A Transect Through a Clastic-swamp to Peat-swamp Ecotone in the Springfield Coal, Middle Pennsylvanian Age of Indiana, USA

TOM L. PHILLIPS

Department of Plant Biology, University of Illinois, 505 South Goodwin Avenue, Urbana, IL 61801

WILLIAM A. DiMICHELE

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

Permineralized fossil plants in coal balls were collected along a kilometer transect through an organic-rich shale in the Springfield Coal in southwestern Indiana. The organic shale is an upper bench of the Springfield Coal in an area where the coal is split into an upper and lower bench by a complex system of clastics that originated as a splay. The clastic wedge, described as the Folsomville Member / Leslie Cemetery paleochannel, is up to 6 km wide and 15 m thick. The transect begins approximately 100 m from the edge of the clastic wedge that splits the coal seam and follows the upper bench of coal over and toward the center of the clastic wedge. The dominant elements of the vegetation were the lycopsid tree Paralycopodites brevifolius *and several species of medullosan pteridosperms. This report confirms the ecotonal habitats of this vegetation.*

INTRODUCTION

Terrestrial tropical environments of the Pennsylvanian Period, best known as the coal age, are represented by innumerable dioramas that portray bizarre plants in family portrait settings, usually gathered around light gaps in dark forests of giant club mosses. The inaccuracy of such reconstructions, based on analogy with modern plants and forests, has become increasingly apparent. Whole plant reconstructions, life-history studies, and quantitative ecological analyses have revealed unique properties both of coal-age plants and the vegetation they comprised. Peat-forming forests were but one part of diverse wetland environments of the tropical coastal plains (e.g., Scott, 1978). Furthermore, the peat-forming forests themselves were complex, and included a variety of recurrent assemblages associated with different physical conditions (e.g., DiMichele and Phillips, 1994).

Peat-forming mires are best known from coal balls—concretions in coal seams that preserve the structural peat stages of the coal (Scott and Rex, 1985). Most coal balls entomb the original organic fabric of the peat in calcium carbonate. Preservation is often exceptionally good, a taphonomic factor that encouraged generations of paleobotanists to study the morphology and systematic biology of coal-swamp plants (Phillips et al., 1973; Andrews, 1980). The development of quantitative methods (Phillips et al., 1977) led to wide ranging studies of coal-swamp ecology, partic-
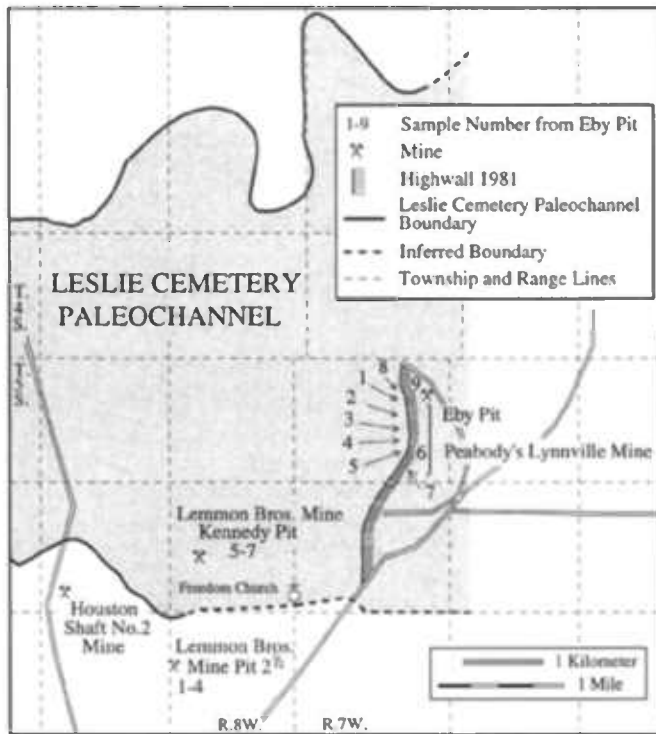
ularly of American deposits (Phillips et al., 1985; Raymond, 1988; Feng, 1989; DiMichele et al., 1991; Pryor, 1993), which complemented the morphological work.

Coal balls generally are recovered from commercially minable coal seams in the course of mining. Thus, nearly all these analyses have focused on the plants of peat substrates. However, coal balls or coal-ball like preservation also occur in impure coals that more accurately may be called organic shales. We report here on such a deposit that preserves a vegetation transitional between peat and clastic substrate swamp habitats. The vegetation is distinctive, and has been identified in deposits from thick coal seams, but mostly in association with underclays and clastic partings (DiMichele and Phillips, 1988). This report confirms its association with ecotonal environments.

GEOLOGICAL SETTING

Materials studied in this analysis were collected in the Eby Pit of the Peabody Coal Company Lynnville Mine, located on Indiana highway 61 between the towns of Boonville and Lynnville in Warrick County, Indiana (Figure 1). Coal balls were collected from deposits in the Degonia Springs 7 ½' Quadrangle, E ½ Section 6, T5S R7W. Coal balls occurred in the upper bench of the Springfield Coal Member of the Carbondale Formation (Petersburg Formation in Indiana usage), which is upper Middle Pennsylvanian. This is late Desmoinesian in age, equivalent to the late Westphalian D in European stratigraphic terminology.
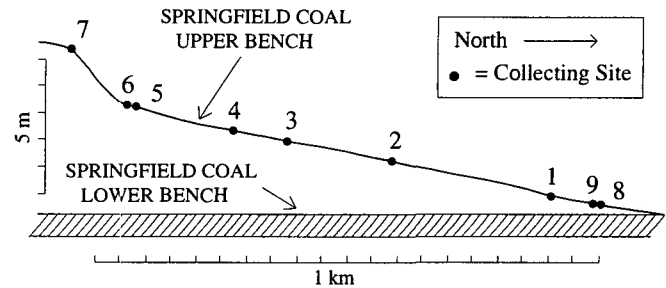
The geology of this locale is discussed in detail by Eggert et al. (1983) and Willard et al. (1995). The Springfield Coal in the Eby pit is split into two benches. The benches are separated by a complex of mudstone and sandstone, part of an interconnected system of channel-form rock bodies 1.6–6.0 kilometers in width that forms a split in the Springfield Coal. Eggert (1982) mapped these rocks as the Folsomville Member. The Folsomville Member may be as much as 15 m thick in the Eby pit. The main (lower) bench of the Springfield Coal dips steeply into the area of split coal and varies from 0.6 to 1.5 m in thickness (Willard et al., 1995). The upper bench of the Springfield Coal, continuous with the main coal bed at the edge of the split, is present over most of the Folsomville Member and varies widely in character. In some sections, it appears as a normally bright-banded bituminous coal. In other areas, it appears as a clastic-rich coal or organic shale and in some cases,

FIGURE 1—Location of Peabody Coal Company Lynnville Mine, Eby pit, at the time coal balls were collected in the early 1980's. Collecting sites in transect are numbered. Coal balls also were collected from other local mines shown on the map. The area of split Springfield coal within the Leslie Cemetery Paleochannel is shaded.

FIGURE 2—North-south transect through Eby pit. Coal-ball collecting sites, in the thin upper bench of split coal, are numbered. Profiles were collected at sites 8 and 9; coal balls were collected from a single horizon at sites 1 to 7.

the clastic-rich layers may be intermixed with more coaly layers or grade upward into a normally bright-banded coal. According to Eggert et al. (1983) the upper bench most commonly has a distinctly shaley lower facies near the margin of the split. The organic interval in the upper bench may vary in thickness from a few centimeters to nearly 1 meter. Overlying the coal is the black, fissile Turner Mine Shale Member, which is up to 0.7 m thick. It may contain marine invertebrates at its base, and these may be mixed with the uppermost layers of the upper bench of Springfield Coal. The Turner Mine Shale is, in turn, overlain by the St. David Limestone Member, which may be up to 1.5 m thick in the areas we examined, contains an open marine fauna, and may be clastic rich in the lower two-thirds of its thickness. Both the Turner Mine Shale and the St. David Limestone tend to be somewhat thicker above the area of the Folsomville Member and split Springfield Coal than above adjacent areas of unsplit coal.

The Folsomville Member has been interpreted by Eggert and coworkers (Eggert, 1982, 1984; Eggert and Adams, 1984; Eggert et al., 1983; Willard et al., 1995) as a large splay, composed of floodplain and channel facies. Most of the clastic fill is composed of a series of migrating channels and associated overbank clastic deposits formed in backswamps. Plant growth within the channel belt is indicated by occasional immature paleosols, which are evidenced by in situ roots in blocky mudstones. Compressions of the plants that presumably colonized the flood plain have been described by Willard et al. (1995). Eggert (1982) used the name Leslie Cemetery Paleochannel to de-

scribe this feature genetically. Clastic deposition in the paleochannel took place while peat continued to accumulate in the adjacent Springfield Coal mire. As the channel filled, organic mucks formed in swamps between the margins of the mire and the active channel belt. These mucks gradually prograded over the coarser clastics of the paleochannel belt, perhaps as the local base level rose and clastic deposition in the channel began to slacken. Locally, purer peat then developed above the swamp mucks, forming the highly variable upper bench of the Springfield Coal.

MATERIALS AND METHODS

The coal balls examined in this study occur entirely within the clastic-rich upper bench of the Springfield Coal near the margin of the paleochannel where the clastic lower facies of the upper bench is best developed (Eggert et al., 1983; Willard et al., 1995). Coal balls were collected at nine sites in a roughly north to south transect 850 m in length (Fig. 1), and at an additional locality approximately three kilometers to the west of the transect. The collecting sites in the transect are numbered 1–9, and the western outlier is site 12. Collections from sites 10 and 11, in the vicinity of site 12, were too poorly preserved for further analysis; those from site 3 were removed from the analysis due to small sample size. In addition to in situ specimens, a random sample of coal balls was collected at site 12; some of the illustrative material is derived from this random sample. Sites 1–7 are collections from a single zone of coal balls near the top of the organic shale bed (Fig. 2). Sites 8, 9, and 12 are profiles that include zones from two or more horizons in the organic shale (Table 1). A detailed lithologic description of the transect can be found in Willard et al. (1995). The entire coal ball transect falls between stratigraphic sections 6 and 8 in figure 3 of Willard et al. (1995). Coal-ball site 4 of the present paper corresponds to stratigraphic section 7 of Willard et al. (1995).

Throughout the coal-ball transect, the upper bench of coal is primarily an organic shale with coaly stringers. Shale laminae contain numerous plant fragments preserved as compressions and detritus. Due to its variation in character, the upper bench was sampled for proximate analysis only in areas where it displayed a conspicuously coaly aspect; Eggert (1984) and Willard et al. (1995) report high ash values of 13.6% and 30.7% respectively, compared with values from 5%–14% typical of the lower bench

TABLE 1—Coal-ball profiles from the Eby Pit.

	Zone	Thickness	
SITE 8			
Top	Zone 1	7 cm	
	Zone 2	6 cm	
	Coaly shale	8 cm	
	Zone 3	3 cm	
	Coaly shale	7 cm	
	Zone 4	6 cm	
	Coaly shale	30 cm	
	Zone 5	3 cm	
Bottom	Coaly shale	25 cm	
SITE 9			
Top	Zone 1	6 cm	
	Zone 2	5 cm	
	Zone 2/3		
	Zone 3	5 cm	
Bottom	Zone 4	6 cm	
SITE 12			
Top	Dark gray shale	18 cm	with plant debris
	Zone 1	30 cm	
	Zone 2	41 cm	
Bottom	Light Gray underclay with Stigmarian axes		

of coal in the split. Certainly, if the coal-ball-bearing coaly shale had been sampled for ash, values would have been much higher than those reported for normally bright banded coal.

Coal balls were collected and analyzed quantitatively according to the techniques described in Phillips et al. (1977). Samples were cut transversely, and cellulose acetate peels were prepared from the cut surfaces. Peels were attached to a transparent acetate sheet marked with a matrix of numbered, cm-square grids. The plant-organ type and its taxonomic affinity were recorded for each grid. Fusain, mineral matter, and invertebrate shells were noted. Data were compiled by site, or by zone if there were multiple zones at a site. Initial analyses include all un-identified and root material. For ecological analysis, roots are eliminated because they may have penetrated the litter layers from later vegetational stands. Exceptions to this are some roots of the *Psaronius* aerial root mantle. The inner root mantle was evidently entirely aerial, and it is counted as such. However, for roots of the outer mantle, we have found no objective means to separate aerial from subterranean portions. As a compromise solution, we arbitrarily count one-half of all outer roots as aerial.

Analysis of the data is presented in several forms. Raw data for the transects and profiles appears in Figure 3, illustrating the relative proportions of identified categories by major plant group, unidentified categories of plants, invertebrates, or clastic matter in the coal balls. Fusain (mineral charcoal) content of collections (Table 2) is based on a data set from which all non-plant materials have been removed and the remaining abundances normalized to 100% aggregate abundance. Finally, all ecological analyses are performed with data normalized to 100% identified aerial tissues, from which roots and material not identifiable to major plant group have been removed.

Exploratory ecological analyses were performed with SYSTAT version 5.1 for Windows (Wilkinson et al., 1992). Data were ordinated with non-metric multidimensional

scaling in two dimensions. Euclidian distance was used as the metric because data were continuously variable in character. Cluster analysis was performed using the un-weighted pair groups method of analysis (referred to as average linkage in SYSTAT). Taxa used in the quantitative ecological analysis were reduced to the lowest taxonomic level for which reliable whole-plants could be constructed from dispersed organs. Lycopsids, small ferns, cordaites, and some small pteridosperms are treated best as whole plants. Medullosans, *Psaronius* tree ferns, several small pteridosperms, and sphenopsids are well characterized from isolated organs, but few of these can be assembled reliably into whole-plant species. Table 3 shows the data matrix used in the ordination and cluster analysis. Table 2 provides a complete list of taxa identified and species diversity (richness) for each assemblage. Medullosan diversity was estimated using "species" of foliage, which was more common than ovules, and, at all but one site, more diverse; medullosan stem and rachis segments are difficult to identify to species at the present time (but see Beeler, 1983; Pryor, 1990). *Psaronius* diversity was estimated using reproductive organs, which in some instances can be correlated with specific types of reproductive structures (Lesnikowska, 1989). Although three types of Marattialean reproductive organs were found in Eby pit assemblages, only one *Psaronius* stem type was encountered, but it does correlate with one of the common types of reproductive organ.

Specimens used in this analysis are housed in the Paleobotanical Collections Facility at the University of Illinois, Champaign-Urbana. The coal-ball numbers and the surface area quantified for each site, or zone at a site, are presented in Table 2. Peels of illustrated specimens are housed in the Paleobotanical Collections of the National Museum of Natural History; USNM catalogue numbers appear in the captions of the figures that reference the respective specimen.

RESULTS

Whole-peat Composition

The major group composition of the transect sites and zones is illustrated in Figure 3. Four major groups of vascular plants comprise the whole-peat composition: lycopsids, pteridosperms, ferns, and sphenopsids, in descending order of abundance. Cordaites are rare to absent. At sites 1–7 percent abundance of lycopsids and pteridosperms are almost equal, with the largest divergence at site 7 (Table 4).

This transect of sites, summed and treated as a single horizon, yields peat composed 43.9% of lycopsids and 43% of pteridosperms. This is by far the highest abundance of pteridosperms reported from such a large collection. The shoot/root ratio of sites 1–7 is 2.9, one of the highest ever reported from a large coal-ball data set. This results in large part from the great abundance of pteridosperm tissues, mostly foliage (76%).

As will become apparent in subsequent presentations of the data, one lycopsid in particular, *Paralycopodites brevifolius*, accounts for the bulk of the tissue at most sites, with two species of the Lepidodendraceae (*Lepidodendron hickii* and *Lepidophloios hallii*) also contributing heavily

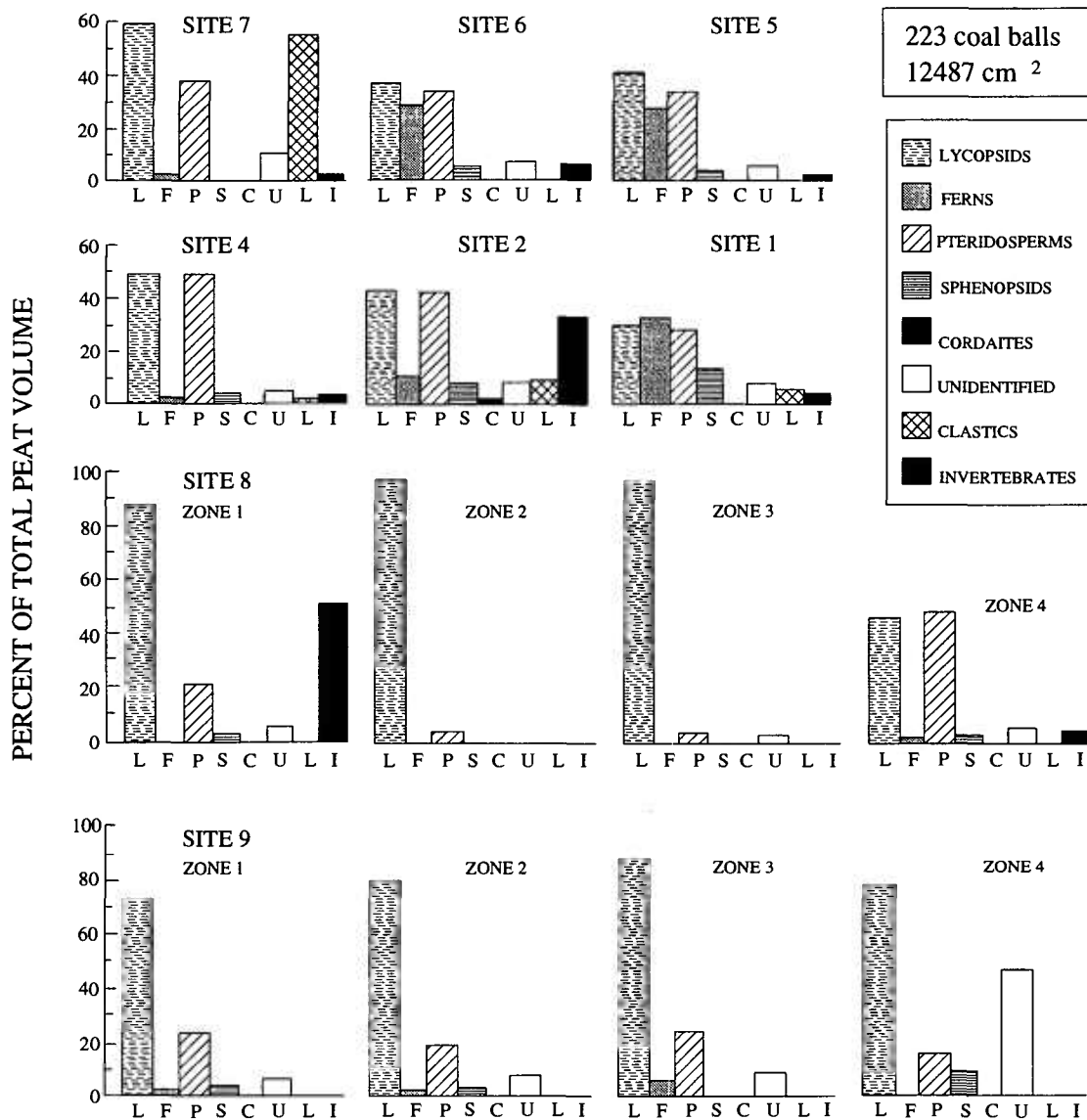COAL BALL SAMPLES, PEABODY LYNNVILLE MINE
EBY PIT, SITES 1-9

FIGURE 3—Whole peat composition of coal-ball samples from each of the nine transect sites. Sites 8 and 9 consisted of multiple zones; zone 1 is uppermost in each profile (see Table 1).

to the peat, especially at sites 8 and 9. On a whole-peat basis, sites 8 and 9 also have high shoot/root ratios, 2.6 and 3.2 respectively, averaged across the whole profile. Nevertheless, much of the lycopsid and pteridosperm tissues are root systems. At site 12 the shoot/root ratio is 1.5. Unidentified plant tissues are of relatively low abundance, usually < 10% except at lowermost zones of Sites 8 and 9 where they represent 22.2% and 43.3% of the peat, respectively.

Fusain (mineral charcoal) is of minor importance in the coal-ball deposits (Table 2). Several zones in profile 8 had no detectable fusain. Zone 4 at site 9 had the highest abundance, at 24.3%, but this was due almost entirely to two large fragments of lycopsid bark and cortical tissue. Ex-

cluding the anomalously high fusain levels in Site 9, Zone 4, the average amount of charcoal per assemblage is 2.5%. Such a fusain abundance is relatively low compared to other late Middle Pennsylvanian coals that have been analyzed quantitatively (Phillips and DiMichele, 1981; DiMichele and Phillips, 1988; DiMichele et al., 1991).

Transverse sections of four typical coal-ball faces are illustrated in Figures 4 and 5, and show peat fabric and the mix of organs. Eby pit coal balls are similar preservationally to almost all other known coal-ball deposits in general character. The peat is composed mostly of fragmentary large organs surrounded by a matrix of more detrital and organic material. Preservation of the Eby peats is relatively good, including the presence of delicate parenchyma-

TABLE 2—Coal-ball samples analyzed from the Eby Pit.

Site	cm² Analyzed	University of Illinois accession numbers	% Fusain	Species richness
1	672	26776–26791	1.2	11
2	2366	26792–26823	0.3	12
4	6191	26828–26920	2.4	14
5	516	26928–26934	0.8	10
6	962	26935–26964	1.7	13
7	165	26965–26966	7.3	11
8-1	55	28368–28373	0	5
8-2	34	28384–28386	0	3
8-3	238	28392–28405	0	2
8-4	526	28406–28414	3.4	12
9-1	251	28374, 28375, 28377 28381–28383	3.6	8
9-2	309	28387, 28367*, 28388*	1.6	9
9-3	99	28389, 28391 28367*, 28388*	6.1	6
9-4	103	28422	24.3	3
12-1	4098	36859–36916	3.7	15
12-2	901	36930–36953	5.3	12
12-float		36751–36774		
		*coal balls preserving more than one zone	3.8 (average) 2.4 (average with 9-4 excluded)	

Species identified:

Lycopsids (see Bateman et al., 1992 for taxonomy):

   Trees: *Paralycopodites brevifolius, Lepidopholios hallii, Lepidodendron hickii, Synchysidendron resinosum*

   Ground cover: *Hizemodendron serratum*

Ferns:

   Trees (taxa based on the whole plant assemblages of Lesnikowska, 1989): *Psaronius "gnomus" (Scolecopteris gnoma), P. magnificus (S. latifolia), P. "altissima" (S. altissimus)*

   Ground cover: *Ankyropteris brongnartii*

   Liana: *Anachoropteris involuta*

Sphenopsids:

   Trees: *Calamodendron americanum, Arthropitys communis (Calamocarpon)*

   Ground cover: *Sphenophyllum plurifoliatum*

Cordaites:

   Tree: *Pennsylvanioxylon nauertianum*

Pteridosperms:

   Trees: *Medullosa* species based on foliage types: *Alethopteris lesquereuxii, A. sullivantii, Neuropteris rarinervis,* unidentified alethopteriod, *Medullosa* species based on ovule types: *Hexapterospermum* sp., *Pachytesta saharasperma, P. stewartii, P. illinoense,* cf. *P. hoskinsii,* cf. *P. gigantea*

   Ground cover: *Callistophyton boysettii*

   Liana: *Heterangium (Conostoma leptospermum)*

Incertae sedis:

   Epiphyte ?: *Stellastelara parvula*

tous tissues in many organs. As can be seen from the faces illustrated, slight compression has resulted in general dorsi-ventral flattening. The degree to which peats are flattened varies greatly among coals and among zones of coal balls in a single coal, and can be much greater than that illustrated. The general fabric of the Eby peats is "open," meaning that well-preserved larger organs are embedded in a matrix of detrital peat and small fragmentary litter. Small roots, particularly those of medullosans, are abundant and widely scattered in some coal balls (Fig. 4A) but usually do not penetrate large litter. Surface decay levels were relatively low, peat accumulation relatively rapid, and consequent repeated penetration by roots from different forest stands limited. These preservational characteristics apply to assemblages dominated almost exclusively by medullosan pteridosperms (Figs. 4A and 5B) or those in which medullosans and the lycopsid *Paralycopodites* codominate (Figs. 4B and 5A). Where lepidodendracean lycopsids were most abundant, peat tended to be more poorly preserved with higher levels of tissue decay.

Marine invertebrates occur in each of the collections from sites 1–7 and in two zones of the profile at site 8. Detailed examination of oriented coal balls indicates that a lag of shelly material was deposited on the top of the upper bench of the peat; a number of coal balls indicate erosion of the uppermost layers of the organic mud followed by or as-

TABLE 3—Data matrix for ordination. Abundances of taxa are given for each site or zone.

Taxa									Sample sites							
	eby1	eby2	eby4	eby5	eby6	eby7	eby8x1	eby8x2	eby8x3	eby8x4	eby9x1	eby9x2	eby9x3	eby9x4	eby12x1	eby12x2
Stelastellara parvula	0	0.06	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0.16
Pennsylvanioxylon nauertianum	0	0.06	0	0	0	4.1	0	0	0	0	0	0	0	0	0	0
Psaronius spp.	33.11	9.23	2.72	28.6	27.14	7.1	0	0	0	0	0	0.41	3.79	0	10.9	8.64
Lepidophloios hallii	2.97	1.31	6.11	1.54	0.71	4.1	4.64	0	0	7.12	2.78	5.78	1.26	0	5.31	62.48
Lepidodendron hickii	0	0	0	0	0	0.6	0	0	0	0.56	0	53.3	68.34	0	4.06	6.85
Hizemodendron serratum	0	0	0	0	0	0	0	0	0	9.68	1.74	8.26	5.06	0	0.89	0
Synchysidendron resinosum	0	0.25	0.5	0	0.43	0	0	5.55	0	0	12.5	0	1.26	0	7.92	2.55
Paralycopodites brevifolius	18.65	35.79	31	29.37	22.03	13.6	0	88.88	0	0.85	0	0	0	0	24.07	0.95
unidentified Lepidodendraceae	4.56	1.19	0	0.77	5.32	0	81.37	0	96.88	10.81	43.75	11.15	11.39	74.28	7.76	8.77
Anachoropteris involuta	0.19	0	0.04	0	1.15	0	0	0	0	0.84	1.74	0.41	0	0	0.07	0
Ankyropteris brongnartii	0	0	0	0.21	0	0	0	0	0	0	0	0	0	0	0	0
Callistiophyton boysettii	0	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterangium sp.	0	0	0.02	0	0	0.6	0	0	0	0.28	0	0.41	0	0	0.2	0.11
Medullosa spp.	31.73	44.89	55.74	37.36	38.01	62.7	11.62	5.55	3.11	65.52	33.33	19.42	8.85	19.99	26.37	0.76
Sutcliffia insignis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.91
Arthropitys communis	0.59	0	0.82	0	0.14	1.2	2.32	0	0	1.7	0.87	0	0	5.71	1.44	1.11
Calamodendron americanum	5.55	3.2	0.62	0.51	2.15	5.3	0	0	0	0	0	0	0	0	0.69	0
Sphenophyllum plurifoliatum	2.57	3.95	0.57	1.8	2.87	0.6	0	0	0	1.42	5.28	0.41	0	0	10.96	0.79

TABLE 4—Lycopsid and pteridosperm percentage abundances from coal balls of the Eby pit transect.

Site	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Lycopsids	29.1	41.6	50	47.6	39.4	38.0	59.2
Pteridosperms	27.7	41.2	50	47.7	32.2	32.3	38.2

sociated with deposition of a shell lag (Fig. 5A). A similar deposit was reported in the Herrin coal in association with coal balls (DeMaris et al., 1983), and has been observed in the Upper Pennsylvanian Calhoun coal (Mamay and Yochelson, 1962). Figure 5 illustrates coal balls in which invertebrates have been incorporated into the peat matrix. In most instances, as in Figure 5B, the invertebrate shells appear to have been introduced into the peat from above through the activity of burrowing invertebrates. This is indicated by sharp boundaries between the invertebrate-rich muds and adjacent peats, and by the disposition of the invertebrate deposits, cutting across the peat fabric from top to bottom. However, in other cases, as illustrated in Figure 5A, invertebrate shells are well mixed within the peat fabric, possibly occurring contemporaneously with peat deposition or, through reworking of the top of the peat, shortly after it ended. Figure 5A illustrates two layers of coal balls. The top layer, composed of several small coal balls, is a homogeneous mixture of marine mud and finely detrital peat. In the lower layer, marine invertebrates are concentrated in the center of the coal ball, but also appear to be interstitial elements of the peat. It appears possible that brackish to marine waters may have entered the Leslie Cemetery paleochannel as base level changed and drowned at least the final swamp vegetation.

Ecological Analysis

Plant assemblages of the Eby pit can be divided into two major types. The first, which accounts for 10 of the 16 assemblages analyzed, is dominated by medullosan pteridosperms or codominated by medullosan pteridosperms and the lycopsid tree *Paralycopodites brevifolius*. The other assemblages are dominated by lycopsids, either *Lepidodendron hickii, Lepidophloios hallii,* or indeterminate lepidodendracean lycopsid tissues assignable to either of these closely related species (Figure 6). Two small assemblages, site 9 zone 1 and site 9 zone 4, show overlap in these otherwise disparate dominant elements. In these two cases, lepidodendracean tissues are most abundant, but medullosans also are of importance in the assemblage. *Lepidophloios hallii* is widespread and occurs in abundances of < 10% in nearly all assemblages (Table 3); this is consistent with its widely dispersed seed-like propagules.

The distinction between the two major kinds of communities (assemblages) is shown very clearly in the ordination (Fig. 6) and cluster analyses (Fig. 7). Assemblages 8–1, 8–3, and 9–4 are dominated by tissues that were identifiable only to the level of Lepidodendraceae. In the mechanics of the statistical analysis, these are coded as a unique taxon different from the identifiable species of the Lepidodendraceae that probably produced the tissue, thus leading to a more distinct separation than is warranted. It is likely that these assemblages were dominated by *Lepi-*

dophloios hallii, and share the low species diversity, particularly the rarity of ground cover and ferns, which typifies dominance by this species (DiMichele and Phillips, 1988). Figure 7 shows that assemblage 8–2, strongly dominated by *Paralycopodites brevifolius,* does not cluster closely with the other *P. brevifolius–Medullosa* assemblages, a consequence of its relatively low proportion of medullosans and high lycopsid dominance.
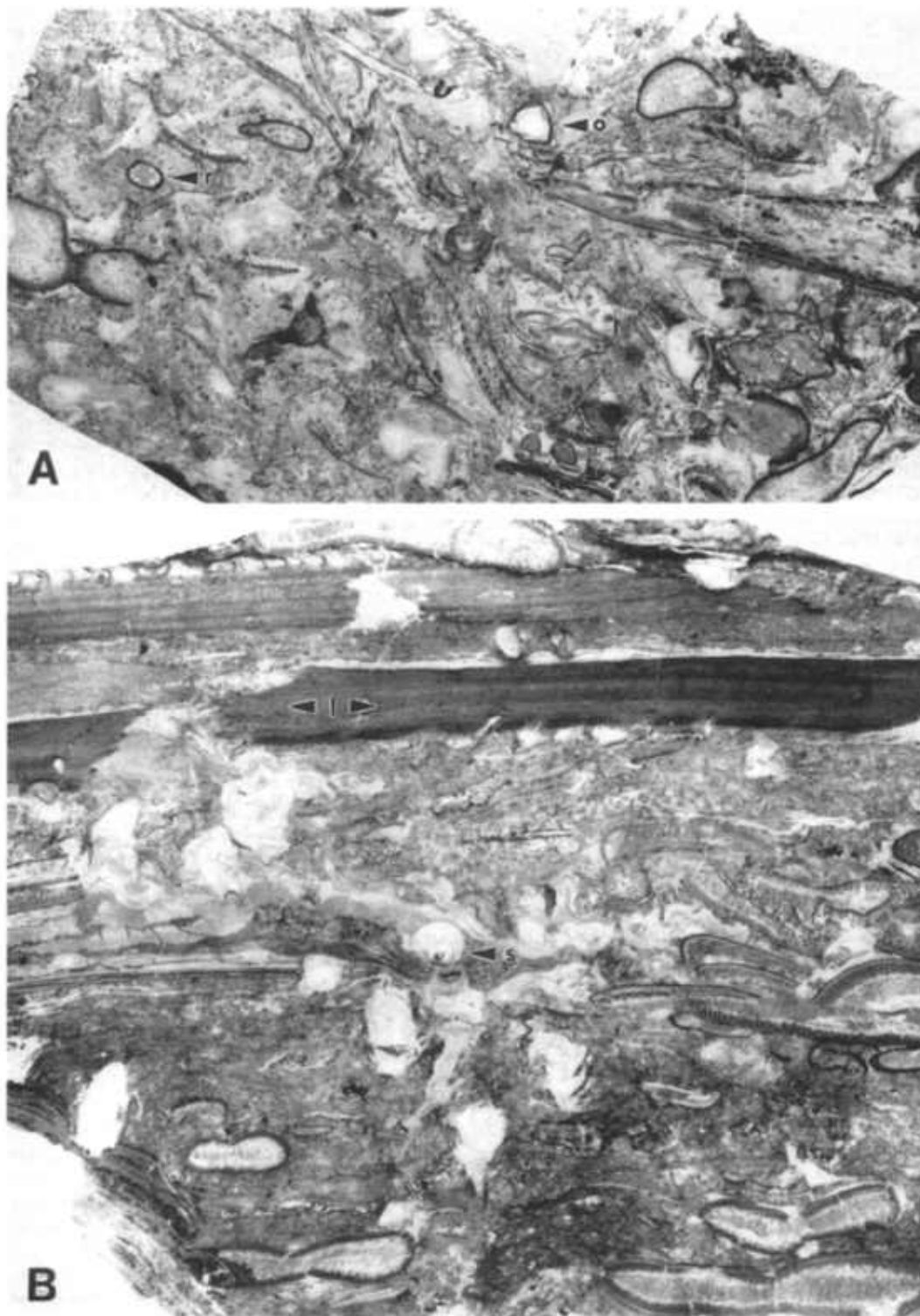
Taxonomic Considerations

Species identified in the samples and the species diversity at each site are presented in Table 2. Selected taxa are illustrated in Figures 8 and 9. Overall, there are either 22 or 24 species in the entire Eby pit assemblage, depending on whether *Medullosa* is typified by foliage (four species) or ovules (six species). Considerable changes in the taxonomy of arborescent lycopsids in the past 15 years are summarized in Bateman et al. (1992). The five species of five lycopsid genera that occur at the Eby pit are widely known from late Westphalian D coals in the United States and have distinctively different vegetative anatomies and reproductive organs, rendering them highly differentiable even in fragmentary preservation. All the lycopsids were trees except for *Hizemodendron serratum,* which had a sprawling, ground-cover growth form (Baxter, 1965).

For *Psaronius* tree ferns, we followed the taxonomic usage of Lesnikowska (1989), who correlated the various vegetative organs with each other and with reproductive structures. The only stems encountered in the collections were those of *Psaronius magnificus,* which is characterized by a highly distinctive aerenchymatous stem cortex and limited root mantle (Rothwell and Blickle, 1982); *P. magnificus* correlates with the reproductive structure *Scolecopteris latifolia.* No distinct stem remains were found for the two other reproductive forms, *Scolecopteris gnoma* and *S. altissima.* Only two small ferns were encountered. *Anachoropteris involuta* occurred widely in low abundance; reproductive organs of *Ankyropteris brongniartii* occurred in one coal ball.
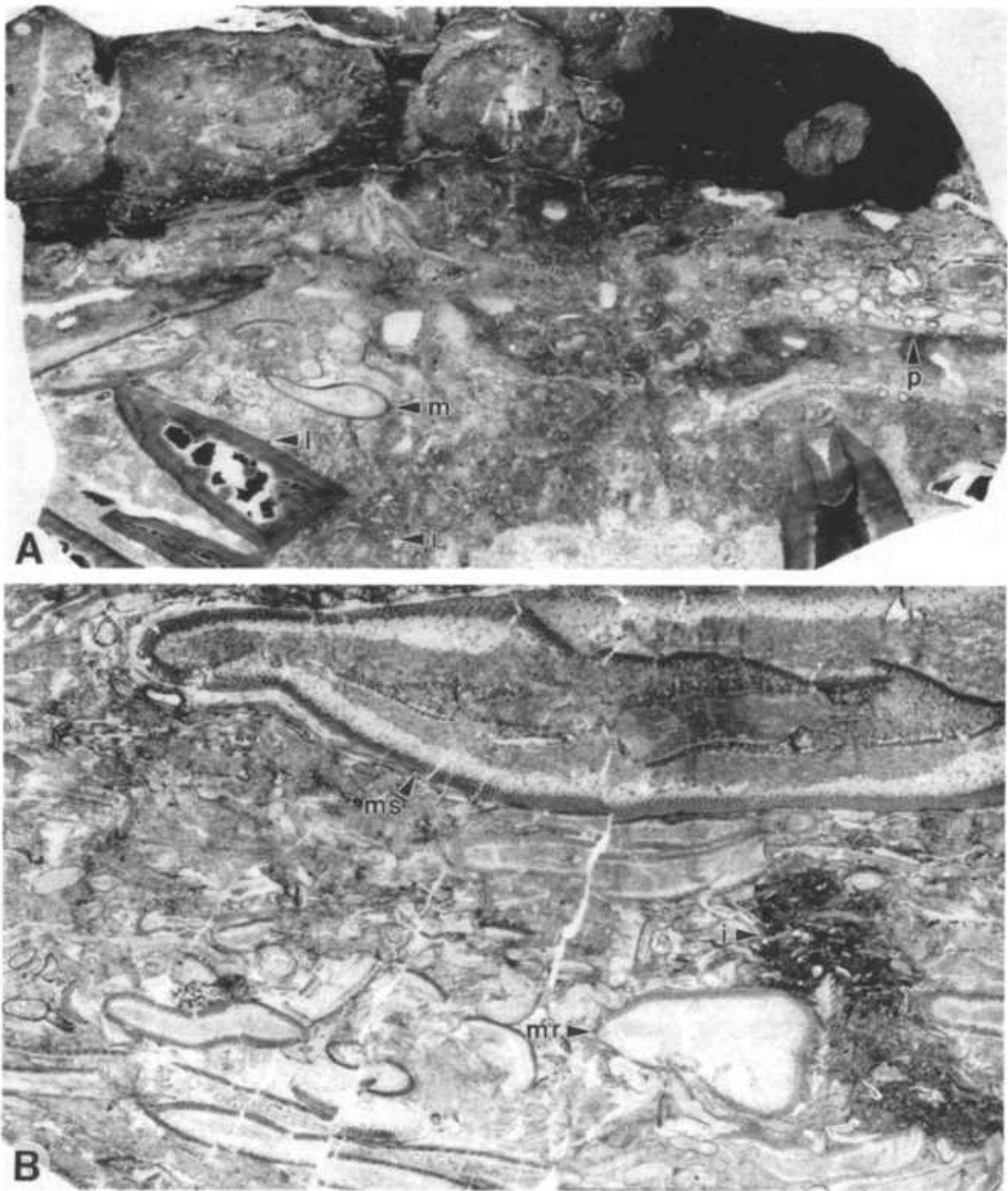
The sphenopsid assemblage was typical of the late Westphalian D. The two calamite species were probably small, upright shrubs or trees forming thickets. Included are *Arthropitys communis,* the probable source of *Calamocarpon*-type reproductive organs, and *Calamodendron americanum,* an uncommonly encountered species in most other coal-ball deposits. *Sphenophyllum plurifoliatum* had a sprawling ground-cover growth habit and was distributed widely, being absent in only one instance from those assemblages heavily dominated by lepidodendracean lycopsids.

Of the seed plants, cordaites were quite rare, as is typical for coals younger than middle Westphalian D. Small pteridosperms also were rare. *Heterangium* of a form that produced *Conostoma leptospermum* ovules, a possible vine (Pigg et al., 1987), was found in low abundances in several assemblages; *Callistophyton boysetii,* which had a sprawling habit (Rothwell, 1981), was identified from its reproductive organs in a single coal ball. The vegetative remains of arborescent pteridosperms are difficult to identify to species and, for the most part, are poorly correlated with reproductive organs or foliage types. The clearest generic distinction is between *Sutcliffia,* which produced *Re-*

FIGURE 4—Transverse sections of coal balls; each natural size (1 X). (A) Medullosan-dominated peat; speckled pattern created by bundles of sclerenchyma cells in the peripheral cortex of medullosan rachises. r = medullosan root; o = medullosan ovule (*Pachytesta*). UI 36886 A, site 12–1; USNM 494802. (B) Peat composed of medullosans and lycopsids. Medullosans can be identified in cross section by the typically speckled pattern, created by sclerenchyma bundles in their cortical tissues. Note the heavily decayed major framework components. I = Periderm of the lycopsid *Paralycopodites brevifolius* with attached leaf bases, shown in longitudinal section (see Fig. 8A for higher magnification image). s = lycopsid stigmarian rootlets. UI 26838 D top, site 4; USNM 494803.

FIGURE 5—Transverse sections of coal balls. (A) Mixed coal balls composed of plants and marine invertebrates. i = invertebrate shells; l = lycopsid periderm; p = *Psaronius* tree fern aerial root mantle; m = medullosan rachis. Opaque/black areas are coal. 0.75 ×. UI 26801 A bot, site 1; USNM 494804. (B) Mixed coal ball with invertebrates localized in possible burrow filling (i). Most of the other remains are medullosan rachis (mr) or stem (ms) segments. 1 ×. UI 26859 D bot, site 4; USNM 494805.

ticulopteris-type foliage, and *Medullosa,* which is associated with a number of foliage and ovule types. Four types of medullosan foliage occurred widely: *Alethopteris lesquereuxii, A. sullivantii, Neuropteris rarinervis,* and a foliage type that we have not identified to species (thin lamina with highly melanic mesophyll). These vary in relative proportions in different assemblages; any one species may be the most abundant locally. *Reticulopteris* foliage was
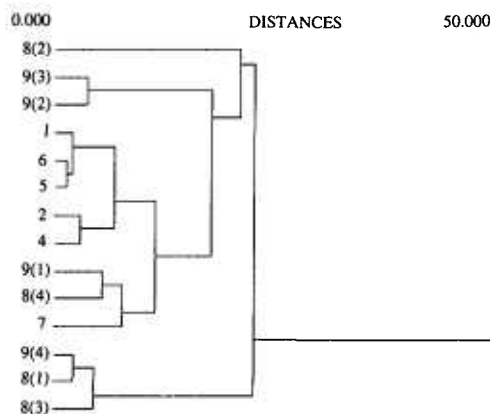
FIGURE 6—Non-metric multidimensional scaling ordination of coal ball assemblages from nine Eby pit transect sites and site 12 (see text). Zones for sites 8, 9, and 12 are shown in parentheses. Except for zone 12(2), all assemblages with positive Axis 1 scores are dominated by either or both *Medullosa* and *Paralycopodites*. All assemblages with negative Axis 1 scores, plus 12(2), are dominated by species of the Lepidodendraceae, *Lepidodendron* and *Lepidophloios*.

common only in the one assemblage that also had abundant *Sutcliffia insignis* rachises.

Six types of ovules were identified with the following patterns of occurrence: *Pachytesta illinoensis* occurred in five assemblages, and was the only ovule in four of these; *Hexapterospermum* sp. was represented by a single specimen in an assemblage (12–1) that included several *Pachytesta saharasperma* (which occurred no where else), *Pachytesta illinoensis,* and an unidentified large ovule; *Pachytesta stewartii* and a large ovule, possibly *Pachytesta gigantea,* occurred only once and in the same assemblage;

FIGURE 7—UPGMA cluster analysis of 14 assemblages from the Eby pit transect. Numbers refer to sites and, where appropriate, zones (in parentheses). Assemblages 1, 2, 4, 5, 6, 7, 9(1), and 8(4) are dominated by medullosan pteridosperms, or codominated by medullosans and the lycopsid *Paralycopodites.* Assemblages 8(1), 8(2), 8(3), 9(2), 9(3), and 9(4) are dominated by lycopsids. Of these, all are dominated by *Lepidodendron* or *Lepidophloios* of the Lepidodendraceae, except for 8(2), which is composed nearly entirely of *Paralycopodites.*

Pachytesta hoskinsii occurred as a single specimen in an assemblage with no other identifiable ovule types; unidentifiable fragments of ovules occurred in several of the assemblages.

The total species diversity in the entire data set is fairly typical of a well sampled, late Westphalian D assemblage from one basic environmental type. Diversity is lower than that found in profiles from thick coals where a number of subenvironments are sampled. Total area sampled in this analysis was 17,486 cm^2, which is a relatively large area, comparable to the vertical profiles composed of multiple zones collected from other localities. Only a few of the species occur at only one collecting site, including *Sutcliffia insignis, Callistophyton boysetii,* and *Ankyropteris brongniartii.* Cordaites were the only major tree group to occur at as few as two sites. All others had wider distributions (estimating *Medullosa* diversity from foliage rather than ovules). The compositional consistency over a large area suggests that sampling has captured the major elements of the vegetation.

DISCUSSION

Pennsylvanian-age peat-forming environments are among the best known of any types of fossil deposits, both taxonomically and ecologically, due to the exquisite three-dimensional preservation afforded by coal balls. For the most part, however, coal balls have given us insights into the vegetation of peat-forming mires. Floras of clastic environments are known mostly from compression and impression preservation, and appear to be dominated by different species from those of peat-forming environments (Scott, 1978; Pfefferkorn and Thomson, 1982; Gastaldo et al., 1995). The different forms of preservation limit the cross comparability of peat and clastic floras, both of

which grew in the tropical wet lowlands. For this reason, the coal balls from the Eby pit are an important bridge between the vegetation of peat and clastic swamps, and were important in the reconstruction of the landscape of the Springfield peat swamp illustrated in Phillips and Cross (1991).

The Eby flora appears to have grown in swampy lowlands fringing the peat mire along the margin of the Leslie Cemetery channel floodplain. Such swamp areas were probably stagnant much of the time with occasional floods carrying in fine clays. The deposit appears to have alternated between clastic muck and thin intervals of relatively pure peat. The coal-ball phases appear to have formed within the thin peat-rich layers, although inorganic material and peat were intermixed in coal balls from several sites. Coal balls frequently were surrounded on all sides by clastic organic shales. For much of its extent, the organic shale deposit is underlain by a well-developed underclay (Willard et al., 1995). In addition, the juncture of the main coal bench and thin upper bench is not marked by extensive interfingering. These observations indicate that clastic swamps formed late within the life of the Folsomville splay, in conjunction with a change in local base level that ultimately became a marine incursion. Elevated water tables within the splay may have encouraged the development of clastic swamps. The marine units overlying the Springfield are thicker within the area of the Folsomville clastics, which is consistent with a more prolonged period of deposition there.

Root systems of all the major plant groups, including medullosans, were common in the coal balls, and the thinness of the peat zones insures that many plants were rooted in muck and had access to much higher nutrient levels than plants of thick peat substrates. This is reflected in the sizes of plants, such as *Paralycopodites brevifolius,* which appear to be considerably greater in the Eby coal balls than in coal balls from other, less clastic-rich peat-substrate sites, such as the Secor coal (DiMichele et al., 1991) and Herrin coal (DiMichele and Phillips, 1988). The compositional makeup of the vegetation, particularly the low diversity and relative abundance of ground cover, and relatively low proportions of free-sporing tree ferns, are consistent with a commonly flooded substrate.
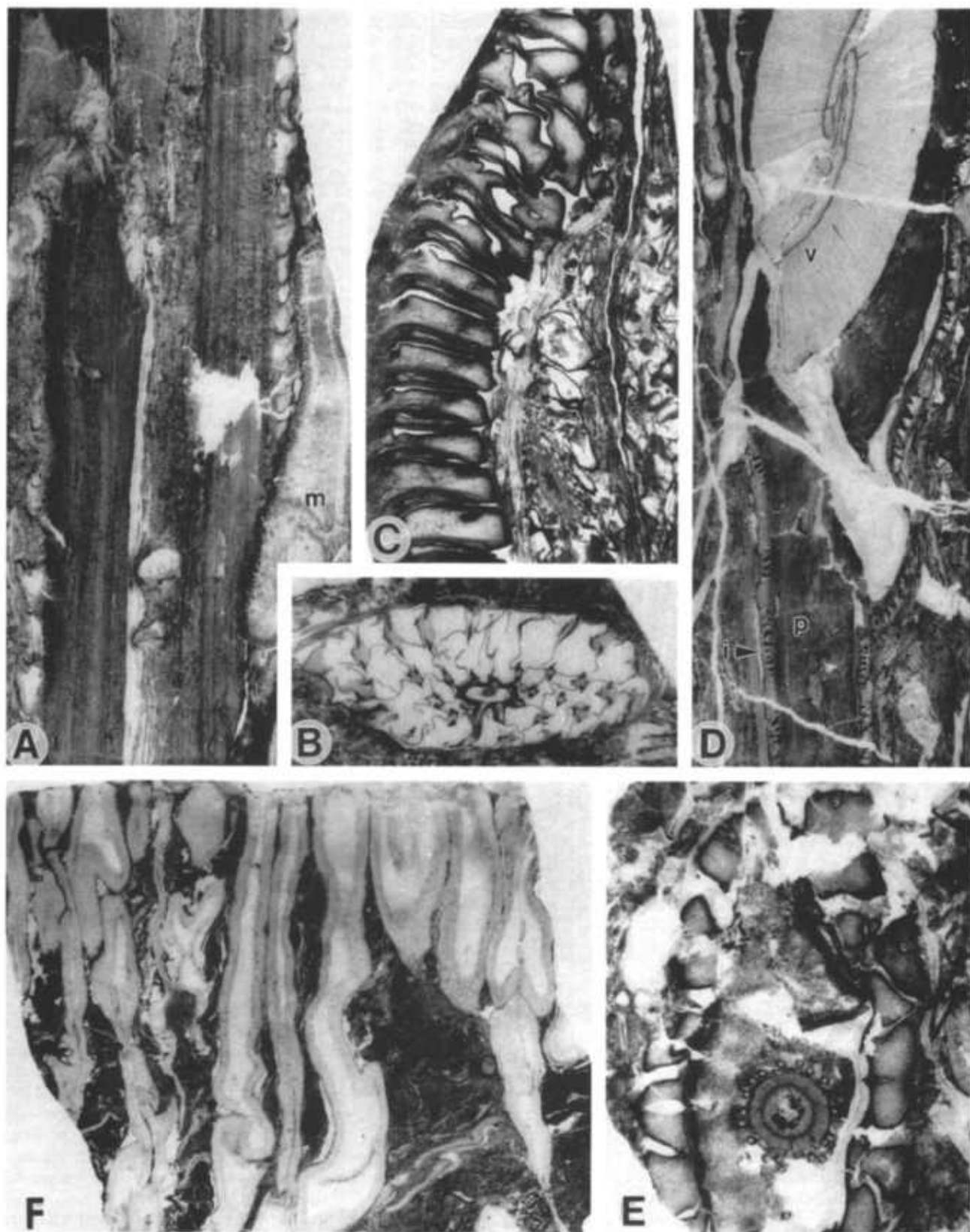
Dominant Plants of the Eby Pit Flora

The dominant elements in the Eby pit flora represent two distinct types of swamp floras. The more typical of the two is dominated by lycopsids of the family Lepidodendraceae— *Lepidophloios hallii* and *Lepidodendron hickii. Lepidophloios* species are relatively more common in coal-ball floras of the Westphalian than in compression floras, and they are important to dominant elements of many peat-forming mires, indicated both by macrofossil and palynological studies (Phillips et al., 1985; DiMichele and Phillips, 1995). Typically such assemblages are associated with bright-coal macerals and moderate ash levels, indicating some flooding and probably persistent water cover (e.g., Eble and Grady, 1990). Gastaldo (1987) reports *Lepidophloios* in deep-water clastic swamps of the Westphalian A in association with low-diversity communites, paralleling the patterns of *Lepidophloios*-dominated assemblages from Westphalian D
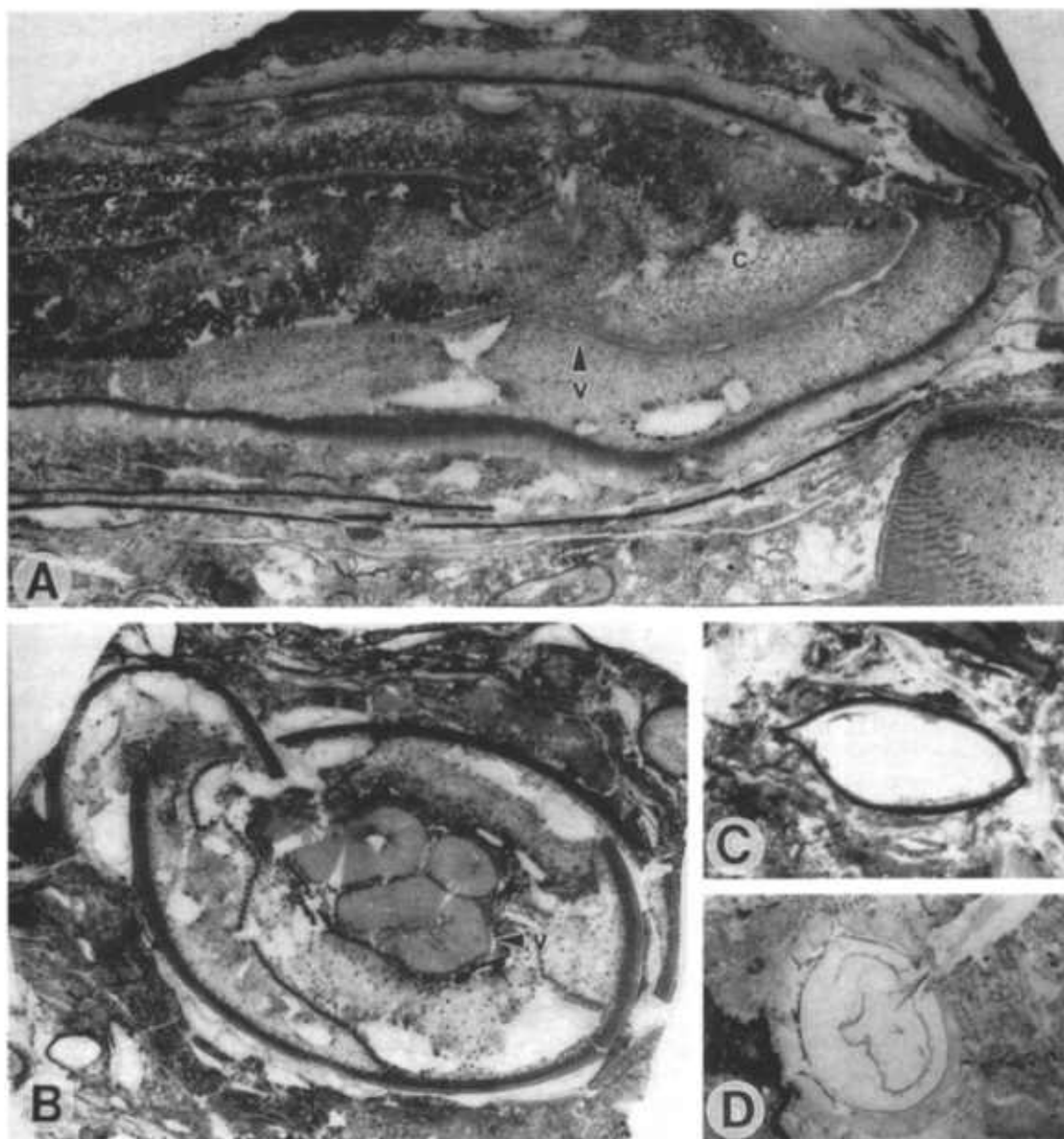
coals (DiMichele and Phillips, 1988). *Lepidodendron,* in contrast, is more common in compression-impression floras than in coal-ball floras throughout the Westphalian, where it occurs in a wide variety of habitats from organic-clastic swamps (Lamboy and Lesnikowska, 1988) to back-swamps along channel margins, generally in association with relatively diverse vegetation (Gastaldo, 1987). *Lepidodendron* appears to have been considerably less diverse on peat substrates, although *L. hickii* occurs in coal-balls throughout the Westphalian and is of occasional importance (DiMichele, 1983; Calder, 1993). Willard (1989a, b) contrasted *Lycospora* spore assemblages produced by the Lepidodendraceae in clastics and coal, and also found distinctive species composition.

The assemblage less often found in Westphalian-age coal balls is that dominated by medullosans and the lycopsid *Paralycopodites brevifolius.* Ample evidence supports the dominance of medullosans in wet floodplain environments of the Westphalian (see Pfefferkorn and Thomson, 1982, for discussion), where they were diverse. The foliage genera *Neuropteris sensu lato,* recently subdivided into several genera by Cleal and Shute (1995), *Alethopteris, Paripteris, Linopteris,* and *Reticulopteris* consist of numerous well delimited species. A few of the species known from compression-impression preservation also have been reported from coal balls, including *Neuropteris scheuchzeri* (Beeler, 1983), *Neuropteris ovata* (Beeler, 1983), *Neuropteris rarinervis* (Oestry-Stidd, 1979), *Alethopteris lesquereuxii* (Baxter and Willhite, 1969), *Alethopteris sullivantii* (Leisman, 1960), *Alethopteris serlii sensu lato* (Mickle and Rothwell, 1982), *Alethopteris bohemica* or *A. grandinoides* (Mickle and Rothwell, 1982) and *Linopteris* sp. (Stidd et al., 1975—probably *Reticulopteris münsteri).* We have encountered several additional forms in the course of our quantitative studies, although the numbers appear to be small. So, in general, only a small subset of medullosans appears to have crossed regularly between clastic floodplain habitats and peat-substrate mires. Furthermore, there are no reported medullosan foliage species unique to ancient peat-substrate habitats. Medullosans have been reported as dominant elements in some organic-clastic swamp deposits from both the Westphalian (Lamboy and Lesnikowska, 1988) and Stephanian (DiMichele, unpublished data), but species again are drawn from those already known to inhabit both peat and mineral substrates.

The other dominant plant in this environment is *Paralycopodites brevifolius,* probably represented in compression preservation by *Ulodendron majus* (Thomas, 1967), which, in American compression floras at least, is quite rare. *Paralycopodites brevifolius* is known from the Lower Carboniferous and occurs sporadically in coal-ball deposits throughout the Westphalian (DiMichele, 1980), often in association with clastic-and-fusain enriched portions of coal seams. The occurrence of *Paralycopodites brevifolius* and medullosan pteridosperms is a recurrent theme in many coal-ball assemblages throughout the Westphalian, first occurring in the Westphalian A (DiMichele and Phillips, 1995). Where it has been possible to correlate recurrent "communities" with physical environmental indicators, this kind of assemblage is strongly associated with high levels of mineral matter in the coal, with clastic partings or with the underclay (all seen in the Herrin coal; DiMichele and Phillips, 1988), with rotted peat (such as in

FIGURE 8—Plants from Eby pit coal balls. (A) Longitudinal section of *Paralycopodites brevifolius* periderm with attached leaf bases. m = transverse section of medullosan rachis. 1.5 ×. UI 26838 D top; USNM 494803. (B) Oblique transverse section of *Flemingites* cone, produced by *Paralycopodites brevifolius*. 3 ×. UI 26939 B bot; USNM 494806. (C) Longitudinal section of *Lepidophloios hallii* leaf cushions. 3 ×. UI 36771 B bot; USNM 494807. (D) Transverse section of *Synchysidendron resinosum* stem. v = vascular cylinder; p = flattened periderm; i =

FIGURE 9—Plants from Eby pit coal balls. (A) Transverse section of *Psaronius magnificus* showing characteristic aerenchymatous cortex (c). v = primary vascular strands. 1.5 ×. UI 26929 C bot; USNM 494811. (B) Transverse section of *Medullosa* stem. Vascular bundles (v) are located in the center of the stem, ensheathed by the bases of petioles; sclerotic bundles are concentrated in the outer parts of the cortex of the leaf bases. 1 ×. UI 36757 C top; USNM 494812. (C) Longitudinal section of medullosan ovule, *Pachytesta saharasperma*. 3 ×. UI 36880 B bot; USNM 494813. (D) Oblique section of medullosan ovule *Pachytesta illinoensis*. 1 ×. UI 26793 B bot; USNM 494814.

the Secor coal of Oklahoma; DiMichele,et al., 1992), or more broadly with "planar" mire conditions that were distant from marginal areas but still subject to nutrient enrichment (Calder, 1993). Thus, the inference of association with distinctive ecotonal conditions was made by aggregation of data from many point sources (i.e., individual

small zones in coal ball profiles or through incremental palynological analysis). The Eby pit site is the first collection to demonstrate the close and clear association of this flora with distinctly clastic swamp conditions over an extended local area.

The Eby pit transect covers a distance of about 1 km,

←

expanded interareas between leaf cushions, with form diagnostic of *Synchysidendron*. 1.5 ×. UI 36754 C bot; USNM 494808. (E) Transverse section of terminal stem segment of *Synchysidendron resinosum*. Specimen has characteristic large leaf cushions, pith with nests of sclerotic cells, and leaf cushions ensheathed in the middle cortex by cells with resin-like contents. 3 ×. UI 36878 A; USNM 494809. (F) Oblique longitudinal section of stigmarian rootlets from a lycopsid rhizomorphic root system; these rootlets appear to be attached to a common stigmarian main axis. 1 ×. UI 26903 B bot; USNM 404810.

from sites 8 and 9 at the northern end through sites 1 to 7, proceeding from north to south. Nearly all of this transect is dominated by the *Paralycopodites*—medullosan community type. Only near the edge of the upper bench, within 100 m of its union with the lower bench, do assemblages appear that are dominated by lycopsids of the Lepidodendraceae, *Lepidophloios hallii* and *Lepidodendron hickii*. Medullosans remain common in these lepidodendracean assemblages, but *Paralycopodites* abundances are greatly reduced. As such, they are similar to the lycopsid-dominated assemblages described by Gastaldo (1987) near paleochannels or splays. Within the site 8 profile in particular, there is an oscillation of the two community types in successive zones. The abundance of medullosans within the marginal lepidodendracean assemblages reflects the high levels of clastic matter in the swamp.

Coal balls occur within the unsplit Springfield Coal in three mines between 3 and 4.5 km from the Eby pit. These sites also contain large percentages of medullosan pteridosperms and a great variety of lycopsids. In fact, the Springfield Coal in western Indiana has perhaps the most diverse arborescent lycopsid assemblage of any of the major Westphalian coals we have examined, including *Lepidophloios hallii, Lepidodendron hickii, Paralycopodites brevifolius, Sigillaria* sp., *Hizemodendron serratum, Diaphorodendron scleroticum, Synchysidendron resinosum,* and *Sublepidophloios* sp., all in dominant to subdominant abundances. However, in the coal-ball profiles from the unsplit Springfield Coal, assemblages typical of other late Westphalian coals predominate, with the *Paralycopodites*–medullosan assemblages occurring rarely (DiMichele and Phillips, 1995).

Comparisons with Coal-ball Studies from Spain

Thus far there is only one other report of extremely high pteridosperm abundances (48%, as a percentage of individual specimens) in coal-ball deposits (Beckary, 1987), from NW Spain in a seam of Namurian C–Westphalian A age. This represents the only deviation from lycopsid dominance in the European Westphalian. As in the Eby Pit, the Spanish coal balls are mixed (plant material and marine invertebrates). In contrast to the Eby Pit, however, all of the other major plant groups (ferns, lycopsids, sphenopsids and cordaites) occurred as approximately equal numbers of specimens in the Spanish coal balls; shoot/root ratios were inferred to be considerably lower, and preservation was sometimes poor.

Occurrences of Mixed (Plant-Marine Invertebrate) Coal Balls

The concept of mixed coal balls, containing both plants and animals, was first elaborated by Mamay and Yochelson (1962). Two types of coal balls were described in this study: a homogeneous type with plant and animal remains fully intermixed, and a heterogeneous type with distinct segregation. Such coal balls are sometimes found in the top zones of coal-ball deposits and have been recorded widely in the Middle and Upper Pennsylvanian in the United States (Mamay and Yochelson, 1962) and in the Middle Carboniferous of the Donets Basin (Zaritsky, 1968). Reports have been exceedingly rare in Western Europe (Holmes and Scott, 1981). Marine invertebrate fossils were first reported in coal balls of the Springfield Coal from several abandoned mines in the Boonville, Indiana area (Boneham, 1976). The study indicated animal remains in not more than 5% of the coal balls; however, none of the coal balls were found in place in the coal. Animal studies of some of the coal balls from site 12 at Eby Pit led to the description of beautifully preserved conodont assemblages by Rexroad (1993) and the interpretation that the animals lived in a nearby mud-trapping, salt-water mire not subjected to major fluctuations in salinity.

Palynological Studies

Willard (1993) studied the palynology of the Springfield Coal throughout its extent in Indiana, Illinois, and western Kentucky. She identified large-scale gradients within the coal, particularly in the relative abundances of tree-fern and lycopsid spores. Tree-fern spores are characteristically the most abundant spores in Springfield samples. Areas distant from contemporaneous paleochannels are dominated by the fern spore *Thymospora pseudothiessenii,* and by a broad spectrum of lycopsid spores. In contrast, areas of unsplit coal near paleochannels have a broad spectrum of tree-fern spores in codominant abundances. Lycopsids are of secondary importance throughout most of the areal extent of the coal, with *Lycospora* producing forms of greatest importance; *Lycospora* was produced by members of the Lepidodendraceae and by *Paralycopodites.* Only near the Folsomville/Leslie Cemetery paleochannel complex were lycopsids dominant, represented particularly by *Lycospora* spp., and tree-fern spores of secondary importance. *Lycospora orbicula,* produced by *Paralycopodites,* is particularly abundant in the upper bench of the coal near the paleochannel (Willard et al., 1995). These patterns of spore distribution are consistent with the coal-ball patterns from the Eby pit and nearby mines.

Transects have been reported from a number of other coals of Westphalian age. Virtually all of these combine palynology with examination of coal petrology and geochemical analyses. For example, Eble et al. (1994) studied a margin to interior transect in the Lower Pennsylvanian (Westphalian A) Mary Lee coal bed of Alabama; vegetational and associated physical changes in early Middle Pennsylvanian (Westphalian B) coals have been examined for the Springhill Coal of Nova Scotia by Calder (1993) and the central Appalachian Fire Clay coal bed by Eble and Grady (1990); Hower et al. (1994) studied the late Middle Pennsylvanian (Westphalian D) No. 5 Block coal bed from the Appalachians. The transects in each of these coals were long, extending from the margin to the interior parts of the coal bodies, and vertical patterns also were studied. In general, floras show clear evidences of lateral change, especially in areas approaching the margins of the original peat bodies. In these areas, mineral matter and sulfur increase in concentration and are associated with greater plant diversity and floristic changes, often including species more commonly found in compression floras. However, the patterns found in the coals examined in the previously mentioned studies are often variable, reflecting the unique conditions in each of the ancient mires. Calder (1993), for example, found spores of *Paralycopodites* to be a major element of the Springhill coal flora, but in planar

parts of the interior mire, rather than near the clastic-rich base of the seam, above the mineral underclay.

Clastic Swamp Studies

Other studies of vegetational changes along transects in the late Paleozoic include Gastaldo's (1987) report of a long transect from a clastic swamp to a levee environment in rocks of the Lower Pennsylvanian of Alabama. This transect showed marked similarities to patterns found in the coal-bed transects, with increases in diversity and complexity of the vegetation toward the swamp margins and levees. Lycopsid trees, especially *Lepidophloios,* dominated in the low-diversity standing-water swamp deposits; pteridosperms, ferns, sphenopsids, and the lycopsids *Lepidodendron* and *Sigillaria* were abundant in the better drained habitats. On a smaller scale, DiMichele and Nelson (1989) described transects through clastic swamp vegetation in the roof shale of the Springfield Coal in Illinois, from a nearly pure stand of *Sigillaria* to vegetation dominated by pteridosperms. Changes in dominance patterns were abrupt and were inferred to reflect changes in hydrologic conditions.

The variety of patterns revealed in these transects suggests that controls on vegetational distribution in the late Paleozoic were as complex as they are today. Some basic patterns have begun to emerge. For example, the distributional patterns of species of lycopsid trees are increasingly well understood. Basic differences in the physical tolerances and ecological strategies of seed plants, sphenopsids, lycopsids, and ferns may be more clearly marked in the Paleozoic than at any other time in land-plant history. However, in order to use the patterns of the late Paleozoic as part of model systems to understand the effects of environmental change on short-term and long-term vegetational dynamics, it will be necessary to understand individual species tolerances in as much detail as possible, given the challenges presented by the fossil record.

ACKNOWLEDGMENTS

REFERENCES

ANDREWS, H.N., 1980, the Fossil Hunters: Cornell University Press, Ithaca, 421 pp.

BATEMAN, R.M., DIMICHELE, W.A., and WILLARD, D.A., 1992, Experimental cladistic analysis of anatomically preserved arborescent lycopsids from the Carboniferous of Euramerica: An essay on paleobotanical phylogenetics: Annals of the Missouri Botanical Garden, v. 79, p. 500–559.

BAXTER, R.W., 1965, The growth habit of *Lepidodendron serratum* Felix: The Palaeobotanist, v. 14, p. 1–4.

BAXTER, R.W., and WILLHITE, M.R., 1969, The morphology and anatomy of *Alethopteris lesquereuxi* Wagner: University of Kansas Science Bulletin, v. 48, p. 767–783.

BECKARY, S., 1987, Floral-faunal association in the coal balls of the Rosario mine (NW Spain), Namurian C–Westphalian A). Palaeoecological interpretation: Annales de la Societe Geologique du Nord, v. 106, p. 111–115.

BEELER, H.E., 1983, Anatomy and frond architecture of *Neuropteris ovata* and *Neuropteris scheuchzeri* from the Upper Pennsylvanian of the Appalachian Basin: Canadian Journal of Botany, v. 61, p. 2352–2368.

BONEHAM, R.F., 1976, Marine invertebrate fossils in Pennsylvanian coal balls from southern Indiana: Proceedings of the Indiana Academy of Sciences for 1975, v. 85, p. 78–88.

CALDER, J.H., 1993, 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: *in* Cobb, J.C., and Cecil, C.B., eds., Modern and Ancient Coal-forming Environments: Geological Society of America, Special Paper 286, p. 153–180.

CLEAL, C.J., and SHUTE, C.H., 1995, A synopsis of neuropterid foliage from the Carboniferous and Lower Permian of Europe: Bulletin of the Natural History Museum, London (Geology), v 51, p. 1–52.

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 1982–3, 69 p.

DIMICHELE, W.A., 1980, *Paralycopodites* Morey & Morey, from the Carboniferous of Euramerica—a reassessment of generic affinities and evolution of "*Lepidodendron*" *brevifolium* Williamson: American Journal of Botany, v. 67, p. 1466–1476.

DIMICHELE, W.A., 1983, *Lepidodendron hickii* and generic delimitation in Carboniferous lepidodendrid lycopods: Systematic Botany, v. 8, p. 317–333.

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

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., 1994, Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 106, p. 30–90.

DIMICHELE, W.A., and PHILLIPS, T.L., 1995, The response of hierarchically structured ecosystems to long-term climate change: A case study using tropical peat swamps of Pennsylvanian age: *in* STANLEY, S.M., KNOLL, A.H., and KENNETT, J.P., eds., Effects of Past Global Change on Life: National Research Council Studies in Geophysics, p. 134–155.

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

EBLE, C.F., and GRADY, W.C., 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.

EBLE, C.F., GASTALDO, R.A., DEMKO, T.M., and LIU, Y., 1994, Coal compositional changes along a mire interior to mire margin transect in the Mary Lee coal bed, Warrior Basin, Alabama, USA: International Journal of Coal Geology, v. 26, p. 43–62.

EGGERT, D.L., 1982, A fluvial channel contemporaneous with deposition of the Springfield Coal Member (V), Petersburg Formation,

Northern Warrick County, Indiana: Indiana Geological Survey Special Report 28, p. 1–20.

EGGERT, D.L., 1984, The Leslie Cemetery and Francisco distributary channels in the Petersburg Formation (Pennsylvanian) of Gibson County, Indiana, USA: *in* RHAMANI, R.A., and FLORES, R.M., eds., Sedimentology of Coal and Coal-bearing Sequences: Special Publication, International Association of Sedimenologists, v. 7, p. 309–315.

EGGERT, D.L., and ADAMS, S.C., 1984, Distribution of fluvial channel systems contemporaneous with the Springfield Coal Member (middle Pennsylvanian) in southwestern Indiana: Compte Rendu, 9th International Congress of Carboniferous Stratigraphy and Geology, v. 4, p. 342–348.

EGGERT, D.L., CHOU, C.-L., MAPLES, C.G., PEPPERS, R.A., PHILLIPS, T.L., and REXROAD, C.B., 1983, Origin and economic geology of the Springfield Coal Member in the Illinois Basin (Field Trip 9): 1983 Field Trips in Midwestern Geology, v. 2, p. 121–146.

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.

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

GASTALDO, R.A., PFEFFERKORN, H.W., and DiMICHELE, W.A., 1995, Taphonomic and sedimnetologic characterization of roof-shale floras: *in* LYONS, R.C., MOREY, E.D., and WAGNER, R.H., eds., Historical Perspective of Early Twentieth Century Carboniferous Paleobotany in North America (W.C. Darrah Volume): Boulder, Colorado, Geological Society of America Memoir, v. 185, p. 341–352.

HOLMES, J., and SCOTT, A.C., 1981, A note on the occurrence of marine animal remains in a Lancashire coal ball (Westphalian A): Geological Magazine, v. 118, p. 307–308.

HOWER, J.C., EBLE, C.F., and RATHBONE, R.F., 1994, Petrology and palynology of the No. 5 Block coal bed, northeastern Kentucky: International Journal of Coal Geology, v. 25, p. 171–193.

LAMBOY, W., and LESNIKOWSKA, A.D., 1988, Some statistical methods useful in the analysis of plant paleoecological data: PALAIOS, v. 3, p. 86–94.

LEISMAN, G.A., 1960, The morphology and anatomy of *Callipteridium sullivantii*: American Journal of Botany, v. 47, p. 281–287.

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, Champaign-Urbana, 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.

MICKLE, J.E., and ROTHWELL, G.W., 1982, Permineralized *Alethopteris* from the Upper Pennsylvanian of Ohio and Illinois: Journal of Paleontology, v. 56, p. 392–402.

OESTRY-STIDD, L.L., 1979, Anatomically preserved *Neuropteris rarinervis* from American coal balls: Journal of Paleontology, v. 53, p. 37–43.

PFEFFERKORN, H.W., and THOMSON, M.C., 1982, Changes in dominance patterns in Upper Carboniferous plant-fossil assemblages: Geology, v. 10, p. 641–644.

PHILLIPS, T.L., and CROSS, A.T., 1991, Paleobotany and paleoecology of coal: *in* GLUSKOTER, H.J., RICE, D.D., and TAYLOR, R.B., eds., Economic Geology, U.S.: The Geology of North America, v. P-2, p. 483–502.

PHILLIPS, T.L., and DiMICHELE, W.A., 1981, Paleoecology of Middle Pennsylvanian age coal swamps in southern Illinois—Herrin Coal Member at Sahara Mine No. 6: *in* NIKLAS, K.J., ed., Paleobotany, Paleoecology, and Evolution: Praeger Press, New York, v. 1, p. 231–284.

PHILLIPS, T.L., PFEFFERKORN, H.W., and PEPPERS, R.A., 1973, Development of paleobotany in the Illinois Basin: Illinois State Geological Survey Circular, v. 480, p. 1–86.

PHILLIPS, T.L., KUNZ, A.B., and MICKISH, D.L., 1977, Paleobotany of permineralized peat (coal balls) from the Herrin (No. 6) Coal Member of the Illinois Basin: *in* GIVEN, P.N., and COHEN, A.D., eds., Interdisciplinary Studies of Peat and Coal Origins: Geological Society of America, Microform Publication, v. 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 inferences: International Journal of Coal Geology, v. 5, p. 43–109.

PIGG, K.B., TAYLOR, T.N., and STOCKEY, R.A., 1987, Paleozoic seed ferns: *Heterangium kentuckyensis* sp. nov. from the Upper Carboniferous of North America: American Journal of Botany, v. 74, p. 1184–1204.

PRYOR, J.S., 1990, Delimiting species among permineralized medullosan pteridosperms: A plant bearing *Alethopteris* fronds from the Upper Pennsylvanian of the Appalachian basin: Canadian Journal of Botany, v. 68. p. 184–192.

PRYOR, J.S., 1993, Patterns of ecological succession within the Upper Pennsylvanian Duquesne coal of Ohio (USA): Evolutionary Trends in Plants, v. 7, p. 57–66.

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.

REXROAD, C.B., 1993, Conodonts from coal balls in the Springfield coal bed member of the Petersburg Formation (Desmoinesian, Pennsylvanian) in southern Indiana: Proceedings of the Indiana Academy of Sciences, v. 102, p. 83–91.

ROTHWELL, G.W., 1981, The Callistophytales (Pteridospermopsida): reproductively sophisticated Paleozoic gymnosperms: Review of Palaeobotany and Palynology, v. 32, p. 103–121.

ROTHWELL, G.W., and BLICKLE, A., 1982, *Psaronius magnificus* n. comb., a marattialean fern from the Upper Pennsylvanian of North America: Journal of Paleontology, v. 56, p. 459–468.

SCOTT, A.C., 1978, Sedimentological and ecological control of Westphalian B plant assemblages from West Yorkshire: Proceedings of the Yorkshire Geological Society, v. 41, p. 461–508.

SCOTT, A.C., and REX, G., 1985, The formation and significance of Carboniferous coal balls: Philosophical Transactions of the Royal Society, Series B, v. 311, p. 123–137.

STIDD, B.M., OESTRY, L.L., and PHILLIPS, T.L., 1975, On the frond of *Sutcliffia insignis* var. *tuberculata*: Review of Palaeobotany and Palynology, v. 20, p. 55–66.

THOMAS, B.A., 1967, *Ulodendron*: Lindley and Hutton and its cuticle: Annals of Botany, v. 31, p. 775–782.

WILKINSON, L., HILL, M., WELNS, J.P., and BIRKENBEUEL, G.K., 1992, SYSTAT for Windows: Statistics, Version 5 Edition: SYSTAT Inc., Evanston, Illinois, 750 pp.

WILLARD, D.A., 1989a, Source plants for Carboniferous microspores: *Lycospora* from permineralized *Lepidostrobus*: American Journal of Botany, v. 76, p. 820–827.

WILLARD, D.A., 1989b, *Lycospora* from Carboniferous *Lepidostrobus* compressions: American Journal of Botany, v. 76, p. 1429–1440.

WILLARD, D.A., 1993, Vegetational patterns in the Springfield Coal (Middle Pennsylvanian, Illinois Basin): Comparison of miospore and coal-ball records: *in* COBB, J.C., and CECIL, C.B., eds., Modern and Ancient Coal-forming Environments: Geological Society of America Special Paper 286, p. 139–152.

WILLARD, D.A., DiMICHELE, W.A., EGGERT, D.L., HOWER, J.C., REXROAD, C.B., and SCOTT, A.C., 1995, Paleoecology of the Springfield Coal Member (Desmoinesian, Illinois Basin) near the Leslie Cemetery paleochannel, southwestern Indiana: International Journal of Coal Geology, v. 27, p. 59–98.

ZARITSKY, P.V., 1968, The occurrence of so-called faunistic and mixed coal balls in the coals of the Donets Basin: Doklady Akademii Nauk S.S.S.R., v. 180, p. 707–709.