Paleoecological Analysis of Two Early Pennsylvanian Mineral-Substrate Wetlands

JANELLE S. PRYOR[1]
Department of Biological Sciences, Mississippi College, Clinton, MS 39058

ROBERT A. GASTALDO[2]
Department of Geology, Colby College, Waterville, ME 04901-8858

PALAIOS, 2000, V. 15, p. 3–13

The biomass within two Early Pennsylvanian (Langsettian [Westphalian A] equivalent) penecontemporaneous swamp communities was sampled quantitatively to obtain an estimate of the taxonomic contribution to each assemblage. Blocks of organic-rich shale were removed from a clastic parting within the Black Creek Coal, and ~0.5-m² siltstone quadrats were chain-sawed from a clastic swamp community directly above the Bear Creek Coal. Bedding planes were exposed, and the surface areas for each taxon per bedding surface were measured and used as proxies for biomass contribution in each locality. Biomass over a combined area of 5.47 m² was assessed for the Black Creek Coal parting; biomass covering an area of 9.70 m² was evaluated for the assemblage preserved above the Bear Creek coal. In addition to calculating standard diversity indices, this data set was analyzed using cluster analyses and non-metric multidimensional scaling (NMDS) to differentiate variations within the general flora.

Low species diversity characterizes both floras. Diversity indices for both assemblages are very similar, indicating essentially no difference in assemblage composition, despite the difference in edaphic conditions. The Bear Creek Coal wetlands show greater variation in species content, while the mineral-enhanced peat of the Black Creek Coal overlaps this species diversity within a slightly more restricted range of variation. Cluster analysis produced 5 stable clusters, whereas three dimensions of the NMDS analysis provided the best fit to explain the variation among the samples. The dimensions are interpreted as representing abundance of (1) arborescent lycopsids, (2) arborescent and climbing sphenopsids, and (3) pteridosperms. The plant community preserved within the clastic parting of the Black Creek Coal is comparable to that of the community found above the Bear Creek Coal. Hence, vegetation that colonized mineral-substrate soils in Early Pennsylvanian coastal lowlands, whether in peat or non-peat accumulating settings, are very similar. The dominance of pteridosperms in these depositional regimes appears to remain stable throughout the Early and Middle Pennsylvanian and portends community replacements in the Late Westphalian D some 8–10 million years later.

INTRODUCTION

Until recently, very little detailed information has been published about Early Pennsylvanian coastal wetland communities of North America. Most of this information has originated from assemblages preserved in the Black Warrior Basin, where the Pottsville Formation (Langsettian [Westphalian A]; Gillespie and Rheams, 1985) is more than 3000 m thick (Hewitt, 1984). Palynologic and coal petrographic (e.g., Eble et al., 1994), permineralized peat (Winston and Phillips, 1991), biostratigraphic (Lyons et al., 1985), taphonomic (e.g., Gastaldo et al., 1989), and megafloral paleoecologic (Gastaldo, 1987, 1990, 1992; Gastaldo et al., 1991; Demko and Gastaldo, 1992) studies have been conducted primarily on the most productive coal-bearing interval—the Mary Lee Coal Zone. This interval has been the focus of investigation because of extensive strip-mining operations near the basin margin that have exposed these rocks for more than 1000 km² in Walker and Fayette Counties alone.

Many of the other coal zones also preserve megafloral assemblages similar to those reported for the Mary Lee, but limited exposure has restricted collection and analysis, particularly in the lowest part of the section. This contribution focuses on the comparison between biomass proxies of two essentially coeval coastal communities—one in the Bear Creek Coal Zone, the other in the Black Creek Coal Zone—that occupied different soil substrates in the earliest Pennsylvanian. Analysis of biomass allocation in other North American coals has been done (Pryor, 1996; Baker and DiMichele, 1997), but this study provides the first evaluation of penecontemporaneous biomass from an organic-rich (clastic-parting in a peat swamp) and mineral soil (coastal wetland).

Geological Setting

The Black Warrior foreland basin of Alabama contains a thick section of Late Mississippian (Chesterian) and Early Pennsylvanian (Morrowan) rocks that were deposited under strong control of both tectonic and climatic factors, resulting in genetic packages of cyclic sediments (Pashin, 1994a). Each cycle is characterized by a coarsening- and coaling-upward sequence that begins above a fossiliferous ravinement surface/bed over which a basal marine mudstone was deposited. Lithologies within the marine sequence coarsen upward into open- to marginal-marine sandstone that, in turn, are overlain by marginal marine and terrestrial sandstone, mudstone, and coal (Gastaldo

---

[1] Current address: Department of Physiology and Biophysics, University of Mississippi Medical Center, 2500 North State Street, Jackson, MS 39216-4505.

[2] Previous address: Department of Geology, Auburn University, AL 36849.

0883-1351/00/0015-0003/$3.00

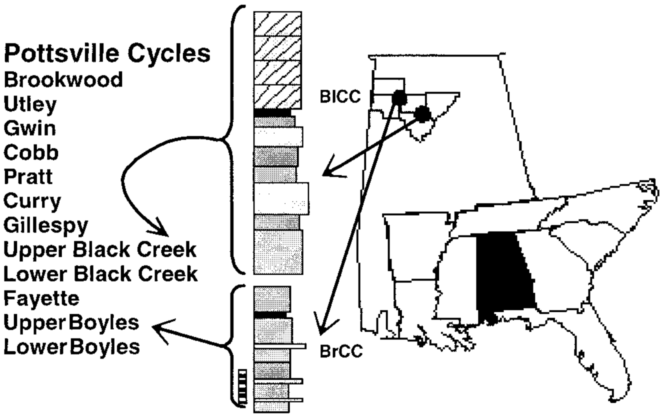

FIGURE 1—Stratigraphic column and location of collecting localities in northwestern Alabama, southeastern United States. BlCC = Black Creek Coal locality; BrCC = Bear Creek Coal locality. Scale bar to left lower corner of stratigraphic column equals 10 feet.

et al., 1993; Pashin, 1994b). Cycles range in thickness from 11 m (35 ft) along the northern basin margin to more than 200 m (700 ft) in the deep subsurface. Thirteen cycles (Fig. 1) have been identified across the basin and represent regional marine-nonmarine depositional continua best explained by allogenic processes (Gastaldo et al., 1993; Pashin, 1994a; Demko and Gastaldo, 1996). Depending upon the time scale used (Menning et al., 1997), duration of Pottsville-type cycles may have ranged between ~0.15 to 0.2 MY.

The Bear Creek Coal represents the terrestrial expression of the Upper Boyles cycle (Fig. 1) and, although it can be traced across the basin (Pashin, 1994a), it crops out only in Franklin County, northwest Alabama. Near the basin margin, the Bear Creek Coal is found in isolated pods restricted to troughs of the underlying quartz arenite, which is interpreted to represent the stranding of offshore sand bars during regression (see Gastaldo et al., 1993). The peat swamp formed above a leached clay horizon (paleosol) in which stigmarian axes and appendages are well preserved. The thickness of the coal varies near the basin margin in this setting, but increases and becomes laterally extensive in the subsurface to the southeast where fully terrestrial deposits have been identified (Pashin, 1994a). The coal is overlain by fluvial overbank and/or tidal deposits, which are indicative of coastal plain transgression.

The Black Creek Coal in this study is exposed in Walker County and is overlain by the Bremen Sandstone (Haas and Gastaldo, 1986), which means that it is the terrestrial expression of the Upper Black Creek cycle (Fig.1). Palynologically, this cycle and those stratigraphically higher have been assigned to the Langsettian (Westphalian A; Eble and Gillespie, 1989). This coal accumulated above a leached, stigmarian-rooted claystone that overlies silty and fossiliferous shale, interpreted to represent back-barrier deposits (Haas and Gastaldo, 1986). Interspersed are medium- to fine-grained sandstones within which medium- to large-scale rippled beds, micro-cross stratification to large-scale cross bedding, and thin low-angle beds are common. These sandstones have been interpreted to represent overwash and shoreface deposits over which terrestrial conditions developed (Haas and Gastaldo, 1986). Although the Black Creek Coal can be traced across the basin, similar to the Bear Creek Coal (Pashin, 1994b), it is overlain by an offshore sandstone body—the Bremen Sandstone—where it crops out at the northern basin margin. Much of the coal and whatever overlying coastal plain and/or marginal marine sediments might have been present were eroded prior to emplacement of this sand body.

Objectives

The current study compares the Westphalian A adpression (sensu Shute and Cleal, 1987) floras preserved within peat and non-peat accumulating wetlands of the Black Warrior Basin coastal plains. Results from a number of actuopaleontologic studies (e.g., Raymond, 1987; Burnham, 1989, 1990, 1994; Burnham et al., 1992) indicate that heterogeneity of the source vegetation is reflected in autochthonous plant-litter accumulations, and that this plant debris can be used to produce reliable reconstructions of the source-plant community (Gastaldo et al., 1995). The fossil assemblages analyzed from within the Black Creek Coal and the roof rock of the Bear Creek Coal represent autochthonous and parautochthonous plant-litter deposits (see Gastaldo et al., 1995). Hence, there is a very high probability that the preserved megaflora accurately reflects the original taxonomic composition of the vegetation within these ancient swamps. Thus, sampling the Black Creek and Bear Creek assemblages should be closely analogous to sampling the vegetation of the parent-plant communities.

MATERIALS AND METHODS

Slabs of organic-rich shale, ranging in thickness from 9 to 13 cm, over a lateral extent of approximately 4 m, were manually excavated from within the Black Creek Coal at Smith Lake Dam (T. 13 S., R. 5 W., Sec. 6, Lewis Smith-Lake Dam 7.5′ USGS Quadrangle; Haas and Gastaldo, 1986). Blocks of siltstone, measuring 0.5 m^2 and ranging from 1.6 to 4 cm thick, over a lateral area of 10 meters, were excavated with a carbide-tipped chain saw from the overburden of the Bear Creek Coal within the Wilson Mine, Franklin County, AL (T. 8 S., R. 11 W., Sec. 18, Phil Campbell 7.5′ USGS Quadrangle). The orientation of each block was labeled in the field so that the stratigraphic sequence and laterally equivalent blocks could be reconstructed in the laboratory. All sampling was conducted during the mid-1980's.

In the lab, shale and siltstone bedding planes were exposed using wide-bladed chisels and fine spatulas. Bedding surfaces of the Black Creek Coal were exposed at intervals ranging between 0.5 and 1 cm, whereas successive bedding surfaces of the Bear Creek siltstone were exposed at approximately 0.1-to-0.4-cm intervals depending upon adpression density (Appendix). Each bedding surface was covered with a sheet of acetate; exposed plant remains were outlined with a permanent marker and identified to the lowest taxonomic rank (genus and species, if possible) and by plant organ (stem/branch, leaf, cone, rachis, pinnule(s), seeds, megaspores). A total of 5.47 m^2 and 9.70 m^2 of surface area were analyzed in this way for the Black Creek and Bear Creek Coals, respectively (Appendix).

TABLE 1—Species Richness (S), the inverse of Simpson ($D = 1/\Sigma((n_i(n_i - 1))/(N(N\text{-}1)))$, where n_i equals the number of observations of the i^{th} species), Shannon ($H' = -\Sigma p_i \ln p_i$, where p_i is the proportional abundance of the i^{th} species), and evenness ($e = H'/\ln S$) indices for the Early Pennsylvanian non-peat (Bear Creek Coal) and peat (Black Creek Coal) accumulating communities.

	Species richness (S)	Simpson index (D)	Shannon (H′)	(e)
Bear Creek Roof-Shale	15	0.36	1.32	0.49
Black Creek Parting	9	0.28	1.33	0.60

Tracings were photocopied along with a cm-scale for calibration purposes. The perimeter and surface area of each plant fragment per bedding plane were calculated using a digitizing pad, PC-Digitize and SigmaScan V 3.01, and an 8088-based computer. Data were entered into a spreadsheet wherein total surface area of each slab was calculated.

Cover (i.e., surface area in cm^2) was summarized for each taxon for each bedding surface. Genera in each assemblage were monospecific, and some orders were represented by only a single species. Hence, although the data in Tables 1–4 and the Appendix *appear* to be tabulated on the taxonomic level of genus or order, they are actually at species level. Whenever a plant fragment could not be identified taxonomically without doubt, it was identified to plant-organ type (if possible) and assigned to "miscellaneous" (MSC category; Appendix).

Percent vegetative biomass (i.e., percent cover) for each taxon on each bedding plane was calculated from total number of cm^2 of vegetative biomass for the species, divided by the total surface area of the slab layer. "Total Percent Biomass" for a sample was equal to the sum of percent vegetative biomass values for all plant taxa present, including MSC (Appendix). The Simpson (D) and Shannon-Weaver (H') diversity indices, along with evenness (e), were calculated for each locality (Magurran, 1988; Ludwig and Reynolds, 1988). DiMichele et al. (1991) have shown that different methods for estimating species abundances in adpression assemblages result in similar approximations of species richness and rank-order abundance.

Pearson product-moment correlations were calculated among species to test for multicollinearity (Table 1). Multicollinearity and singularity are statistical problems that occur when variables are highly correlated (Tabachnick and Fidell, 1989). Multicollinearity occurs when variables have correlations greater than 0.90; singularity occurs when variables are perfectly correlated (Tabachnick and Fidell, 1989). From a purely statistical standpoint, when variables are multicollinear or singular, they contain redundant information and can weaken the statistical validity of the analysis (Tabachnick and Fidell, 1989). In cluster analyses, redundant variables could lead to inflated values for measures of similarity between objects being clustered (Dillon and Goldstein, 1984).

Proximity matrices were calculated using abundance of individual plant taxa as variables and bedding surfaces (slab layers) as "cases" or "OTUs" ("operational taxonomic unit", i.e., objects being clustered). The samples were clustered using Czekanowski Coefficient (Grieg-Smith, 1983) with the Average Linkage (UPGMA) clustering algorithm using NTSYS-pc version 1.60 (Rohlf, 1990). The Czekanowski Coefficient was specifically chosen because it makes pairwise comparisons between samples of vegetation, based upon the number and the biomass of species that are common to the two samples:

$$\text{Czekanowski Coefficient}_{(\text{sample A, sample B})} = 2MC/(MA + MB) \qquad (1)$$

where MA = total percent biomass in sample A; MB = total percent biomass of sample B; MC = summation from species 1 to species *n* (minimum value for percent biomass for species *i* in sample A or sample B). A similarity matrix for the Czekanowski Coefficient was generated by a program written by Pryor in Borland's TurboPascal for Windows because this similarity index was not available in NTSYS-pc (Rohlf, 1990). Average linkage (UPGMA) was chosen for the clustering algorithm because it is a robust general-purpose algorithm that has yielded reliable results in previous plant paleoecological studies (Pryor, 1996). An external validation of cluster solutions was done by an analysis using the Centroid Average (WPGMC) clustering algorithm in NT-SYS-pc.

Cluster solutions from the analyses were determined visually. A mean profile for each cluster was calculated using the average and standard deviation of the percent biomass for each plant taxon from the shale samples grouped within the cluster (Table 3). These mean profiles were used to interpret the results of the cluster analysis. Clusters were also compared with the raw data for bedding planes (i.e., height of slab; Appendix) to determine if sam-

TABLE 2—Pearson product-moment correlations between plant taxa. LYU = unidentified lycopsid; LYD = *Lepidodendron*; CAL = *Calamites*; PT = pteridosperm; NR = *Neuropteris* foliage; AL = *Alethopteris* foliage; SPH = *Sphenopteris pottsvillea*; COR = Cordaitales.

	LYU	LYD	CAL	PT	NR	AL	SPH	COR
LYU	1.00							
LYD	−0.01	1.00						
CAL	0.00	−0.04	1.00					
PT	−0.14	−0.16	0.12	1.00				
NR	−0.14	−0.06	−0.18	0.11	1.00			
AL	−0.07	−0.03	−0.04	−0.03	−0.01	1.00		
SPH	−0.05	−0.03	−0.06	−0.07	0.05	−0.03	1.00	
COR	0.05	−0.03	0.12	−0.03	−0.10	0.07	−0.01	1.00

TABLE 3—Mean profiles of plant = biomass estimates for clusters of samples (derived from cluster analysis using Czekanowski coefficient with UPGMA clustering algorithm). Dominant plant taxa for each cluster are highlighted. LYU = unidentified lycopsid; LYD = *Lepidodendron*; CAL = *Calamites*; PT = pteridosperm; NR = *Neuopteris* foliage; AL = *Alethopteris* foliage; SPH = *Sphenopteris pottsvillea*; COR = Cordaitales; MSC = miscellaneous plant debris.

Cluster 1 n = 1	LYU	LYD	CAL	PT	NR	AL	SPH	COR	MSC
	0.00	**16.50**	0.00	1.61	0.00	0.00	0.00	0.00	0.00
Cluster 2 n = 2	LYU	LYD	CAL	PT	NR	AL	SPH	COR	MSC
Avg.	**46.60**	0.51	0.00	12.68	0.12	0.00	0.00	0.00	11.61
S.D.	**13.20**	0.51	0.00	6.49	0.12	0.00	0.00	0.00	11.61
Cluster 3 n = 10	LYU	LYD	CAL	PT	NR	AL	SPH	COR	MSC
Avg.	0.04	0.00	0.08	6.52	0.10	0.02	0.00	0.01	**16.81**
S.D.	0.10	0.00	0.23	1.70	0.19	0.06	0.01	0.04	**20.25**
Cluster 4 n = 1	LYU	LYD	CAL	PT	NR	AL	SPH	COR	MSC
	0.00	0.00	**54.67**	**31.18**	0.00	0.00	0.00	0.00	1.21
Cluster 5 n = 67	LYU	LYD	CAL	PT	NR	AL	SPH	COR	MSC
Avg.	1.91	0.00	2.51	**30.10**	0.36	0.02	0.03	0.04	4.15
S.D.	4.88	0.02	4.91	**16.83**	0.64	0.06	0.13	0.17	7.96

ple clusters correlated with differences in successional stages or with differences in collecting locality (Table 4).

The Czekanowski Coefficient matrix was also analyzed with non-metric multidimensional scaling (NMDS), using NTSYS-pc version 1.60 (Rohlf, 1990). A final stress value of 0.10 for a *k*-dimensional analysis was used to indicate the goodness of fit of the data in *k*-dimensional space (Rohlf, 1990). Pearson product-moment correlations of dimensions with plant taxa were used to interpret the dimensions resulting from the NMDS analysis (Table 4).

Samples with similar species profiles (i.e., similar proportions of the same taxon) have been interpreted to represent samples from the same microassemblage (viz., successional stage or microhabitat). In a cluster analysis, samples with similar species profiles should form homogeneous groupings. Thus, the clusters (of samples) formed in the statistical analysis should represent similar successional stages or microhabitats from within the plant communities. The mean profile (i.e., averaged proportions of species) of each cluster of samples should then represent the generalized species profile for the particular microassemblage. NMDS was used in conjunction with cluster analysis to determine underlying gradients within the source plant community or depositional environment and the relationships among the discrete groupings of samples formed in the cluster analysis.

TABLE 4—Correlations between plant taxa and clusters of shale samples (derived from cluster analysis); between plant taxa and NMDS dimensions; and between clusters and NMDS dimensions. Correlation values were calculated as Pearson product-moment correlations. LYU = unidentified lycopsid; LYD = *Lepidodendron*; CAL = *Calamites*; PT = pteridosperm; NR = *Neuropteris* foliage; AL = *Alethopteris* foliage; SPH = *Sphenopteris pottsvillea*; COR = Cordaitales; MSC = miscellaneous plant debris.

		MDS dimension		
Taxon	Cluster	1	2	3
LYU	−0.33	0.33	**0.65**	0.18
LYD	−0.41	−0.34	−0.28	0.48
CAL	−0.01	**0.65**	0.14	−0.25
PT	0.17	0.00	0.48	**−0.89**
NR	0.15	−0.27	−0.03	−0.14
AL	−0.04	−0.04	−0.01	−0.02
SPH	0.12	−0.07	−0.04	0.02
COR	0.04	0.25	0.09	0.00
MSC	−0.27	−0.09	−0.24	0.21
Cluster	1.00	0.27	0.18	−0.42

RESULTS AND INTERPRETATIONS

Taxonomic diversity in both assemblages is low, numerically dominated by pteridosperm stem and rachial (leaf axis) debris. Isolated pinnules or pinnae of cf. *Neuralethopteris schlehani* are very common in both assemblages, appearing in a large number of samples from each locality (Appendix). Other pteridosperm foliage is represented by *Sphenopteris pottsvillea* and *Alethopteris lonchitica.* Numerically, *Sphenophyllum* leaves are the next most common element in the Bear Creek assemblage (in supplemental material from the locality that was not used in the present study), but are absent in the blocks from the Black Creek locality. The majority of the material assigned to the MSC category were roots of uncertain taxonomic affinity, interpreted as probably pteridospermous in origin.

Diversity indices were calculated using all taxonomic rankings and plant parts, assuming that each represented one distinct biological entity (see below). Results, presented in Table 1, indicate that both communities have low D, H', and e values. Low diversity indices have been interpreted to be indicative of communities that exist under physically or chemically stressed conditions, and/or those

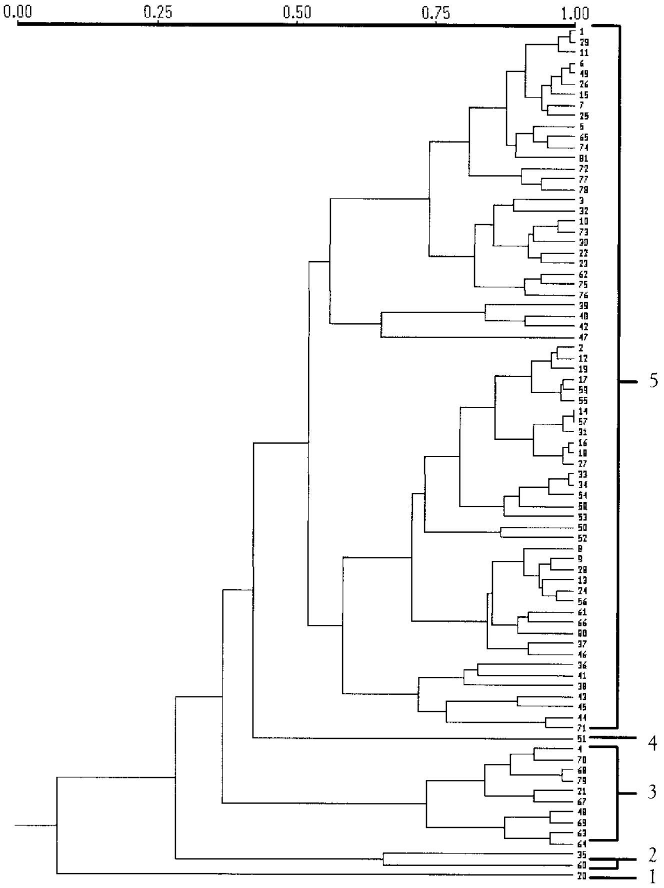

FIGURE 2—Dendrogram representing cluster solution from Czekanowski Coefficient—Average Linkage (CZAL) cluster analysis of plant biomass data from Black Creek and Bear Creek coals. Sequence of samples (from bottom to top): Cluster 1–20; Cluster 2–60, 35; Cluster 3–4, 63, 69, 48, 67, 21, 79, 68, 70, 4; Cluster 4–51; Cluster 5–71, 44, 45, 43, 38, 41, 36, 46, 37, 80, 66, 61, 56, 24, 13, 28, 9, 8, 52, 50, 53, 58, 54, 34, 33, 27, 18, 16, 31, 57, 14, 55, 59, 17, 19, 12, 2, 47, 42, 40, 39, 76, 75, 62, 23, 22, 30, 73, 10, 32, 3, 78, 77, 72, 81, 74, 65, 5, 25, 7, 15, 26, 49, 6, 11, 29, 1.

that experience low levels of environmental stability (Hughes, 1986). Low evenness values, on the other hand, indicate that the assemblages are dominated by only a few taxa. Inasmuch as these assemblages originate from wetland environments, these results are not surprising.

Correlation Matrices

Correlation coefficients for all taxonomic combinations are less than 0.2 (Table 2). This indicates the absence of multicollinearity among species. Therefore, these taxa can be used as variables for deriving proximity matrices for cluster analyses. The results also indicate that the assemblage components represent discrete biological entities.

Cluster Analyses

The Czekanowski Coefficient—Average Linkage (CZAL) analysis produced what could be interpreted as 5 or 6 distinctive clusters (Fig.2). Analysis of the data matrix with the centroid algorithm yielded similar results, indicating that the clusters were stable (i.e., particular samples were repeatedly grouped together, regardless of algorithm used in the analysis and, thus, most likely represented real phenomena rather than computational artifacts).

The mean profiles for the 5th and "6th" clusters (identified as clusters "5a" and "5b" in Appendix) showed the same rank-order abundance of taxa, with the values for means on the same order of magnitude. The only difference between these two mean profiles were the values for PTR (cluster 5a: 41.3 ± 14.66, $n = 37$; cluster 5b: 16.3 ± 4.69, $n = 30$); a t-test of the equality of the means indicated no significant difference between these values ($t' = 1.585$, $t'_{.05} = 2.041$, $P > 0.05$; Sokal and Rohlf, 1981). Thus, these two groups of samples were interpreted to be subsamples of the same large cluster.

Mean profiles for the 5-cluster solution of the Czechanowski Coefficient—Average Linkage analysis are shown in Table 3. Comparison of mean profiles for different clusters indicates that cluster 1 represents samples in which debris from *Lepidodendron* (a lycopsid) was the dominant taxon in the litter. The samples in cluster 2 are characterized by debris from an unidentified (degraded) arborescent lycopod and an increased proportion of pteridosperm debris. The samples that characterize cluster 3 are dominated by miscellaneous plant debris (predominately roots of uncertain taxonomic affinity) that had undergone aerial or subaerial degradation prior to burial and preservation. These samples are found dispersed as 1 or 2 layers in several different slabs from each locality. This suggests that this cluster may reflect a short-term dry interval, where the substrate either was exposed above the water level or the debris had accumulated to heights above the water table, allowing plants to become established and root into the substrate. The sample in cluster 4 is characterized by a large amount of both calamite and pteridosperm detritus. The majority of the bedding surfaces group in cluster 5, which is characterized by a dominance of pteridosperms.

There was a particular trend of specific sample clusters when they were compared within successive layers within the same slabs (Appendix). This is interpreted to reflect the presence of a single community type rather than an indication that the clusters pertain to different stages of ecological succession. Comparison of clusters among different sample blocks or collection localities (Appendix; Fig. 3) indicates that clusters do not relate directly to ecological differences in the collection sites. The majority of the samples were grouped into a single large cluster (cluster 5), while the other four clusters (i.e., clusters 1–4) contained relatively few samples (Appendix; Table 3). Together, these factors strongly indicate that the floral assemblages and, hence, the original communities of both the Black Creek Coal parting and the Bear Creek wetland are very similar, fitting the pteridosperm-dominated species profile for cluster 5. Clusters 1–4 are interpreted to represent very localized, small-scale heterogeneity in the flora. Such heterogeneity may be the result of edaphic spatial differences within the mire or might represent temporal perturbation caused by stochastic windfalls of canopy lepidodendralean (clusters 1 and 2) or calamitalean (cluster 4) trees.

Non-metric Multidimensional Scaling Analysis

Non-metric multidimensional scaling (NMDS) was used to extract underlying factors contributing to the patterns

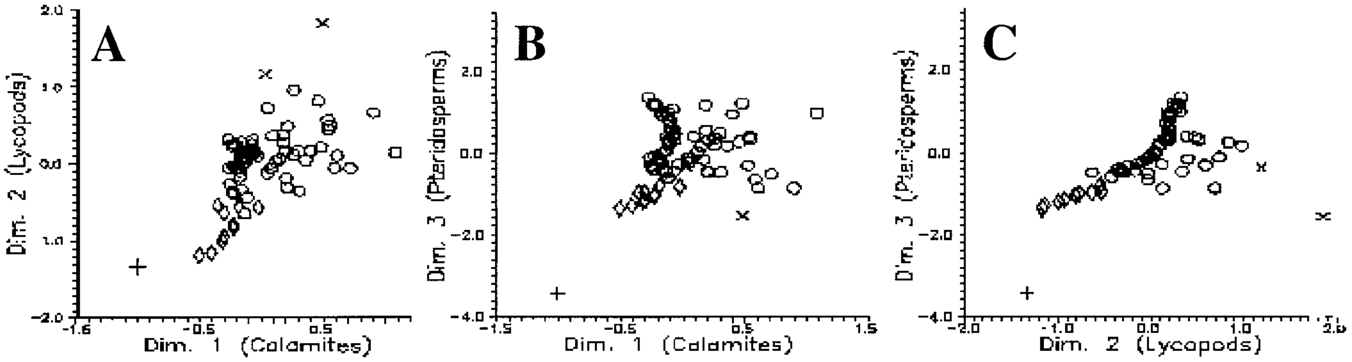

FIGURE 3—Ordination of clusters of shale samples (clusters derived from cluster analysis) onto NMDS dimensions (derived from non-metric multidimensional scaling analysis of the plant biomass data from the Black Creek and Bear Creek Coals). + = Cluster 1; X = Cluster 2; ◊ = Cluster 3; □ = Cluster 4; ○ = Cluster 5. (A) Dimension 1 (representing abundance of calamites) versus Dimension 2 (abundance of lycopsids). (B) Dimension 1 (abundance of calamites) versus Dimension 3 (abundance of pteridosperms). (C) Dimension 2 (abundance of lycopsids) versus Dimension 3 (abundance of pteridosperms).

in the data. The objective in a NMDS analysis is to find the solution with the fewest number of dimensions and the lowest stress value (best fit of the data). The three-dimension solution resulting from the NMDS analysis had a stress value of 0.23, indicating a relatively good fit with the data. Further increase in number of dimensions in the NMDS solution did not significantly decrease the final stress value (i.e., produce a better fit to the data), whereas a decrease in the number of dimensions increased the final stress value (i.e., produced a worse fit to the data).

In order to interpret the phenomena producing the variation in the data that is detected by a NMDS dimension, correlation values were calculated between various variables and the NMDS dimensions (Table 4). The variables used for this correlation included the biomass estimates for the plant taxa (including the MSC category) and the clusters derived from the cluster analysis; the formula used for calculating r was the Pearson product-moment correlation (Rohlf, 1990). Dimension 1 is correlated with the calamites, Dimension 2 with the unidentified lycopsid species, and Dimension 3 with pteridosperms (Table 4).

To visualize the relationship among clusters in multidimensional space, samples belonging to different clusters (derived in the previous CZAL cluster analysis) were ordinated onto the NMDS dimensions (Fig. 3). In all three ordinations, the samples in cluster 5 occupied the central region of the axes, whereas clusters 1–4 tended to occupy extreme positions on the axes. This lends further support to the previous interpretation that cluster 5 represents the most common floristic profile for the collecting localities, and that clusters 1–4 represent samples that are “outliers.” These latter assemblages may be temporally localized replacements in the floristic composition, but not necessarily successional changes in the flora. There is no evidence for a repetitive pattern of sere development through either stratigraphic section.

The samples in clusters 1 and 2, in which *Lepidodendron* and the unidentified arborescent lycopsid dominated, respectively (Table 3), are found at the opposite ends of Dimension 2 (Fig. 3A, C), which correlated with biomass of lycopsids. This arrangement might indicate that an underlying factor may have controlled the distribution of lycopsid species, such as an edaphic gradient, at the two collecting localities. A strong edaphic gradient has been demonstrated by Gastaldo (1987) for contemporaneous communities in the southern Appalachians, and similar distributions are well documented in younger peat and non-peat accumulating mires (e.g., DiMichele and DeMaris, 1987).

In addition, samples (OTUs) were also identified by collection locality, and ordinated onto the NMDS dimensions (Fig. 4). There is a great deal of overlap among the samples from the Black Creek and Bear Creek mires. Samples from the Black Creek coal parting show a very tightly clustered pattern, whereas data points from the Bear Creek roof-shale swamp are more widely dispersed on the graphs. This suggests that, although there is a good deal of overlap in the floristic composition of the two plant communities, the samples from within the Black Creek peat mire show a more limited range of variation than those in the clastic swamp above the Bear Creek coal.

DISCUSSION

The floras of the two Early Pennsylvanian (Langsettian [Westphalian A]) plant communities in this study are both dominated by pteridosperms and show fairly low species diversity (Table 1), the latter of which is consistent with what has been reported for other Carboniferous wetland assemblages (Wing and DiMichele, 1995). Although Simpson’s dominance (D) index is sensitive to the abundances of the common taxa and the Shannon index is strongly correlated with richness, results from both assemblage data are nearly identical. This indicates that there are essentially no community differences despite the fact that the Bear Creek assemblage grew in a clastic swamp (siliciclastic substrate) and the Black Creek assemblage was rooted in a mineral-rich organic muck.

For both localities, the plant organs found in the deposit include lepidodendralean rooting organs (*Stigmaria*) that penetrate the carbonaceous shale or other miscellaneous roots which are probably autochthonous elements, as well as aerial plant parts that are possibly parautochthonous (minimal aerial transport from the source plants in a forested area located very near the site of accumulation and deposition; Behrensmeyer and Hook, 1992). The concentration of rachial axes would infer that these branch-like structures fell into shallow standing water (high in tannic

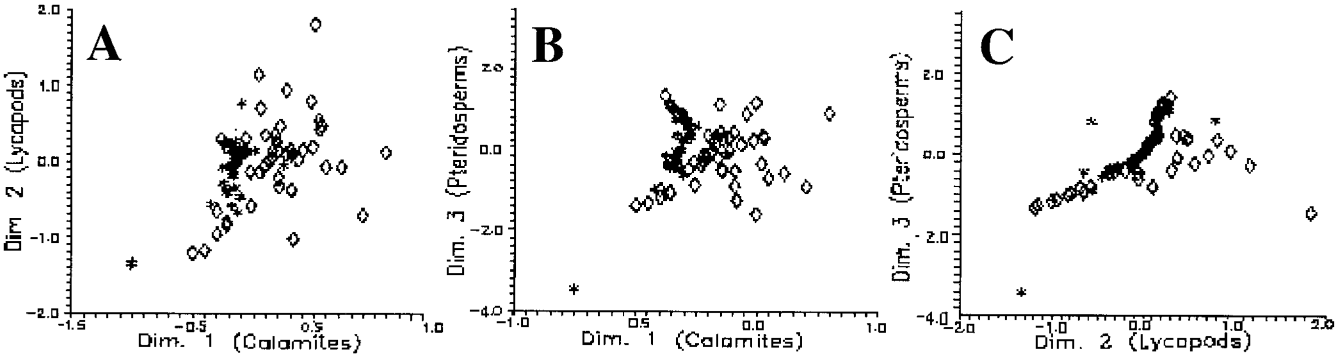

FIGURE 4—Ordination of shale samples from different collecting localities onto NMDS dimensions (derived from non-metric multidimensional scaling analysis of the plant biomass data). ✱ = Black Creek Coal parting; ◊ = Bear Creek Coal overburden. (A) Dimension 1 (representing abundance of calamites) versus Dimension 2 (abundance of lycopsids). (B) Dimension 1 (abundance of calamites) versus Dimension 3 (abundance of pteridosperms). (C) Dimension 2 (abundance of lycopsids) versus Dimension 3 (abundance of pteridosperms).

acids to allow for their preservation; Gastaldo and Staub, 1999) and were not transported. There is no indication of axial alignment in the plant assemblage, which would be indicative of aqueous transport. These factors suggest that the aerial debris (leaves, rachises, etc.) fell off the source plant and were quickly buried. There is no taphonomic evidence that would indicate that most of the plant material accumulated for long periods and then was washed collectively into the site of accumulation, or that the deposits were reworked at a later time. Thus, there is no indication of long-term taphonomic time-averaging of the assemblages (Behrensmeyer and Hook, 1992).

The flora preserved above the Bear Creek Coal is interpreted to represent an autochthonous/parautochthonous obrusion deposit ("smothered bottom" burial event), resulting from one or more, short-term depositional events (Gastaldo et al., 1995) as a result of either autocyclic or allocyclic processes (Demko and Gastaldo, 1996). This assemblage represents the community that colonized an immature soil following burial of the Bear Creek peat by siliciclastics. The duration of this community is difficult to determine in absolute terms, but may indicate a period of deposition on the order of 10^1 but somewhat less than 10^2 years. This estimate is based upon the fact that: (1) a large proportion of pteridosperm pinnae and pinnules are well preserved, which would indicate rapid burial of these plant parts prior to decay (Burnham, 1993); (2) pteridosperm stems and frond axes are silt-cast, indicating a moderate residence time on the swamp floor prior to burial (Gastaldo et al., 1989); and (3) a sparse distribution of aerial rooting structures vertically and subhorizontally penetrate the deposit without disturbance of primary structures, which would be indicative of a short duration of colonization. Hence, the Bear Creek Coal assemblage is believed to represent a single wetland community in space and time.

The flora preserved within the Black Creek Coal parting also is an autochthonous assemblage, but may represent the response of vegetation to perturbation of the peat swamp by increased overbank sedimentation. Due to limited outcrop exposure, the aerial extent and geometry of this parting is not known, preventing any interpretation regarding the paleotopography of, and the conditions for, the accumulation. Although it is fairly difficult to get an accurate estimate of the sedimentation rates of this organic-rich shale, its maximum thickness of 13 cm indicates this assemblage may be more time-averaged than that of the Bear Creek. Winston (1989) determined the compaction ratio for Medullosan frond axes (*Myeloxylon*; 2.5:1 to 10.6:1) comparing specimens preserved in coal balls (permineralized peat) with those in the adjacent coal. Using his average ratio of 5.5:1 (Winston, 1989, table 1), the decompacted thickness of the original Black Creek parting would be approximately 71.5 cm. The parting is located in the lowest part of the coal seam, and initial accumulation rates in the basal parts of modern peat swamps have been reported to approach 3 mm/year (Anderson and Muller, 1975). Using these figures as estimates, the pteridosperm-dominated parting could represent as much as 238 years of accumulation. Such a duration should be sufficient to demonstrate evidence of primary successional changes in the vegetation if it existed.

The analysis of stratigraphically constrained data demonstrates that very few successional changes occurred during mineral enrichment of this peat swamp. Hence, it is probable that the plant debris in the shale originated from a mature plant community during a stable stage of ecological succession. This interpretation is consistent with the floristic patterns demonstrated among the samples (i.e., with the majority of the samples containing similar species profiles) and with the interpretation of the pattern of the small number of "outlier" samples. The rank-order abundance of biomass proportions of plant taxa in these outliers are very different, probably representing stochastic small-scale disturbances within a larger stable community. This stability of plant communities is consistent with patterns documented from other Pennsylvanian localities (DiMichele and Phillips, 1996).

Medullosan pteridosperms are interpreted to have been moderate-sized trees (Pfefferkorn et al., 1984; Wnuk and Pfefferkorn, 1987) attaining heights of up to 10 m. Depending upon the taxon, the growth habit of these trees varied from being solitary and free-standing to poly-specific clusters comprised of communally supported individuals. Phillips (1981) demonstrated that Medullosan pteridosperms increased in importance as contributors to peat mires until the Late Carboniferous (Duckmantian [Westphalian B] to Westphalian D) whereupon they reached their zenith in the Stephanian. These pteridosperm-dominated forests inhabited mineral- (nutrient-) rich or mineral-enriched peat that was better drained and possibly fire-prone (Phillips and DiMichele, 1998), including sites in close proximity to river channels and regions that had been subjected to widespread siliciclastic deposition. This replacement in peat-swamp vegetation temporally followed a similar pattern of turnover in the non-peat accumulating wetlands of the Late Carboniferous (Pfefferkorn and Thomson, 1982; Gastaldo et al., 1995).

Gastaldo (1987) demonstrated that pteridosperm-sigillarian forests were restricted to near channel, levee, and back levee sites across a Langsettian (Westphalian A) swamp-to-levee transect in a mineral-substrate wetland. Such near-channel, wetland sites are characterized by a better drained inceptisol and generally experience an absence of standing water (Gastaldo, 1989; Gastaldo and Huc, 1992). And, although siliciclastic-enriched partings in the Mary Lee coal preserve a moderate (25–40%) to a low-to-moderate (5–45%) pteridosperm signal in the palynologic (Eble et al., 1994) and coal petrographic (Winston, 1989) spectra, respectively, there has been little quantitative macrofloral evidence (e.g., Gastaldo, 1990), until now, to demonstrate this relationship in the Early Pennsylvanian.

The flora of the Mid-to-Late Pennsylvanian is fairly well documented from European and American deposits of adpressions and permineralized peat (coal balls—Scott, 1977, 1978, 1979, 1984; Rowe and Galtier, 1989; Winston and Phillips, 1991; DiMichele and Hook, 1992; Galtier, 1997; Phillips and DiMichele, 1998). In the U.S., the Mid-to-Late Pennsylvanian pattern of pteridosperm-dominated, clastic-enriched peat first identified by Phillips (1981) can now be extended back at least to the Early Pennsylvanian (Langsettian [Westphalian A]) based upon adpression assemblages. The fact that mineral-rich histosols (organic soils) were colonized by arborescent seed plants immediately following the Mid-Carboniferous boundary event establishes their ecological role very early in the Pennsylvanian. Although similar data are not yet available for the earliest Pennsylvanian or Late Mississippian peats (e.g., Silesian basin coals of the Czech Republic), several workers (e.g., Purkynovà, 1977; Havlena, 1982; Gastaldo et al., 1998) have noted a marked increase in arborescent pteridosperm taxa in roof-shale floras of central Europe. Hence, it is highly probable that Namurian-aged arborescent pteridosperms of the same taxonomic affinities as those found in the Langsettian (Westphalian A) were capable of colonizing mineral-enriched peat substrates in addition to wetland inceptisols. The ecological constraints on pteridosperm habitats in coastal wetlands appear, then, to be established very early in the Carboniferous.

CONCLUSIONS

(1) Paleoecological analysis of two penecontemporaneous, autochthonous megafloral assemblages—one preserved in the roof shale of the Bear Creek Coal (inceptisol) and the other in a clastic parting of the Black Creek Coal (mineral-enriched histosol)—indicates that both are low-diversity assemblages that are pteridosperm-dominated.

(2) Analysis of the data using the Czekanowski Coefficient—Average Linkage (CZAL) technique resulted in the identification of 5 distinctive clusters that are characterized by: *Lepidodendron* (lycopsid) debris (cluster 1); unidentified (degraded) lycopod and pteridosperm debris (cluster 2); miscellaneous roots and degraded aerial detritus, possibly indicating a short dry interval (cluster 3); calamitean and pteridosperm debris (cluster 4); and dominance of pteridosperm detritus (cluster 5).

(3) Each assemblage is interpreted to represent a single plant community based on the fact that no linear trend of specific sample clusters could be identified when bedding planes of each sample suite were compared within stratigraphic order. Hence, it is believed that each assemblage represents one community rather than different stages of wetland ecological succession. Both plant assemblages, though, were very similar, regardless of the substrate on which each grew.

(4) Results from non-metric multidimensional scaling (NMDS) analyses support the interpretation that cluster 5 represents the general floristic profile for the collecting localities, and that clusters 1–4 represent "outliers" or small, temporally localized heterogeneity (?response to local perturbation) in the floristic composition.

(5) The Mid-to-Late Pennsylvanian pattern of pteridosperm-dominated, clastic-enriched peat mires can now be extended back at least to the Early Pennsylvanian (Langsettian [Westphalian A]) based upon adpression assemblages, confirming previously published palynologic and coal petrographic interpretations. The ecological niche of arborescent pteridosperms in coastal wetlands appears to have been established very early in the Carboniferous, and persisted into the Permian.

ACKNOWLEDGMENTS

The authors would like to thank C.A. Haas, S.M. McCarroll, and D. Douglass for risking life and limb during the collection of the material used in this study; D. Douglass, S. Meredith, and E. Malkoff for the endless hours of slabbing, tracing, and digitizing bedding surfaces; R.G. Hamilton for insightful comments regarding the ecological interpretations of the data analyses; and W.A. DiMichele, R. Lupia, and C.E. Savrda for constructive comments for revision of the manuscript.

REFERENCES

ANDERSON, J.A.R., and MULLER, J., 1975, Palynological study of a Holocene peat and a Miocene coal deposit from NW Borneo: Review of Palaeobotany and Palynology, v. 19, p. 291–351.

BAKER, R.A., and DIMICHELE, W.A., 1997, Biomass allocation in Late Pennsylvanian coal-swamp plants: PALAIOS, v. 12, p. 127–132.

BEHRENSMEYER, A.K., and HOOK, R.W., RAPPORTEURS, 1992, Paleoenvironmental contexts and taphonomic modes: *in* BEHRENSMEYER, A.K., DAMUTH, J.D., DIMICHELE, W.A., POTTS, R., SUES, R.-D., and WING, S.L., eds., Terrestrial Ecosystems Through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals: University of Chicago Press, Chicago, p. 15–136.

BURNHAM, R.J., 1989, Relationships between standing vegetation and leaf litter in a paratropical forest: Implications for paleobotany: Review of Palaeobotany and Palynology, v. 58, p. 5–32.

BURNHAM, R.J., 1990, Paleobotanical implications of drifted seeds and fruits from modern mangrove litter, Twin Cays, Belize: PALAIOS, v. 5, p. 364–370.

BURNHAM, R.J., 1993, Time resolution in terrestrial macrofloras: Guidelines from modern accumulations: *in* KIDWELL, S.M., and BEHRENSMEYER, A.K., eds., Taphonomic approaches to time resolution in fossil assemblages: Short Course in Paleontology, n. 6, p. 57–78.

Burnham, R.J., 1994, Patterns in tropical leaf litter and implications for angiosperm paleobotany: Review of Palaeobotany and Palynology, v. 81, p. 99–113.

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

Demko, T.M., and Gastaldo, R.A., 1992, Paludal environments of the Lower Mary Lee coal zone, Pottsville Formation, Alabama: Stacked clastic swamps and peat mires: International Journal of Coal Geology, v. 20, p. 23–47.

Demko, T.M., and Gastaldo, R.A., 1996, Eustatic and autocyclic influences on deposition of the Lower Pennsylvanian Mary Lee Coal zone, Warrior Basin, Alabama: International Journal of Coal Geology, v. 31, p. 3–19.

Dillon, W.R., and Goldstein, M., 1984, Multivariate Analysis: Methods and Applications: John Wiley & Sons, Inc., New York, 587 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., 1996, Clades, ecological amplitudes, and ecomorphs: phylogenetic effects and persistence of primitive plant communities in the Pennsylvanian-age tropical wetlands: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 124, p. 83–105.

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

DiMichele, W.A., Hook, R.W., Beerbower, R., Boy, J.A., Gastaldo, R.A., Hotton, N., III, Phillips, T.L., Scheckler, S.E., Shear, W.A., and Sues, H.-D., 1992, Paleozoic terrestrial ecosystems: *in* Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, R.-D., and Wing, S.L., eds., Terrestrial Ecosystems Through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals: University of Chicago Press, Chicago, p. 205–325.

Eble, C.F., and Gillespie, W.H., 1989, Palynology of selected coal beds from the central and southern Appalachian basin: Correlation and stratigraphic implications: *in* Characteristics of the Mid-Carboniferous Boundary and Associated Coal-bearing Rocks in the Appalachian Basin: 28th International Geological Congress Guidebook, T352, p. 61–66.

Eble, C.F., Gastaldo, R.A., Demko, T.M., and Liu, Y., 1994, Coal compositional changes along a swamp interior to swamp margin transect in the Mary Lee Coal bed, Warrior Basin, Alabama, U.S.A.: International Journal of Coal Geology, v. 26, p. 43–62.

Galtier, J., 1997, Coal-ball floras of the Namurian-Westphalian of Europe: Review of Palaeobotany and Palynology, v. 95, p. 51–72.

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

Gastaldo, R.A., 1989, Preliminary observations on phytotaphonomic assemblages in a subtropical/temperate Holocene bayhead delta: Mobile Delta, Gulf Coastal Plain, Alabama: Review of Palaeobotany and Palynology, v. 58, p. 61–84.

Gastaldo, R.A., 1990, Early Pennsylvanian swamp forests in the Mary Lee coal zone, Warrior Basin, Alabama: *in* Gastaldo, R.A., Demko, T.M., and Liu, Y., eds., Carboniferous coastal environments and paleocommunities of the Mary Lee coal zone, Marion and Walker Counties, Alabama: A Guidebook for Field Trip VI, 39th Annual Meeting Southeastern Section of the Geological Society of America, Tuscaloosa, Alabama: Geological Survey of Alabama, p. 41–54.

Gastaldo, R.A., 1992, Regenerative growth in fossil horsetails (*Calamites*) following burial by Alluvium: Historical Biology, v. 6, p. 203–220.

Gastaldo, R.A., and Huc, A.Y., 1992, Sediment facies, depositional environments, and distribution of phytoclasts in the Recent Mahakam River delta, Kalimantan, Indonesia: PALAIOS, v. 7, p. 574–591.

Gastaldo, R.A., and Staub, J.R., 1999, A Mechanism to Explain the Preservation of Leaf Litters Lenses in Coals Derived from Raised Mires: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 1–14.

Gastaldo, R.A., Demko, T.M., Liu, Y., Keefer, W.D., and Abston, S.L., 1989, Biostratinomic processes for the development of mud-cast logs in Carboniferous and Holocene swamps: PALAIOS, v. 4, p. 356–365.

Gastaldo, R.A., Demko, T.M., and Liu, Y., 1991, A mechanism to explain persistent alternation of clastic and peat-accumulating swamps in Carboniferous sequences: Bulletin Société géologique de France, t. 162, p. 299–305.

Gastaldo, R.A., Demko, T.M., and Liu, Y., 1993, The application of sequence and genetic stratigraphic concepts to Carboniferous coal-bearing strata: An example from the Black Warrior basin, USA: Geologische Rundschau, v. 82, p. 212–226.

Gastaldo, R.A., Pfefferkorn, H.W., and DiMichele, W.A., 1995, Taphonomic and Sedimentologic Characterization of "Roof-Shale" floras: *in* Lyons, P., Wagner, R.H., and Morey, E., eds., Historical Perspective of Early Twentieth Century Carboniferous Paleobotany in North America: Geological Society of America Memoir 185, p. 341–352.

Gastaldo, R.A., Purkynová, E., Šimůnek, Z., Drábková, J., and Eble, C.F., 1998, Vegetational persistence patterns in coastal and continental interiors of the Carboniferous icehouse, Silesian Coal Basin, Czech Republic: Pan European Palaeobotanical Congress, Krakow, Poland, Abstracts.

Gillespie, W.H., and Rheams, L.A., 1985, Plant megafossils from the Carboniferous of Alabama, U.S.A.: *in* Escobeda, J.L., Granádos, L.F., Melendez, B., Pignatelli, R., Ray, R., and Wagner, R.H., eds., Diéxieme Congrés International de Stratigraphie et de Géologie du Carbonifere, v. 2, p. 191–202.

Grieg-Smith, P., 1983, Quantitative Plant Ecology: University of California Press, Berkeley, 359 p.

Haas, C.A., and Gastaldo, R.A., 1986, Flood-tidal deltas and related back barrier systems: Breman sandstone, "Pottsville" Formation, Black Warrior Basin, Alabama: *in* Neathery, T.L., ed., Centennial Field Guide Southeastern Section of the Geological Society of America, v. 6, p. 181–183.

Havlena, A., 1982, The Namurian of Upper Silesia: Floral breaks, lithological variations, and the Mid-Carboniferous boundary problem: *in* Ramsbottom, W.H.C., Saunders, W.B., and Owen, B., eds., Stratigratigraphic data for a Mid-Carboniferous Boundary, Leeds, p. 112–119.

Hewitt, J.L., 1984, Geologic overview, coal, and coalbed methane resources of the Warrior Basin—Alabama and Mississippi: *in* Rightmire, C.T., Eddy, G.E., and Kirr, J.N., eds., Coal Bed Methane Resources of the United States: American Association of Petroleum Geologists Studies in Geology Series, n. 17, p. 73–104.

Hughes, R.G., 1986, Theories and models of species abundance: American Naturalist, v. 128, p. 879–899.

Ludwig, J.A., and Reynolds, J.F., 1988, Statistical Ecology: A Primer on Methods and Computing: John Wiley & Sons, New York, 337 p.

Lyons, P.C., Meissener, C.R., Jr., Barwood, H.L., and Adinolfi, F.G., 1985, Megafloral sequence and North American and European correlations of the upper part of the Pottsville Formation of the Warrior coal field, Alabama, U.S.A.: *in* Escobeda, J.L., Granádos, L.F., Melendez, B., Pignatelli, R., Ray, R., and Wagner, R.H., eds., Diéxieme Congrés International de Stratigraphie et de Géologie du Carbonifere, v. 2, p. 203–245.

Magurran, A.E., 1988, Ecological Diversity and its Measurement: Princeton University Press, Princeton, 179 p.

Menning, M., Weyer, D., Drozdzewski, G., and van Amerom, H.W.J., 1997, Carboniferous time scales revised 1997: Use of geologic time indicators from Central and Western Europe: Geologische Rundshau, v. 86, p.

Pashin, J.C., 1990, Subsurface framework of the Black Creek-Cobb coal-bearing interval, Black Warrior Basin, Alabama: Geological Society of America, Abstracts with Programs, v. 22, no. 4, p. 56.

Pashin, J.C., 1994a, Cycles and stacking patterns in Carboniferous rocks of the Black Warrior foreland basin: Transactions of the Gulf Coast Association of Geological Societies, v. 44, p. 555–563.

Pashin, J.C., 1994b, Flexurally influenced eustaic cycles in the Pottsville Formation (Lower Pennsylvanian), Black Warrior Basin, Alabama: SEPM Concepts in Sedimentology and Paleontology, v. 4, p. 89–105.

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

Phillips, T.L., 1981, Stratigraphic occurrences and vegetational patterns of Pennsylvanian pteridosperms in Euramerican coal swamps: Review of Palaeobotany and Palynology, v. 32, p. 5–26.

Phillips, T.L., and DiMichele, W.A., 1998, A transect through a clastic-swamp to peat-swamp ecotone in the Springfield Coal, Middle Pennsylvanian age of Illinois, USA: PALAIOS, v. 13, p. 113–128.

Pryor, J.S., 1996, The Upper Pennsylvanian Duquesne Coal of Ohio (USA): Evidence for a dynamic peat accumulating swamp community: International Journal of Coal Geology, v. 29, p. 119–146.

Purkynová, E., 1977, Namurian flora of the Moravian part of the Upper Silesian coal basin: *in* Holub, V.M., and Wagner, R.H., eds., Symposium on Carboniferous Stratigraphy: Ústředni Ústav Geologicky, Praha, p. 289–301.

Raymond, A., 1987, Interpreting ancient swamp communities: Can we see the forest in the peat?: Review of Palaeobotany and Palynology, v. 57, p. 217–231.

Rohlf, F.J., 1990, NTSYS-pc: Numerical Taxonomy and Multivariate Analysis System. Version 1.60. Applied Biostatistics Inc., Setauket NY.

Rowe, N.P., and Galtier, J., 1989, A Lower Carboniferous plant assemblage from La Serre (Montagne Noire, France). Part I: Review of Palaeobotany and Palynology, v. 61, p. 239–271.

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 of the Yorkshire Geological Society, v. 41, part 4, no. 33, p. 461–508.

Scott, A.C., 1979, The ecology of Coal Measure floras from northern Britain: Proceedings of the Geological Association, v. 90, p. 97–116.

Scott, A.C., 1984. Studies on the sedimentology, palaeontology and palaeobotany of the Middle Coal Measures (Westphalian B, Upper Carboniferous) at Swillington, Yorkshire. Part I. Introduction: Transactions of the Leeds Geological Association, v. 10, p. 1–16.

Shute, C.H., and Cleal, C.J., 1987, Palaeobotany in museums: Geological Curator, v. 4, p. 553–559.

Sokal, R.R., and Rohlf, F.J., 1981, Biometry (2nd ed): Freeman, New York, 859 p.

Tabachnick, B.G., and Fidell, L.S., 1989, Using Multivariate Statistics: Harper & Row, New York, 509 p.

Wing, S.L., and DiMichele, W.A., 1995, Conflict between local and global changes in plant diversity through geologic time: PALAIOS, v. 10, p. 551–564.

Winston, R.B., 1989, Characteristic features and compaction of plant tissues traced from permineralized peat to coal in Pennsylvanian coals (Desmoinesian) from the Illinois Basin: International Journal of Coal Geology, v. 6, p. 21–41.

Winston, R.B., and Phillips, T.L., 1991, A structurally preserved, Lower Pennsylvanian flora from the New Castle Coal Bed of Alabama: Geological Survey of Alabama, Circular 157, 21 p.

Wnuk, C., and Pfefferkorn, H.W., 1987, A Pennsylvanian-age terrestrial storm deposit: Using plant fossils to characterize the history and process of sediment accumulation: Journal of Sedimentary Petrology, v. 57, p. 212–221.

ACCEPTED SEPTEMBER 9, 1999

APPENDIX

Compilation of raw data for each sampled bedding surface, including biomass estimates (percent surface area covered by plant taxon), cluster (derived from cluster analysis), and NDMS dimension coordinates. SAMPLE IDENTIFICATION NOTATION: BCC-1 and BCC-2 represent the organic-rich shale parting from the Black Creek Coal; L1 through L19 indicates Layer 1 through Layer 19; Slabs 1–7 indicate siltstone from above the Bear Creek coal; LA through LM indicates Layer A through Layer M. DATA: Sample height = distance of layer from bottom of shale slab (in cm); Ttl Area = total surface area of bedding surface; Ttl # = total number of identifiable plant fragments. PLANT TAXA: LYU = unidentified lycopsid; LYD = *Lepidodendron*; CAL = *Calamites*; PT = pteridosperm; NR = *Neuralethopteris* foliage; AL = *Alethopteris* foliage; SPH = *Sphenopteris pottsvillea*; COR = Cordaitales; MSC = miscellaneous plant debris.

OTU	SLAB and layer	Sample height	Ttl area (cm^2)	Ttl #	LYU	LYD	CAL	PT	NR	AL	SPH	COR	MSC	Cluster	Dim. 1	Dim. 2	Dim. 3
1	BCC-1-L1	13	615	4	0	0	0	22.36	0	0	0	0	0	5b	−0.14	0.03	−0.05
2	BCC-1-L2	12.5	777	17	0.58	0	0	56.71	0	0	0	0	0	5a	−0.17	0.3	−1.01
3	BCC-1-L3	11.5	885	13	0.06	0	0	11.3	0	0	0	0	0	5b	−0.12	−0.43	0.59
4	BCC-1-L4	11	1947	59	0.33	0	0	7.66	0.6	0.2	0	0	0.49	3	−0.36	−0.54	0.95
5	BCC-1-L5	10	2341	33	0.05	0	0	16.25	0.2	0	0	0	0	5b	−0.18	−0.16	0.26
6	BCC-1-L6	9.5	1582	12	0	0	0	19.18	0	0	0	0	0	5b	−0.19	−0.04	0.11
7	BCC-1-L7	9	2155	50	0.04	0	0	20	1.13	0	0	0	0.1	5b	−0.23	−0.02	0.06
8	BCC-1-L8	8.5	2229	38	0.03	0	0	26.78	0.48	0.28	0	0	0	5a	−0.12	0.09	−0.25
9	BCC-1-L9	8	2275	39	0	0	0	31.61	0.71	0.07	0.26	0	0	5a	−0.08	0.17	−0.42
10	BCC-1-L10	7.5	2224	25	0	0	0	13.42	0.21	0	0	0	0	5b	−0.17	−0.32	0.42
11	BCC-1-L11	7	1904	24	0.05	0	0	21.52	0.29	0	0.31	0	0	5b	−0.18	0.04	0
12	BCC-1-L12	6	2022	11	0	0	0	59.91	0	0	0	0	0	5a	−0.19	0.26	−1.08
13	BCC-1-L13	5	2466	25	0.07	0	0	29.33	0.06	0	0.25	0	0.76	5a	−0.07	0.14	−0.33
14	BCC-1-L14	4.5	2642	41	0.08	0	0	43.22	0.47	0	0	0	0.27	5a	−0.11	0.15	−0.76
15	BCC-1-L15	4	2599	21	0	0	0	17.73	0	0	0	0	2.35	5b	−0.18	−0.09	0.19
16	BCC-1-L16	3	2432	31	0	0	0	38.44	0.41	0	0	0	0	5a	−0.1	0.17	−0.62
17	BCC-1-L17	2	2336	30	0	0	0	50.33	0.05	0	0	0	2.67	5a	−0.13	0.19	−0.91
18	BCC-1-L18	1	2122	31	0	0	0	38.46	0.03	0	0	0	2.8	5a	−0.1	0.18	−0.62
19	BCC-1-L19	0.5	1325	13	0	0	0	53.78	0	0	0	0	0	5a	−0.13	0.2	−0.99
20	BCC-2-L1	13	469	3	0	16.5	0	1.61	0	0	0	0	0	1	−1.01	−1.33	3.43
21	BCC-2-L2	12	707	14	0	0	0	9.17	0	0	0	0	0	3	−0.19	−0.55	0.78

APPENDIX

Continued.

OTU	SLAB and layer	Sample height	Ttl area (cm²)	Ttl #	LYU	LYD	CAL	PT	NR	AL	SPH	COR	MSC	Cluster	Dim. 1	Dim. 2	Dim. 3
22	BCC-2-L3	11	728	30	0	0	0	12.87	1.43	0	0	0	0	5b	−0.23	−0.38	0.42
23	BCC-2-L4	10	729	29	0	0	0	14.687	1.46	0	0	0	0	5b	−0.26	−0.26	0.31
24	BCC-2-L5	9.5	683	29	0.23	0	0	29.6	1.71	0	0	0	0	5a	−0.12	0.18	−0.34
25	BCC-2-L6	9	754	31	0	0	0	18.65	1.7	0	0	0	0	5b	−0.27	−0.05	0.12
26	BCC-2-L7	8.5	720	11	0	0	0	19.52	0.24	0.19	0	0	0	5b	−0.2	−0.03	0.1
27	BCC-2-L8	7.5	1817	18	0	0	0	37.26	0	0	0	0	0.91	5a	−0.09	0.18	−0.59
28	BCC-2-L9	6.5	1939	20	0	0	0	33.31	0.21	0	0	0	8.98	5a	−0.07	0.17	−0.47
29	BCC-2-L10	5.5	1851	25	0	0	0	22.11	0.11	0	0	0	6.28	5b	−0.16	0.03	−0.03
30	BCC-2-L11	4.5	1779	27	0	0	0	13.66	0.7	0	0.96	0	2.06	5b	−0.24	−0.35	0.37
31	BCC-2-L12	3	2115	25	0	0	0	44.86	0.34	0	0	0	0.78	5a	−0.12	0.18	−0.8
32	BCC-2-L13	2	1202	36	0.17	0	0	10.89	2.06	0	0	0	6.22	5b	−0.14	−0.64	0.47
33	BCC-2-L14	1	1628	8	0	0	0	68.54	0	0	0	0	0	5a	−0.25	0.27	−1.21
34	BCC-2-L15	0.5	726	6	0	0	0	66.75	0	0	0	0	0	5a	−0.22	0.27	−1.19
35	Slab1-LA		886	19	59.8	0	0	6.19	0	0	0	0	0	2	0.48	1.85	1.53
36	Slab1-LB		1280	92	14.66	0	0	22.69	0	0	0.1	0	0.25	5a	0.04	0.73	0.09
37	Slab1-LC		2543	199	7.77	0	2.09	31.71	0	0	0	0.03	0.19	5a	0.2	0.5	−0.33
38	Slab1-LD		2216	137	13.26	0	6.36	17.7	0	0	0	0	0.52	5a	0.52	0.58	0.29
39	Slab1-LE		2280	132	6.38	0	3.55	9.67	0	0	0	0.43	4.46	5b	0.6	0.12	0.85
40	Slab1-LE		2535	117	4.31	0	7.28	12.02	0.12	0	0	0	5.78	5b	0.71	−0.04	0.51
41	Slab1-LG		1815	132	6.51	0	1.77	21.07	0.02	0	0	0	0.92	5a	0.16	0.39	0.14
42	Slab1-LH		1653	76	4.26	0	4.39	11.06	0.18	0	0	0.1	17.33	5b	0.58	−0.04	0.65
43	Slab2-LA		2853	136	26.18	0	2.41	28.81	0	0	0	0	0	5a	0.25	0.97	−0.2
44	Slab2-LB		2537	137	8.36	0	12.17	29.32	0	0	0	0	0.71	5a	0.54	0.51	−0.35
45	Slab2-LC		1899	92	21.28	0	7.61	30.12	0.01	0	0	0	0.25	5a	0.45	0.83	−0.29
46	Slab2-LD		2297	112	3.85	0	1.07	33.46	0	0	0	0.1	5.88	5a	0.08	0.38	−0.41
47	Slab2-LE		1902	63	0.18	0	7.56	6.21	0	0	0	0	21.33	5b	0.89	−0.68	0.85
48	Slab2-LF		1050	42	0	0	0	4.3	0	0	0	0	24.51	3	−0.41	−1.15	1.29
49	Slab2-LG		1794	73	0	0	0	18.69	0	0.06	0	0	5.91	5b	−0.19	−0.05	0.14
50	Slab3-LA		215	28	0	0	17.21	44.93	0	0	0	0	3.65	5a	0.39	0.19	−0.95
51	Slab3-LB		295	26	0	0	54.67	31.18	0	0	0	0	1.21	4	1.07	0.17	−1
52	Slab3-LC		135	19	0	0	30.16	51	0	0	0	0	0	5a	0.47	0.23	−1.23
53	Slab3-LD		792	66	0	0	10.5	62.69	0	0	0	0	2.27	5a	0.17	0.29	−1.19
54	Slab3-LE		926	125	0	0	0	63.6	1.76	0	0	0	3.61	5a	−0.24	0.23	−1.15
55	Slab3-LF		1172	152	0	0	0	50.42	2.68	0	0	0	3.13	5a	−0.18	0.17	−0.94
56	Slab3-LG		1347	150	0	0	0	30.92	2.29	0	0	0	45.77	5a	−0.14	0.18	−0.4
57	Slab3-LH		1143	26	0	0	0	43.07	0.39	0	0	0	27.95	5a	−0.11	0.15	−0.75
58	Slab3-LI		1173	30	0	0	0	79.59	0.23	0	0	0	12.92	5a	−0.28	0.32	−1.37
59	Slab3-LJ		1085	104	0	0	0	49.69	1.51	0	0	0	17.5	5a	−0.17	0.18	−0.9
60	Slab3-LK		951	60	33.41	1.03	0	19.17	0.24	0	0	0	23.21	2	0.02	1.18	0.34
61	Slab4-LA		3683	230	0.41	0	6.6	32.81	0.08	0	0.25	0.21	0.49	5a	0.29	0.18	−0.47
62	Slab5-LB		3668	259	1.16	0.01	2.3	13.87	0.03	0	0.08	0	0.34	5b	0.19	−0.18	0.44
63	Slab5-LC		3202	159	0.03	0	0	5.45	0.02	0.04	0	0	1.39	3	−0.31	−0.94	1.15
64	Slab5-LD		3378	123	0	0	0	5.07	0	0	0	0	1.99	3	−0.32	−1	1.2
65	Slab5-LE		2264	220	0.15	0	1.08	16.66	0	0	0.02	0.28	1.11	5b	−0.04	−0.11	0.27
66	Slab6-LA		2963	186	0.54	0	3.96	36.06	0.04	0.36	0	0	0.2	5a	0.18	0.18	−0.56
67	Slab6-LB		2808	180	0.04	0	0.75	8.76	0.05	0	0.03	0	1.33	3	−0.03	−0.56	0.83
68	Slab6-LC		2226	126	0	0	0	6.8	0	0	0	0	16.87	3	−0.23	−0.78	1.01
69	Slab6-LD		2120	73	0	0	0	3.99	0.04	0	0	0	14.72	3	−0.51	−1.18	1.35
70	Slab6-LE		1844	71	0	0	0	7.45	0.29	0	0	0.14	45.83	3	−0.31	−0.64	0.96
71	Slab7-LB		2611	109	6.54	0	11.42	30.37	0	0.07	0	1.26	0.57	5a	0.53	0.46	−0.4
72	Slab7-LC		3391	95	0	0	6.91	24.59	0.04	0	0	0	1.48	5b	0.35	0.06	−0.19
73	Slab7-LD		3296	61	0	0	0.43	13.22	0.03	0	0	0	23.2	5b	−0.08	0.33	0.45
74	Slab7-LE		3282	95	0	0.13	1.86	17.13	0.02	0	0	0	2.6	5b	0.04	−0.11	0.22
75	Slab7-LF		3333	177	0.44	0	2.49	12.82	0	0	0	0	17.88	5b	0.2	−0.3	0.47
76	Slab7-LG		3266	145	0.09	0	3.49	12.13	0	0	0	0	4.88	5b	0.3	−0.35	0.48
77	Slab7-LH		3280	155	0	0	2.76	22.41	0	0.01	0	0.02	2.48	5b	0.11	0.04	−0.04
78	Slab7-LI		2812	107	0	0	2.93	25.47	0	0	0	0	1.73	5b	0.14	0.08	−0.18
79	Slab7-LJ		2445	47	0	0	0	6.5	0	0	0	0	60.96	3	−0.23	−0.82	1.04
80	Slab7-LK		2035	132	0	0	5.18	29.26	0	0	0	0	6.79	5a	0.25	0.13	−0.35
81	Slab7-LM		1250	120	0.14	0	2.52	18.75	0.43	0	0	0	0.1	5b	0.07	−0.04	0.13