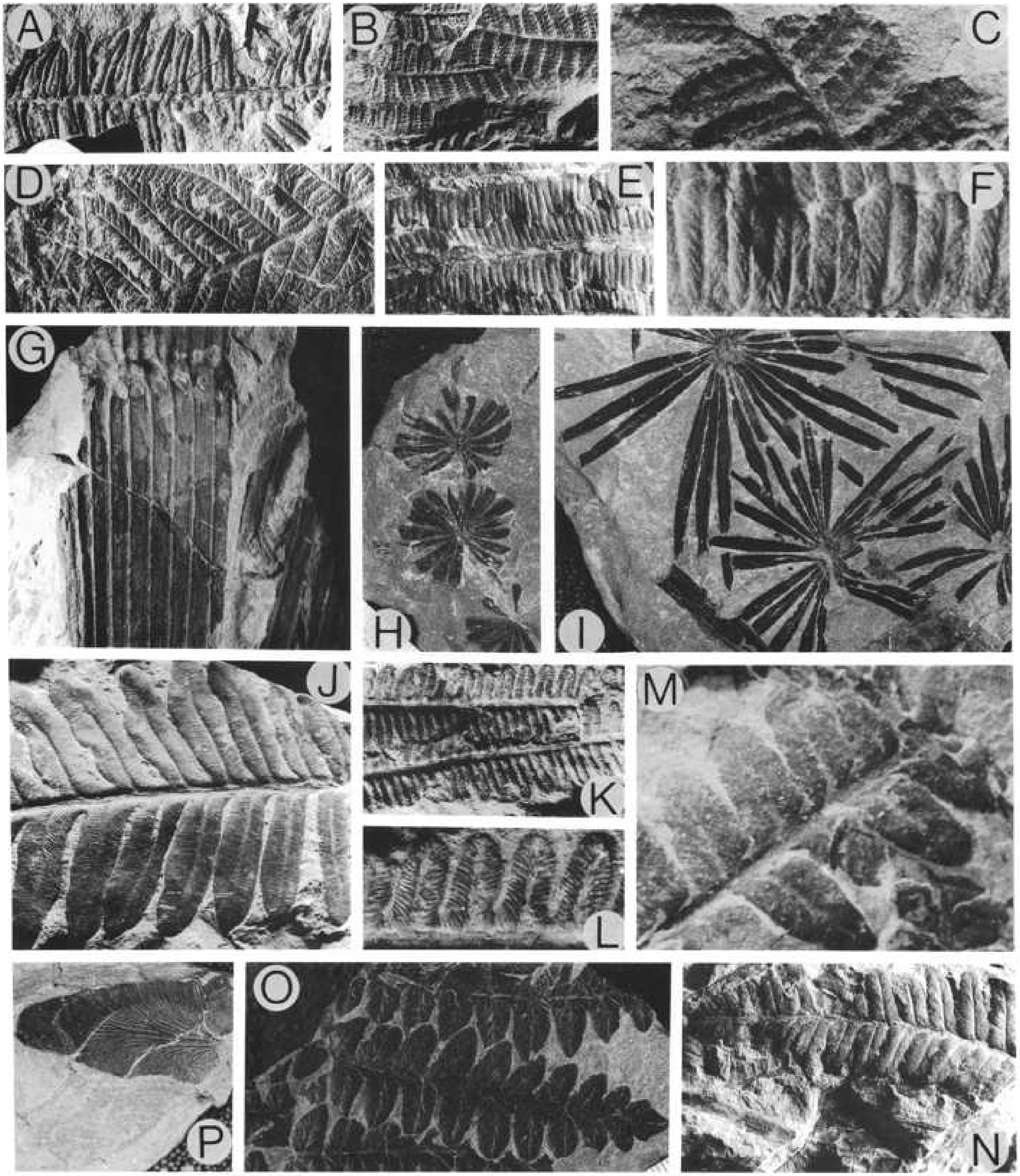
Compression Flora

Twenty-three species of foliage, the best estimates of whole-plant taxa in this analysis, occur in the compression flora if *Sigillaria* sp. is included. Examples of the major taxa are illustrated in Figures 5 and 6. This species richness is lower than the estimated whole-plant richness of the entire peat-swamp assemblage. Species composition of the peat swamp is drawn from a multihabitat landscape, suggested by the floristic analysis, the distribution of fusain, and the assemblage-specific variation in the quality of peat preservation. The compression flora, by contrast, likely represents fewer habitats, drawn from vegetation colonizing a crevasse splay deposit. It may be most comparable to a single coal-ball zone, in which case the species richness of the compression flora would be considerably higher than any encountered in a single peat-swamp habitat. Furthermore, the compression flora probably was deposited during a relatively short period of time compared to the flora of the coal seam, perhaps an order of magnitude less. On a whole-flora level, this would contribute significantly to the apparent lower species richness of the compression assemblage.

The compression flora is typical of middle Desmoinesian (early Westphalian D) floras of the United States (Gillespie and Pfefferkorn, 1979; Pfefferkorn and Thomson, 1982): dominance by medullosan pteridosperms, with an important pecopterid tree-fern component. The vegetation appears to have been structurally diverse, including vines, ground cover, and numerous species of small trees. There is little quantitative information at the generic or specific

→

FIGURE 5—Compression fossils from roof shale of Secor Coal. All ×1 unless noted otherwise. United States National Museum number follows each specimen. **A)** *Pecopteris saraefolia* USNM 455053 **B)** *Pecopteris miltoni* fertile specimen USNM 455054 **C)** *Pecopteris miltoni* ×3 USNM 455054 **D)** *Pecopteris plumos=adentata* USNM 455055 **E)** *Pecopteris hemitelioides* USNM 455056 **F)** *Pecopteris hemitelioides* ×3 USNM



455056 **G)** *Calamites* sp. USNM 455057 **H)** *Annularia sphenophylloides* USNM 455058 **I)** *Annularia stellata* USNM 455059 **J)** *Alethopteris serlii* USNM 455060 **K)** *Alethopteris ambigua* USNM 455061 **L)** *Alethopteris ambigua* ×3 USNM 455061 **M)** '*Mariopteris*' *occidentalis* ×3 USNM 455062 **N)** '*Mariopteris*' *occidentalis* USNM 455062 **O)** *Mariopteris nervosa* USNM 455063 **P)** *Reticulopteris muensteri* USNM 455064.

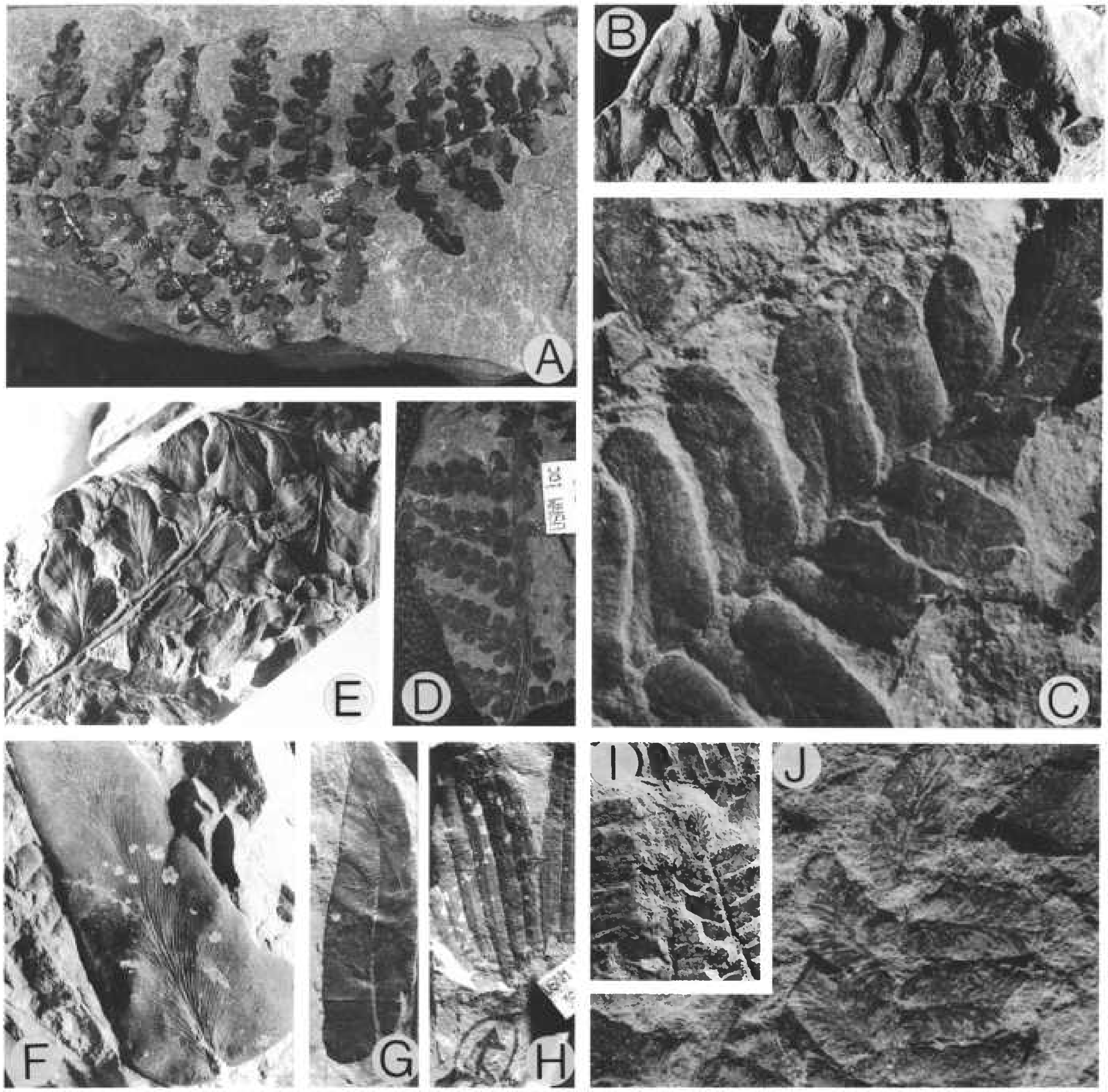


FIGURE 6—Compression fossils from roof shale of Secor Coal. All magnifications ×1 unless noted otherwise. United States National Museum number follows each specimen. **A**) *Eusphenopteris scribani-striata* USNM 455065 **B**) *Neuropteris* cf. *ovata* USNM 455066 **C**) *Neuropteris* cf. *ovata* ×3 USNM 455066 **D**) *Eusphenopteris* sp. USNM 455067 **E**) *Sphenopteris macilenta* USNM 455068 **F**) *Neuropteris osmundae* USNM 455069 **G**) *Neuropteris macrophylla* USNM 455070 **H**) *Holcospermum* sp. USNM 455071 **I**) *Neuropteris rarinervis* USNM 455072 **J**) *Neuropteris rarinervis* ×3 USNM 455072.

levels on Pennsylvanian compression floras (see Scott, 1977, for review; 1978). Consequently it is not possible to assess the distinctiveness of this particular assemblage. It does contain a few unusual elements, such as '*Mariopteris*' *occidentalis*, reported to our knowledge only from the early Desmoinesian of Oklahoma and Kansas, *Reticulopteris muensteri*, and *Sphenopteris macilenta*. However, in general, the dominant elements are species of *Alethopteris*, *Pecopteris*, and *Neuropteris* that occur commonly in strata of equivalent age in the mid-continent. White (1899) published an extensive, but mostly unillustrated, flora of the coal measures from the area near McAlester, Oklahoma.

The diversity of medullosan pteridosperms was similar in the peat swamp and clastic wetlands. Six "species" of medullosan foliage were identified in coal balls, and eight species occur in the compression flora. *Neuropteris rarinervis* is the only species identified in both habitats. However, vagaries resulting from the poor state of the taxonomy of structurally preserved pteridosperm foliage, make comparisons difficult, and there may be greater overlap than suggested by our analysis. It is possible, for example, that what we have identified as *Alethopteris lesquereuxii* in coal balls may be the same as *A. serlii* in compressions, considering the similarity of these two species in compression preservation. Dominance patterns contrast sharply between the two environments. The pteridosperms account for only 3.9% of the coal-ball peat biomass. In the compression flora medullosan foliage accounts for 44.9% of the count data; pteridosperms as a group account for 59.9% of the count data and occur in 86.3% of the quadrats.

The pattern for marattialean ferns is similar to that of pteridosperms. Ferns, mostly marattialeans, account for an average of 5.9% of the peat biomass; they account for 26.2% of the count data from the compression flora, and occur in 45.8% of the quadrats. Marattialean abundance began to reach dominant levels about one-half a stage earlier in clastic lowland habitats than in peat swamps (Pfefferkorn and Thomson, 1982).

Sphenopsids are a minor component of the peat-swamp vegetation and of the compression flora. The average importance of sphenopsids, third overall among major plant groups in the peat swamp, gives the Secor Coal an unusual overall composition. Sphenopsids were important in streamside and in many aggradational environments during the Pennsylvanian (Gastaldo, 1987), but they did not play an important role in most clastic or peat-forming wetlands, despite wide distribution.

SUMMARY

Few coals have received intensive study by paleobotanists, despite the occurrence of coal balls in over 30 coals in the United States alone. Our knowledge of coal-forming floras is derived largely from study of the Union Seam of England, the Hamlin Coal of Kentucky, the Fleming Coal of Kansas, the Springfield, Herrin and Calhoun Coals of Illinois, and the Duquesne Coal of Ohio. The Secor Coal is hardly a household word among the scientists that study coal-forming vegetation. This first detailed examination of the flora and vegetation of the Secor Coal has revealed some interesting and unusual vegetational patterns. We have not, however, encountered many unusual or new taxa in the course of the study. Nonetheless, the Secor Coal reveals clearly the great variety on a common set of themes that appeared in Middle Pennsylvanian peat swamps.

The differences between the peat-swamp and clastic-wetland vegetation also are made clear by comparing a roof-shale to a coal-ball flora. There persists the belief that compression floras of coal roof shales are broadly representative of the peat-forming flora. Although each case must be analyzed independently, it is the exceptional roof flora that is lycopsid dominated and represents a buried peat-swamp forest. The occurrence of lycopsid trunks and stump bases in many underground mines reflects the frequent location of mines in low sulfur coal deposits, which occur most often in proximity to paleochannel systems, and under channel deposits (Hopkins, 1968). It is in such areas that flooding and deposition of channel-borne muds occur during the terminal phases of peat formation (DeMaris et al., 1983); at such times and in such areas forests are most likely to be buried catastrophically. Fossiliferous roof shales represent a wide variety of depositional conditions, and no general inference about their relationship to peat-forming vegetation can or should be made.

ACKNOWLEDGMENTS

We thank Sam Friedman, Oklahoma Geological Survey, for assistance in field work, LeRoy Hemish, Oklahoma Geological Survey, for providing information on the Secor coal, expert opinion on the likely source of coal-balls, and comments on the manuscript, Debra Willard, Smithsonian Institution for computer assistance, Robert A. Gastaldo, Auburn University, for comments on the manuscript, and Mary Parrish, Smithsonian Institution, for preparation of figures. A portion of this work was supported by NSF Grant EAR-8313094 to T.L. Phillips. This is contribution No. 3 from the Evolution of Terrestrial Ecosystems Consortium.

REFERENCES

Branson, C.C., 1962, Pennsylvanian System of the mid-continent: *in* Branson, C.C., ed., Pennsylvanian System in the United States, A symposium, Tulsa, Oklahoma: American Association of Petroleum Geologists, p. 431–460.

Burnham, R.J., Wing, S.L., and Parker, G.G., in press, The reflection of deciduous forest communities in leaf litter: Implications for autochthonous litter assemblages from the fossil record: Paleobiology.

Calder, J.C., in press, The evolution of a ground water-influenced (Westphalian B) peat-forming ecosystem in a piedmont setting: The No. 3 seam, Springhill Coalfield, Cumberland Basin, Nova Scotia: Geological Society of America, Special Publication.

Cecil, C.B., 1990, Paleoclimatic controls on stratigraphic repetition of chemical and siliciclastic rocks: Geology, v. 18, p. 533–536.

Cecil, C.B., Stanton, R.W., Neuzil, S.G., Dulong, F.T., Ruppert, L.F., and Pierce, B.S., 1985, Paleoclimatic controls on Late Paleozoic sedimentation and peat formation in the central Appalachian basin (U.S.A.): International Journal of Coal Geology, v. 5, p. 195–320.

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

Dane, C.H., Rothrock, H.E., and Williams, J.S., 1938, Geology and fuel resources of the southern part of the Oklahoma coal field.

Part 3: The Quinton-Scipio District; Pittsburg, Haskell and Latimer Counties: U.S. Geological Survey Bulletin 847-C, 253 p.
DEMARIS, P.J., BAUER, R.A., CAHILL, R.A., and DAMBERGER, H.H., 1983, Geologic investigation of roof and floor strata: Longwall demonstration, Old Ben mine No. 24—prediction of coal balls in the Herrin Coal: Illinois State Geological Survey, Contract/Grant Report 1983-2, 69 p.
DIMICHELE, W.A., and DEMARIS, P.J., 1987, Structure and dynamics of a Pennsylvanian-age *Lepidodendron* forest: Colonizers of a disturbed swamp habitat in the Herrin (No. 6) Coal of Illinois: PALAIOS, v. 2, p. 146–157.
DIMICHELE, W.A., and PHILLIPS, T.L., 1985, Arborescent lycopod reproduction and paleoecology in a coal-swamp environment of late Middle Pennsylvanian age (Herrin Coal, Illinois): Review of Palaeobotany and Palynology, v. 44, p. 1–26.
DIMICHELE, W.A., and PHILLIPS, T.L., 1988, Paleoecology of the Middle Pennsylvanian age Herrin coal swamp (Illinois) near a contemporaneous river system, the Walshville paleochannel: Review of Palaeobotany and Palynology, v. 56, p. 151–176.
DIMICHELE, W.A., and PHILLIPS, T.L., 1990, Tropical lowland vegetation and climate change in the late Paleozoic: Geological Society of America, Abstracts with Programs, v. 22, p. A76.
EBLE, C., 1988, Palynology and paleoecology of a Middle Pennsylvanian coal bed from the central Appalachian basin: Unpublished Ph.D. Dissertation, West Virginia University, Morgantown, West Virginia, 495 p.
EBLE, C., and GRADY, W., 1990, Paleoecological interpretation of a Middle Pennsylvanian coal bed in the central Appalachian basin, U.S.A. International Journal of Coal Geology, v. 16, p. 255–286.
EHRET, D.L., and PHILLIPS, T.L., 1977, *Psaronius* root systems—morphology and development: Palaeontographica, v. 161B, p. 147–164.
FENG, B.-C., 1989, Paleoecology of an upper Middle Pennsylvanian coal swamp from western Pennsylvania, U.S.A: Review of Palaeobotany and Palynology, v. 57, p. 299–312.
FRIEDMAN, S.A., 1974, An investigation of the coal reserves in the Ozarks section of Oklahoma and their potential uses; Final report to the Ozarks Regional Commission: Oklahoma Geological Survey Special Publication 74-2, 117 p.
FRIEDMAN, S.A., 1978, Desmoinesian coal deposits in part of the Arkoma Basin, eastern Oklahoma: Oklahoma City Geological Society Fieldtrip Guidebook, 62 p.
GASTALDO, R.A., 1987, Confirmation of Carboniferous clastic swamp communities: Nature, v. 326, p. 869–871.
GILLESPIE, W.H., and PFEFFERKORN, H.W., 1979, Distribution of commonly occurring plant megafossils in the proposed Pennsylvanian System Stratotype: *in* ENGLUND, K.J., ARNDT, H.H., and HENRY, T.W., eds., Proposed Pennsylvanian System Stratotype—Virginia and West Virginia: 9th International Congress Carboniferous Stratigraphy and Geology, Guidebook to Fieldtrip No. 1, p. 87–96.
HEMISH, L.A., 1988, Coalescence of the Secor and Secor Rider coal beds in the Shady Grove area, northeastern McIntosh County, Oklahoma, with interpretations concerning depositional environments: Oklahoma Geology Notes, v. 48, p. 100–119.
HENDRICKS, T.A., 1937, Geology and fuel resources of the southern part of the Oklahoma coal field. Part 1. The McAlester District; Pittsburg, Atoka and Latimer Counties: U.S. Geological Survey Bulletin 847-A, 90 p.
HILL, M.O., and GAUCH, H.G., 1980, Detrended correspondence analysis, an improved ordination technique: Vegetatio, v. 42, p. 47–58.
HOPKINS, M.E., 1968, Harrisburg (No. 5) Coal reserves of southern Illinois: Illinois State Geological Survey Circular 431, 25 p.
KENKEL, N.C., and ORLOCI, L., 1986, Applying metric and nonmetric multidimensional scaling to ecological studies: Some new results: Ecology, v. 67, p. 919–928.
LESNIKOWSKA, A.D., 1989, Anatomically preserved Marattiales from coal swamps of the Desmoinesian and Missourian of the midcontinent United States: Systematics, ecology and evolution: Unpublished Ph.D. Dissertation, University of Illinois, Urbana-Champaign, 227 p.
MAMAY, S.H., and YOCHELSON, E.L., 1962, Occurrence and significance of marine animal remains in American coal balls: U.S. Geological Survey Professional Paper 354-I, p. 193–224.
PEARSON, H.L., 1986, Structure and taxonomy of the Carboniferous lycopsid *Anabathra*: Bulletin of the British Museum, Natural History (Geology), v. 40, p. 265–292.
PEPPERS, R.A., 1970, Correlation and palynology of coals in the Carbondale and Spoon Formations (Pennsylvanian) of the northeastern part of the Illinois Basin: Illinois State Geological Survey Bulletin 93, 173 p.
PEPPERS, R.A., 1979, Development of coal-forming floras during the early part of the Pennsylvanian in the Illinois Basin: Guidebook to Fieldtrip No. 9, 9th International Congress Carboniferous Stratigraphy and Geology, part 2, p. 8–14.
PFEFFERKORN, H.W., and THOMSON, M.C., 1982, Changes in dominance patterns in Upper Carboniferous plant-fossil assemblages: Geology, v. 10, p. 641–644.
PFEFFERKORN, H.W., MUSTAFA, H., and HASS, H., 1975, Quantitative Characterisierung ober-karboner Abdruckfloren: Neues Jahrbuch für Geologie und Palaontologie Abhandlung, v. 150, p. 253–269.
PHILLIPS, T.L., and DIMICHELE, W.A., 1981, Paleoecology of Middle Pennsylvanian-age coal swamps in southern Illinois: Herrin Coal Member at the Sahara Mine No. 6: *in* NIKLAS, K.J., ed., Paleobotany, Paleoecology and Evolution, Praeger Press, New York, v. 1, p. 231–281.
PHILLIPS, T. L., and PEPPERS, R.A., 1984, Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence: International Journal of Coal Geology, v. 3, p. 205–255.
PHILLIPS, T.L., KUNZ, A.B., and MICKISH, D.J., 1977, Paleobotany of permineralized peat (coal balls) from the Herrin (No. 6) Coal Member of the Illinois Basin: Geological Society of America, Microform Publication 7, p. 18–49.
PHILLIPS, T.L., PEPPERS, R.A., and DIMICHELE, W.A., 1985, Stratigraphic and interregional changes in Pennsylvanian coal swamp vegetation: Environmental influences: International Journal of Coal Geology, v. 5, p. 43–109.
PRENTICE, I.C., 1980, Multidimensional scaling as research tool in Quaternary palynology: A review of theory and methods: Review of Palaeobotany and Palynology, v. 31, p. 71–104.
PRYOR, J.S., 1988, Sampling methods for quantitative analysis of coal balls. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 63, p. 313–326.
RAYMOND, A., 1988, The paleoecology of a coal-ball deposit from the Middle Pennsylvanian of Iowa dominated by cordaitean gymnosperms: Review of Palaeobotany and Palynology, v. 53, p. 233–250.
READ, C.B., and MAMAY, S.H., 1964, Paleozoic floral zones and floral provinces of the United States: U.S. Geological Survey Professional Paper 454-K, p. 1–33.
ROTHWELL, G.W., and WARNER, S.W., 1984, *Cordaixylon dumusum* n. sp. (Cordaitales): I. Vegetative structures: Botanical Gazette, v. 145, p. 275–291.
SCOTT, A.C., 1977, A review of the ecology of Upper Carboniferous plant assemblages, with new data from Strathclyde: Palaeontology, v. 20, p. 447–473.
SCOTT, A.C., 1978, Sedimentological and ecological control of Westphalian B plant assemblages from West Yorkshire: Proceedings Yorkshire Geological Society, v. 41, p. 461–508.
SELLARDS, E.H., 1908, Fossil plants of the Upper Paleozoic of Kansas: Kansas Geological Survey Report 9, p. 434–467.
VISHER, G.S., 1968, Depositional framework of the Bluejacket-Bartlesville Sandstone: *in* VISHER, G.S., ed., Geology of the Bluejacket-Bartlesville Sandstone of Oklahoma: Oklahoma City Geological Society Fieldtrip Guidebook, p. 33–51.
WHITE, D., 1899, Report on fossil plants from the McAlester Coal

Field, Indian Territory, collected by Messrs. Taff and Richardson in 1897: U.S. Geological Survey, 19th Annual Report (1897–1898), part III—Economic Geology, p. 457–538.
WHITTAKER, R.H., 1975, Communities and Ecosystems, 2nd Edition, MacMillan Publishing Co., New York, 385 p.
WILKINSON, L., 1988, SYSTAT: The System for Statistics, Evanston, Illinois: SYSTAT, Inc., 822 p.
WILLARD, D.A., 1990, Palynology of the Springfield Coal of the Illinois Basin (Middle Pennsylvanian) with quantitative comparison of spore floras and coal-ball peats and implications for paleoecological studies: Unpublished Ph.D. Dissertation, University of Illinois, Urbana-Champaign, 216 p.

ACCEPTED APRIL 21, 1991