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Place vs. time and vegetational persistence: a comparison of four tropical mires from the Illinois Basin during the height of the Pennsylvanian Ice Age

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Abstract

Coal balls were collected from four coal beds in the southeastern part of the Illinois Basin. Collections were made from the Springfield, Herrin, and Baker coals in western Kentucky, and from the Danville Coal in southwestern Indiana. These four coal beds are among the principal mineable coals of the Illinois Basin and belong to the Carbondale and Shelburn Formations of late Middle Pennsylvanian age. Vegetational composition was analyzed quantitatively. Coal-ball samples from the Springfield, Herrin, and Baker are dominated by the lycopsid tree *Lepidophloios*, with lesser numbers of *Psaronius* tree ferns, medullosan pteridosperms, and the lycopsid trees *Synchysidendron* and *Diaphorodendron*. This vegetation is similar to that found in the Springfield and Herrin coals elsewhere in the Illinois Basin, as reported in previous studies. The Danville coal sample, which is considerably smaller than the others, is dominated by *Psaronius* with the lycopsids *Sigillaria* and *Synchysidendron* as subdominants.

Coal balls from the Springfield coal were collected in zones directly from the coal bed and their zone-by-zone composition indicates three to four distinct plant assemblages. The other coals were analyzed as whole-seam random samples, averaging the landscape composition of the parent mire environments. This analysis indicates that these coals, separated from each other by marine and terrestrial-clastic deposits, have essentially the same floristic composition and, thus, appear to represent a common species pool that persisted throughout the late Middle Pennsylvanian, despite changes in baselevel and climate attendant the glacial–interglacial cyclicality of the Pennsylvanian ice age. Patterns of species abundance and diversity are much the same for the Springfield, Herrin, and Baker, although each coal, both in the local area sampled, and regionally, has its own paleobotanical peculiarities. Despite minor differences, these coals indicate a high degree of recurrence of assemblage and landscape organization. The Danville departs dramatically from the dominance–diversity composition of the older coals, presaging patterns of tree–fern and *Sigillaria* dominance of Late Pennsylvanian coals of the eastern United States, but, nonetheless, built on a species pool shared with the older coals.

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1. Introduction

The Pennsylvanian Period of the late Paleozoic has long been recognized as a time of major polar glaciation, concentrated in the southern hemisphere. During this long “ice age,” there were many intervals of glacial advance and retreat (Weller, 1930; Wanless and Weller, 1932), each accompanied by climatic changes throughout the globe (Cecil, 1990). While ice waxed and waned at the poles, major peat-forming mires developed at tropical latitudes, which, undoubtedly, experienced climatic variations as a result of the changes in ice volume. In the latter part of the Middle Pennsylvanian (late Westphalian D), these mires most often corresponded to onset of transgressions following sea-level lowstand, the juncture between glacial maxima and interglacials (Heckel, 1980, 1989). The climate and baselevel effects of glacio-eustasy were superimposed on tectonic movements, which had regional effects on both sea level and sedimentary patterns. The tropical Illinois basin records the interplay of both factors (Langenheim and Nelson, 1992).

The objective of this paper is to examine the similarities and differences of flora and vegetation among four temporally successive mires (“coal swamps”) from the same geographic area. The mires in question are represented today by four economically important coals in the southeastern Illinois Basin, presently western Kentucky and southwestern Indiana (Fig. 1). In stratigraphic order, these are the Springfield, Herrin, Baker, and Danville coal beds (Shaver et al., 1986; Greb et al., 1992; Eble et al., 2001); the Springfield and Herrin coals are in the Carbondale Formation, the Baker and Danville in the Shelburn Formation (Fig. 2).

The vegetation of Carbondale Formation coals is known from the study of fossil spores and pollen preserved in the coal (e.g., Peppers 1996) and from macrofossils preserved in coal balls. Compression–impression fossils, commonly preserved in mudstones and other strata that separate coal beds, generally do not represent peat-forming vegetation, although there are clear ecological and evolutionary relationships and some degree of species overlap (Gastaldo et al., 1995). Data from all sources suggest that vegetation of the Illinois Basin remained remarkably stable through repeated intervals of sea-level and associated climatic changes, either reassembling from refugial

areas or tracking climate to an indeterminate degree, accounting for the recurrence of similar floras and vegetation under similar conditions in successive glacial–interglacial oscillations (DiMichele et al., 1996). However, the late Middle Pennsylvanian of the American midcontinent has its own, unique vegetational signature that contrasts with that of earlier Middle Pennsylvanian mires and of the Late Pennsylvanian. Thus, there is strong evidence against gradually changing species pools. Instead, species pools appear to have turned over rapidly between several intervals of greater stability during which there were lower levels of background origination and extinction. As long as species turnover was low, vegetational structure appears to have been conserved, suggesting some degree of self-regulation, related to, or perhaps simply more recognizable as a consequence of, the ecological peculiarities of the time (DiMichele and Phillips, 1996a,b; DiMichele et al., 2001).

2. Geologic setting

Coal balls for this investigation were collected at four sites: one in southwestern Indiana and three in western Kentucky (Fig. 1). Geologically, these sites are in the Illinois Basin, also known as the Eastern Interior Basin. The basin covers much of Illinois along with southwestern Indiana and western Kentucky. The Illinois Basin is divided into two parts of unequal size by the Rough Creek Fault System. The larger northern part is known as the Fairfield Basin, and the smaller southern part is the Moorman Syncline (Fig. 1). Our Indiana collecting locality is on the eastern shelf of the Fairfield Basin, whereas our three sites in Kentucky lie a short distance south of the axis of the Moorman Syncline. In the western Kentucky study area a fault zone trending ENE, part of the Central Fault Zone, passes about 16 km south of the coal-ball collecting area. These faults appear to have been active during deposition of the strata between the Springfield and Herrin coals, and inactive or only slightly active thereafter (Rogers, 1985). Evidence in support of this interpretation includes thickening of the Kentucky No. 10 coal bed on downthrown blocks, and the localization of sandstones in a graben along the fault zone. The entire Rough Creek Graben, of which the Central Fault Zone is a part, was active

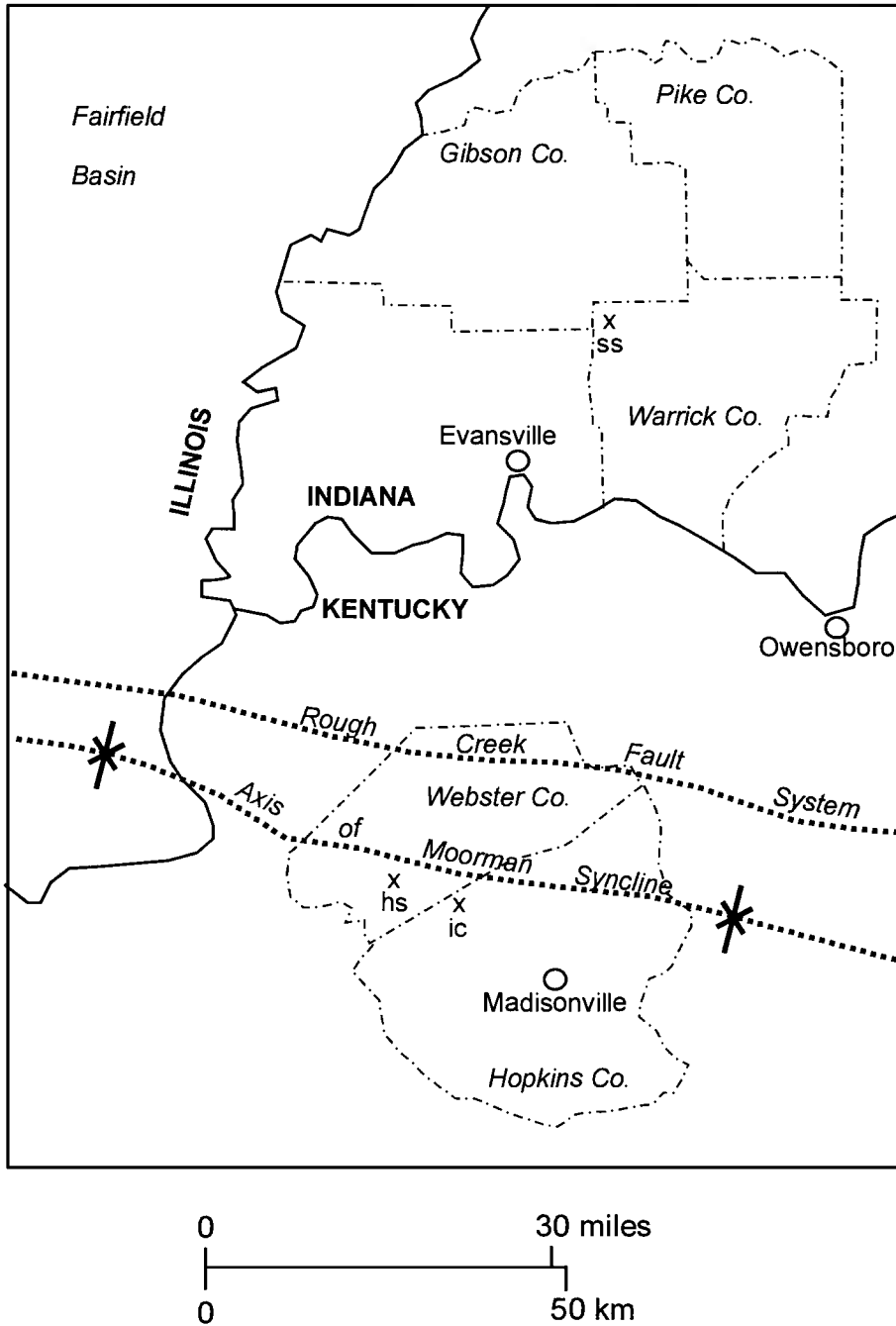


Fig. 1. Location map showing mines where coal balls were collected. hs=Hart & Hart, and J. Smith mines (same location), ic=Island Creek mine, ss=Solar Sources mine.

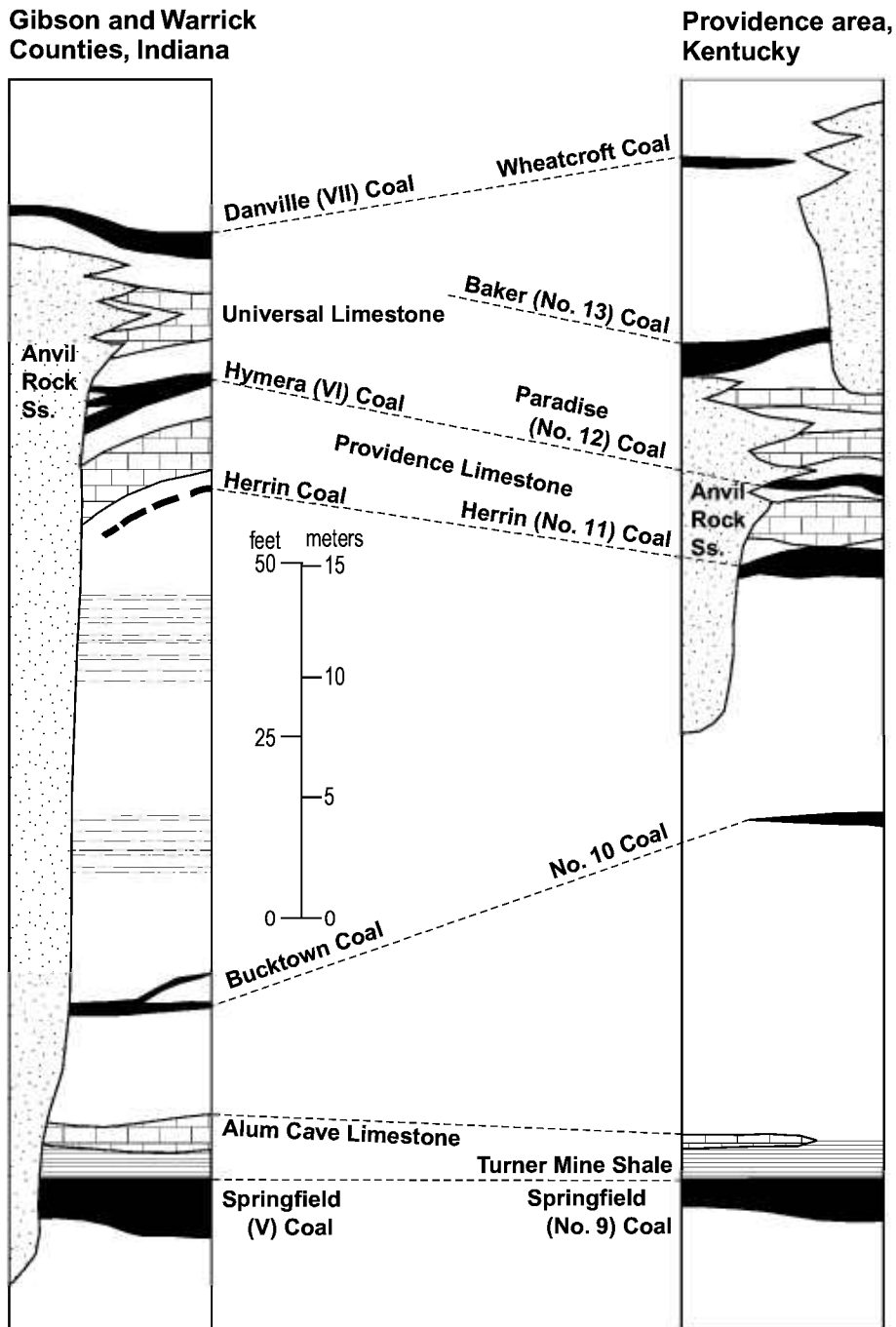


Fig. 2. Stratigraphic columns for the collecting areas. Indiana column based on Wier (1951, 1958) and Eggert (1994); Kentucky column based on Kehn (1966) and Greb et al. (1992). Names of coal beds and other units differ between the states. The Danville and Hymera coals in Indiana previously were called, respectively, the Upper and Lower Millersburg coals.

recurrently throughout Pennsylvanian time (Nelson and Lumm, 1987).

Nearly all of the coal mined in the Illinois Basin comes from rocks of the Desmoinesian or Middle Pennsylvanian age, which is correlative with the Westphalian D Stage of the Upper Carboniferous in western Europe. Coal that is mined occurs in beds 1–4 m thick and is of high-volatile bituminous rank. Most coal in the Illinois Basin is overlain by marine shale or limestone and has a moderate (8–20%) ash yield and high (3–5%) sulfur content. Low-sulfur coal (less than 2% sulfur) is mostly localized in areas where the coal is overlain by non-marine rocks.

The coal balls examined for this study came from four of the most important mineable coal beds in the Desmoinesian Series: the Springfield, Herrin, Baker, and Danville Coals (Fig. 2).

2.1. Springfield coal

Our collection from the Springfield coal was obtained at the Providence No. 1 mine of Island Creek Coal, an underground mine located about midway between Nebo and Providence, Hopkins County, KY. The Providence No. 1 Mine operated by conventional room-and-pillar methods at a depth of 75–90 m below the surface. Large accumulations of coal balls were encountered that hindered mining. On February 26, 1987, Phillips and DiMichele, accompanied by Debra Willard and Phillip J. DeMaris, collected coal balls directly from the working face of the mine.

Three large clusters of coal balls were encountered at the working face of the Providence No. 1 Mine. The largest cluster, where the collection was made, had a core of concentrated coal balls roughly circular in map view and 25–30 m in diameter, surrounded by a rim 3–5 m wide containing scattered coal balls. Two smaller concentrations of coal balls were partially exposed by mining close to the mass that was sampled.

In the area of the Nebo Quadrangle where the coal balls were collected, the Springfield coal ranged from 1.1 to 1.8 m thick (Franklin, 1969). As is typical throughout western Kentucky, the floor was claystone (underclay) and the immediate roof was black, fissile shale (Turner Mine Shale). Above this were clastic strata that coarsened upward from shale to siltstone to sandstone (Rogers, 1985). DeMaris noted that the roof shale near the coal balls contained many large spheroidal

limestone concretions as large as 1 m in diameter. Such concretions are common in the Turner Mine Shale, but these were larger and more numerous than usual.

2.2. Herrin coal

Also, on February 26, 1987, coal balls were collected from the tippel of the Jim Smith Mine, about one mile northwest of Providence in Webster County, KY. The J. Smith Mine was a surface mine that operated in the Herrin (Western Kentucky No. 11) Coal and Baker (Western Kentucky No. 13) Coal.

In this area, the Herrin Coal is generally 1.5–1.8 m thick (Kehn, 1966), and contains the “blue band,” a layer of claystone 5–15 cm thick, about 0.3 m above the base of the coal. The floor is claystone. The immediate roof is dark gray to black, carbonaceous shale, which is subsequently overlain by the Providence Limestone Member. The limestone consists of one or two benches of gray, argillaceous limestone with a marine fauna; it is correlative with the Brereton Limestone of Illinois (Greb et al., 1992).

Because we did not see coal balls in the coal seam at the J. Smith Mine, we do not know what geologic features accompanied them. No faults, paleochannels, or other geologic anomalies are indicated on the geologic quadrangle map (Kehn, 1966).

2.3. Baker coal

Several tons of coal balls were collected in the late 1960s by T.L. Phillips and his students from a waste pile at the abandoned Hart and Hart Coal surface mine (a predecessor to the J. Smith Mine) in the Baker (Western Kentucky No. 13) Coal. The coal balls were mostly concentrated next to a weathered coal exposure and some aggregates could have been essentially in situ, as bypassed obstacles to mining. The location is essentially the same as that of the J. Smith Mine, cited above.

The Providence geologic quadrangle map (Kehn, 1966) shows the outcrop of the Baker Coal and extensive strip mines that operated in this coal. These mines may include Hart and Hart operations, but are not identified specifically. On the stratigraphic column of Kehn's (1966) map, the Baker Coal is shown to vary from 0 to 2.7 m thick. In the adjacent Nebo Quadrangle, a short distance southeast of the area where coal balls were collected, the Baker Coal ranged from 1.1 to 3 m

thick, but was thicker than 1.8 m throughout most of the quadrangle, and splits toward the southeast (Rogers, 1985). The floor may be limestone, shale, or sandstone; the roof is siltstone. The Baker Coal is reported to contain partings and thin interbeds of pyritic or carbonaceous shale and mudstone, and in places is cut out and replaced by sandstone (Kehn, 1966).

Greb et al. (1992) report that although the Baker Coal is not widespread in western Kentucky, the seam is thick and has good quality; the coal block is thickest in belts parallel to paleochannels filled by the Anvil Rock Sandstone. Claystone partings in the Baker Coal thicken toward the channels. The typical roof stratum is either gray silty shale, containing well preserved carbonized fossil plants and “kettlebottoms” (fossil tree stumps), or fine grained sandstone. Based on the geometry of the Baker coal and associated beds, Greb et al. (1992) suggested that the mire may have developed on a flood plain of the Anvil Rock channel system.

2.4. Danville coal

About 1995, a collection of coal balls was presented to T.L. Phillips by D.L. Eggert, then of the Indiana Geological Survey. The coal balls were from the Danville Coal and were collected directly from the coal face at a surface mine operated by Solar Sources, near the town of Elberfeld of northwestern Warrick County, IN (Fig. 1) (Indiana Geological Survey, 2001).

A map by Wier (1958) shows the outcrop of the Lower Millersburg Coal (now called Danville (VII) Coal) and many surface- and deep-mined areas in northwestern Warrick County. In Gibson County, which borders Warrick County on the northwest (Fig. 1), Eggert (1994) reports that the Danville Coal varies from 0.4 to 1.2 m thick and has a moderate ash yield (9–23%) and high (3–5.9%) sulfur content. Eggert (1994, p. 23) states, “. . .the (Danville) coal likely formed from a peat that was deposited in the bay region of a delta. The high sulfur indicates that the peat was exposed to brackish to marine water during or after deposition.”

3. Materials and methods

This study is based on fossil plant remains preserved in coal balls. Coal balls are peat stages of coal,

commonly spheroidal or lens-shaped, and found within coal seams, that were permineralized by calcite, pyrite, or silica prior to significant peat compaction (Phillips et al., 1985; Scott and Rex, 1985). They preserve in microscopic detail the remains of the plants that formed the vegetation of the original mire, including leaves, stems, reproductive organs, and root systems (Phillips et al., 1976). All coal balls examined in this study were preserved as calcium carbonate permineralizations. Organic matter, represented by plant-cell walls, is embedded in the carbonate coal-ball matrix. Plant remains vary in degree of compression and decay, but early diagenetic preservation is indicated by fine tissue details and often minimal decay. Despite early entombment by carbonate, the plant cell walls preserved in coal balls are, nonetheless, coalified to the same rank as the coal bed in which they occur (Lyons et al., 1985). Because of their often exquisite preservation, coal balls have long attracted the attention of paleobotanists (Phillips et al., 1973) and have served to reveal more details of the original composition of Pennsylvanian coals than any other source of information (Phillips and Peppers, 1984; Scott and Rex, 1985).

For this study, the vegetational and plant-organ composition of coal balls was determined quantitatively using a modification of the method developed by Phillips et al. (1976; updated method described in Phillips and DiMichele, 1999). Coal balls were sliced into slabs and the center slab of each was selected for quantitative analysis. The sawed surfaces were etched in a 5% solution of hydrochloric acid, which removes a small amount of the carbonate and leaves the cell walls slightly exposed. The etched surface was flooded with acetone and a clear sheet of thin cellulose acetate was placed on the surface; the acetone softens the acetate, which then envelops the exposed cell walls. Upon drying the acetate film was removed (peeled—hence the reference to the “peel technique”) to provide a thin section of the coal-ball plant material. A 1 cm² grid of clear cellulose acetate was attached to each coal-ball peel. Within each square centimeter, the most common plant part and its taxonomic affinity were identified and recorded, as were the presence of fusain and pyrite, and the male–female affinities of reproductive organs.

Data were summarized by sampling unit: by coal ball for the Danville coal, by coal-ball zone for the Springfield coal, and by whole seam for the Herrin

and Baker coals. A whole-seam random sample of the Springfield coal was created from the profile by averaging taxonomic composition across coal-ball zones. A random sample of the Danville coal was derived by summing the taxonomic counts across the entire coal-ball sample, which then was divided by the total sample size.

Quantitative abundance is reported as whole-plant taxa. Because many plants fall apart after death or during storms, organs, such as stems, leaves, reproductive structures and roots, are usually found isolated, not in attachment to one another. Thus, each “whole plant” represents a summary of organs attributable to a single source plant. Such source plants often are species, but sometimes genera, depending on what is known of the relationships among dispersed organs. In order to calculate relative whole-plant abundances, all unidentified material, 50% of all *Psaronius* roots from the outer mantle, and all roots of lycopsids, pteridosperms, cordaites,

and sphenopsids were removed from the analysis; all fern roots, except those from the inner root mantle of *Psaronius*, also were removed from the biomass calculations. Roots are removed because they may have penetrated from plant communities that developed at a different time from those that produced the aerial litter (except for *Psaronius* inner roots, which are all aerial, and a portion of *Psaronius* outer roots, which are both aerial and penetrate the subsurface). The remaining abundances were added and normalized to 100% identified, accounting for the deleted fraction.

Abundances of fusain and unidentified material are reported separately and reflect percentages in the entire data sets, prior to the deletion of roots and unidentified.

The following data sets were analyzed. All specimens or peels thereof are housed in the Paleobotanical Collections, Department of Plant Biology, University of Illinois, Urbana–Champaign.



Fig. 3. Coal ball from the Springfield coal. Magnification, $\times 1$. Peat is distinctly layered and plant organs are flattened. (1) *Synchysidendron resinosum* axis with leaf cushions. (2) *Lepidophloios hallii* axis: periderm and leaf cushions. (3) *Myeloxylon* (rachis of medullosan pteridosperms) remains. University of Illinois (UI) specimen 36431 D top.

• Springfield coal, Island Creek's Providence No. 1 Mine. The mine is located at 37°23' N, 87°42' W, corresponding approximately to Carter section Sec. 8-K-22, Hopkins County, KY, Nebo 7.5-minute quadrangle. Profile No. 1. Coal-ball numbers 36418–36619, divided into 13 coal-ball collecting intervals (layers), hereafter referred to as zones. Coal-ball zones were determined on the basis of lateral continuity of concretions, characteristic sizes of some coal balls, coal partings, and distinct benches of coal. The collection consists of 202 coal balls with a total middle-peel sampling area of 11,299 cm².

• Herrin Coal, J. Smith Mine. Random Sample No. 1. The tippel of this mine was located at 37°24' 52.5" N, 87°46' 9" W, which corresponds to the NE quarter of Carter section 2-K-21 on the Providence 7.5-minute quadrangle, Webster County, KY. Coal-ball numbers 38100–38300. The collection consists of 210 coal balls with a total middle-peel sampling area of 13,503 cm².

• Baker Coal (Kentucky No. 13), Hart and Hart Coal. Random Sample No. 1. Coal-ball numbers 36628–36750. This mine was located at 37°24' 52.5" N, 87°46' 9" W, which corresponds to the NE

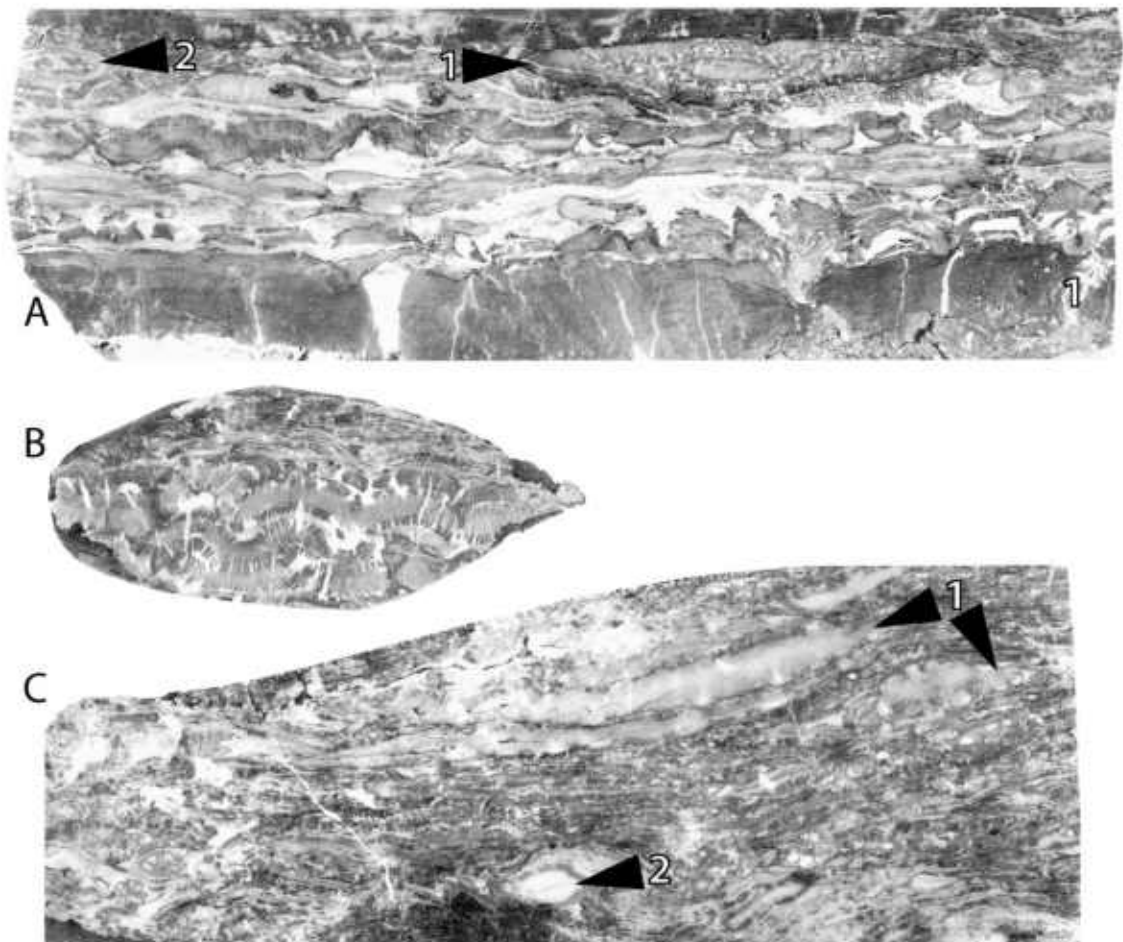


Fig. 4. Coal balls from the Springfield coal. All illustrated at $\times 1$ magnification. (A) Flattened, horizontally layered peat. UI 36574 D top. (1) *Diaphorodendron scleroticum*, stem at top, stem fragment with periderm across bottom. (2) *Etapteris* rachis segment, leaf of the fern *Zygopteris*. (B) Undulate periderm of *Sigillaria*. UI 36562 C. (C) Mixed assemblage with abundant detrital material. UI 36482 C. (1) *Hizemodendron serratum* stems. (2) *Pennsylvanioxydon* axis.

quarter of Carter section 2-K-21 on the Providence 7.5-minute quadrangle, Webster County, KY. The collection consists of 105 coal balls with a total middle-peel sampling area of 11,965 cm². Random Sample No. 2. Coal-ball numbers 37286–37330. The collection consists of 42 large coal balls with a total middle-peel sampling area of 14,738 cm².

• Danville Coal, Solar Sources Mine. Random Sample No. 1. The mine was located at 38°11' N, 87°23' W, in the NW 1/4 of Section 14 and the N 1/2 of Section 15, T4S, R9W of the Elberfeld 7.5-minute

quadrangle, Warrick County, IN. Coal-ball numbers 37105, 37108–37160. The collection consists of 54 coal balls with a total middle-peel sampling area of 2534 cm².

4. Fossil peat taphonomy

Taphonomy is the study of the processes that occur between the death of an organism and its ultimate recovery as a fossil. This can include study

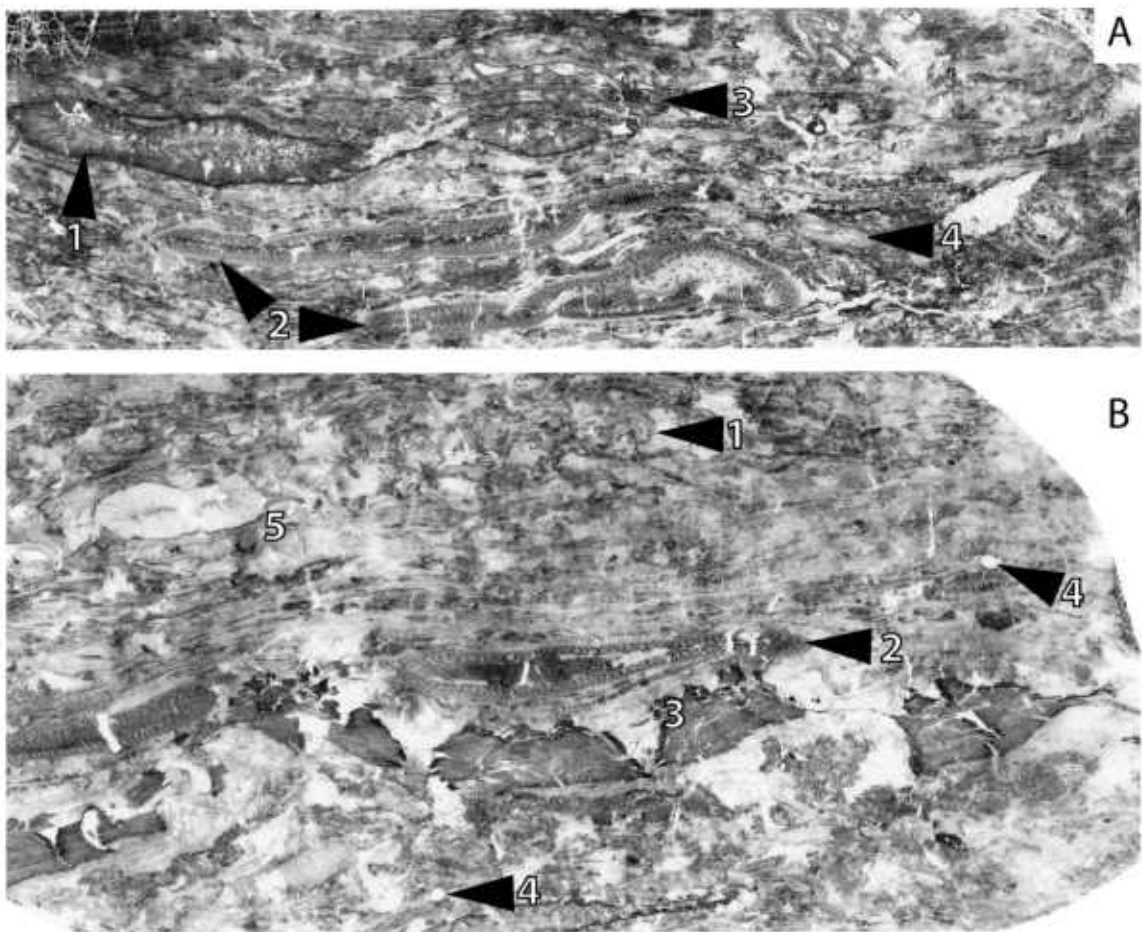


Fig. 5. Coal balls from the Herrin coal. Illustrated at $\times 1$ magnification. (A) Mixed assemblage. UI 36264 D top. (1) *D. scleroticum*. (2) *Myeloxylon*. (3) *Pachytesta* cf. *stewartii*, ovule of *Medullosa*. (4) *Callistophyton boyssetii*, a small ground cover pteridosperm. (B) Mixed assemblage. UI 36238 E top. (1) Inner root mantle of *Psaronius*, a marattalian tree fern. (2) *Myeloxylon*. (3) Outer periderm of *D. scleroticum*. (4) *Callospermarion* (*Taxospermum*), small ovule, probably attributable to *Callistophyton*. (5) Woody cylinder of a stigmarian axis, the rooting system of tree lycopsids.

of sedimentology and geochemistry, as well as the biological aspects of decay and diagenetic alteration (Behrensmeier et al., 1992).

Just as coal balls preserve a record of the parent vegetation of the mires in which they formed, they also

preserve information on physical conditions attendant accumulation and burial history of plant parts. However, the number of interacting variables is large, calling for caution when making interpretations (Covington and Raymond, 1989). Indicators of the ancient environ-

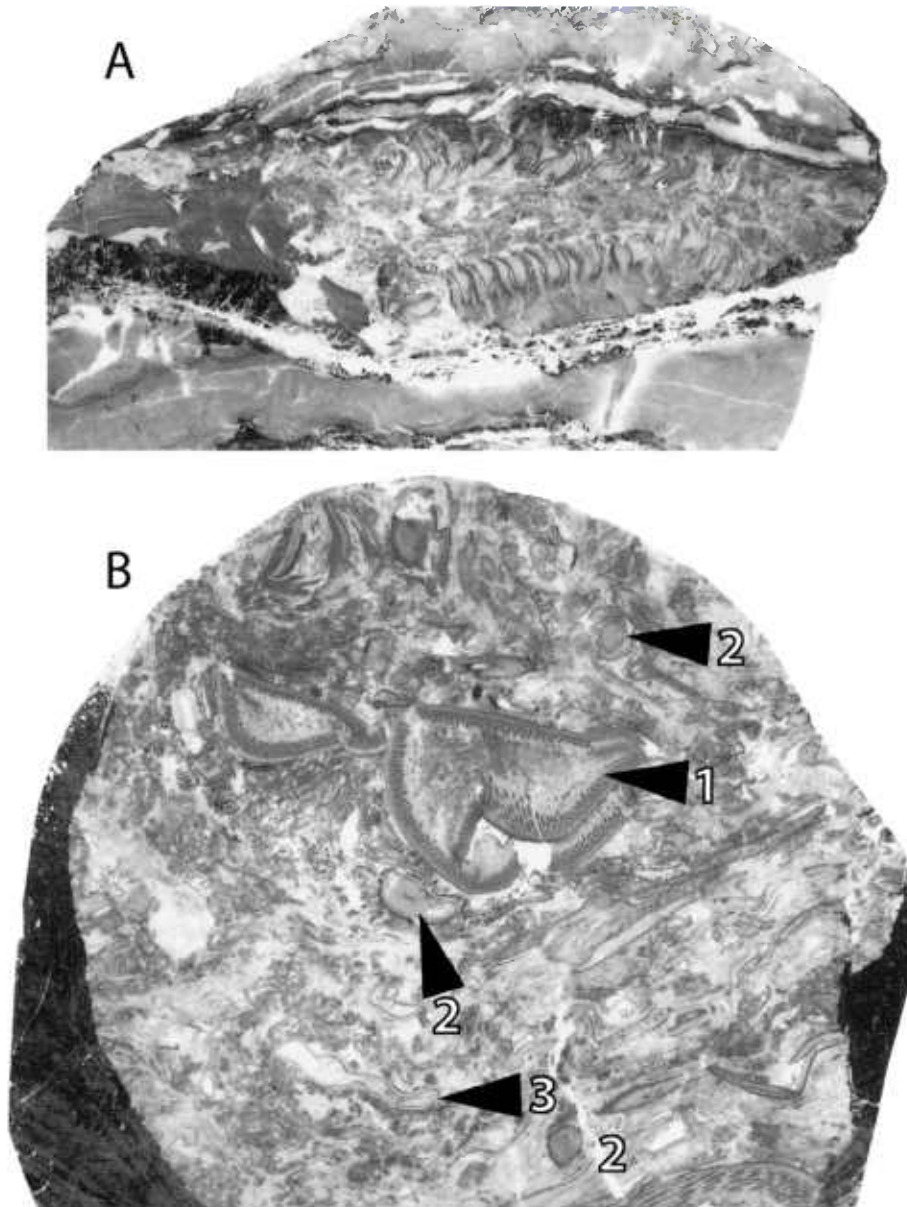


Fig. 6. Coal balls from the Herrin coal. Illustrated at $\times 1$ magnification. (A) *L. hallii* periderm and leaf cushions. UI 36267 A. (B) Mixed assemblage; peat is not flattened but plant axes are broken and orientations are irregular. UI 36290 F. (1) *Myeloxylon*. (2) *C. boyssetii*. (3) *Psaronius* roots from the outer root mantle. These are common in coal balls but, often, are highly flattened and thus difficult to recognize without magnification.

ment preserved in peat include such physical characteristics as charcoal content, indicative of fires, exposure zones often colonized by small plants, or the degree of peat decay. Charcoal is decay-resistant and can be widely transported or reworked. Decay can be inferred by analyses of root penetration (Raymond, 1987; Covington and Raymond, 1989; Pryor, 1993), framework-to-matrix ratio (the ratio of macroscopically preserved plant organs to highly degraded, fine-grained material), indicators of arthropod activity, or the simple preservational state of the plant organs.

The coal balls examined in this study represent an “isotaphonomic” sample. They are all from swampy, waterlogged environments, formed during interglacial periods in the tropics. All preserve plants that could tolerate the extreme conditions of peat substrates. Each sample was permineralized early in peat diagenesis. Yet, there are average preservational differences that must be

considered and that shed light on the some aspects of the prevailing physical conditions in each of the mires.

4.1. Springfield coal

Springfield coal balls (Figs. 3 and 4) were collected in 13 zones permitting intraseam variation to be observed. In general, plant parts within these coal balls frequently are broken and distinctly flattened, giving the fossil peat a very layered look. The layering is accentuated by large pieces of lycopsid bark, which evidently were shed in sheets after plant death. Another characteristic of these coal balls is the abundance of *Psaronius* roots from the outer root mantle, flattened almost to unrecognizability; tree fern outer roots were largely airspaces and thus could be flattened easily if peat burial was not rapid. Pyrite and small detrital matrix debris are common. Although stigmarian roots

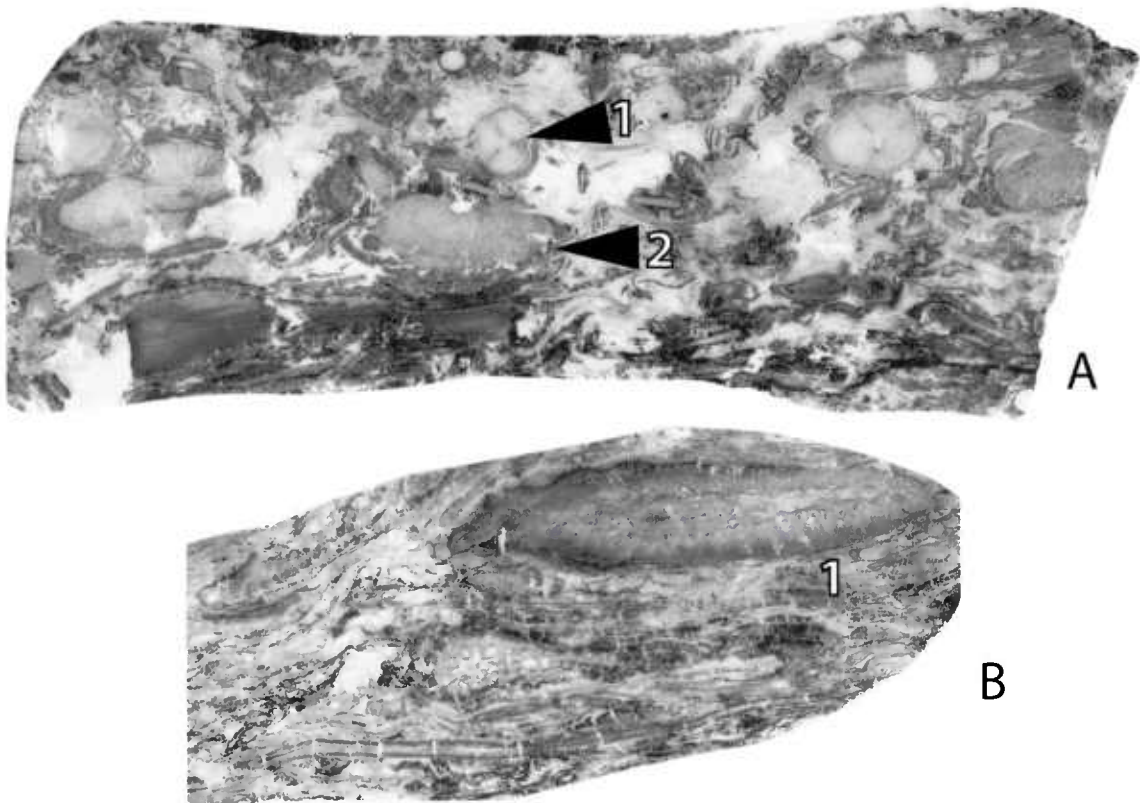


Fig. 7. Coal balls from the Herrin coal. (A) Mixed assemblage of the ground cover plants *Sphenophyllum plurifoliatum* (1), a sphenopsid, and *Callistophyton* (2). A layer of these axes runs across the face of the specimen. UI 36250 B bot. Magnified $\times 1.3$. (B) *S. resinosum* stems mixed with flattened outer roots of *Psaronius*. UI 36246 B bot. Magnified $\times 1$.

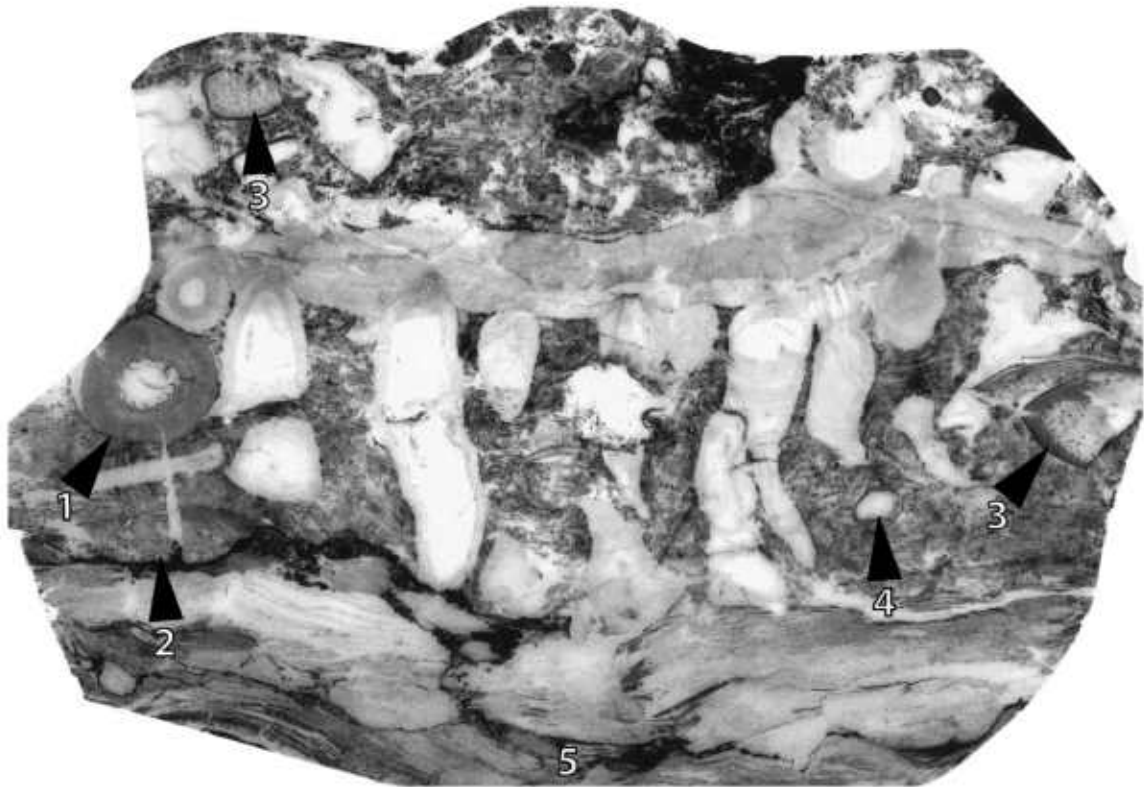


Fig. 8. Coal ball from the Baker coal. Magnified $\times 1$. Large stigmarian axis penetrating peat in upper half. Woody cylinder is visible in the center of the axis; rootlets radiate from both sides of the main axis. (1) *Pennsylvanioxylon* stem. (2) *S. resinosum* stem. (3) *Myeloxylon* rachises. (4) *Lepidocarpon*-megaspore complex of *Lepidophloios*. (5) *Lepidophloios* periderm. UI 36701 E top.

of lycopsid trees are common, they are rarely dense. Cellular preservation is variable. These factors suggest moderate rates of peat accumulation.

4.2. Herrin coal

Herrin coal fossil peats (Figs. 5–7) also may be flattened, but not as consistently as those from the Springfield coal sample. In some instances, flattening appears to have been minimal (Fig. 7A). Root penetration, qualitatively, is more complex than in the Springfield samples; often multiple generations of stigmarian rootlets can be identified. Like the Spring-

field, Herrin peats are high in fine-grained matrix debris. Cellular preservation is variable but can be very good. Unlike the Herrin at other sites where coal balls have been collected and reported (Phillips and DiMichele, 1981; DiMichele and Phillips, 1988), large fragments of lycopsid bark are rare. Many of these factors suggest surface rotting and relatively slow rates of accumulation, allowing repeated episodes of rooting.

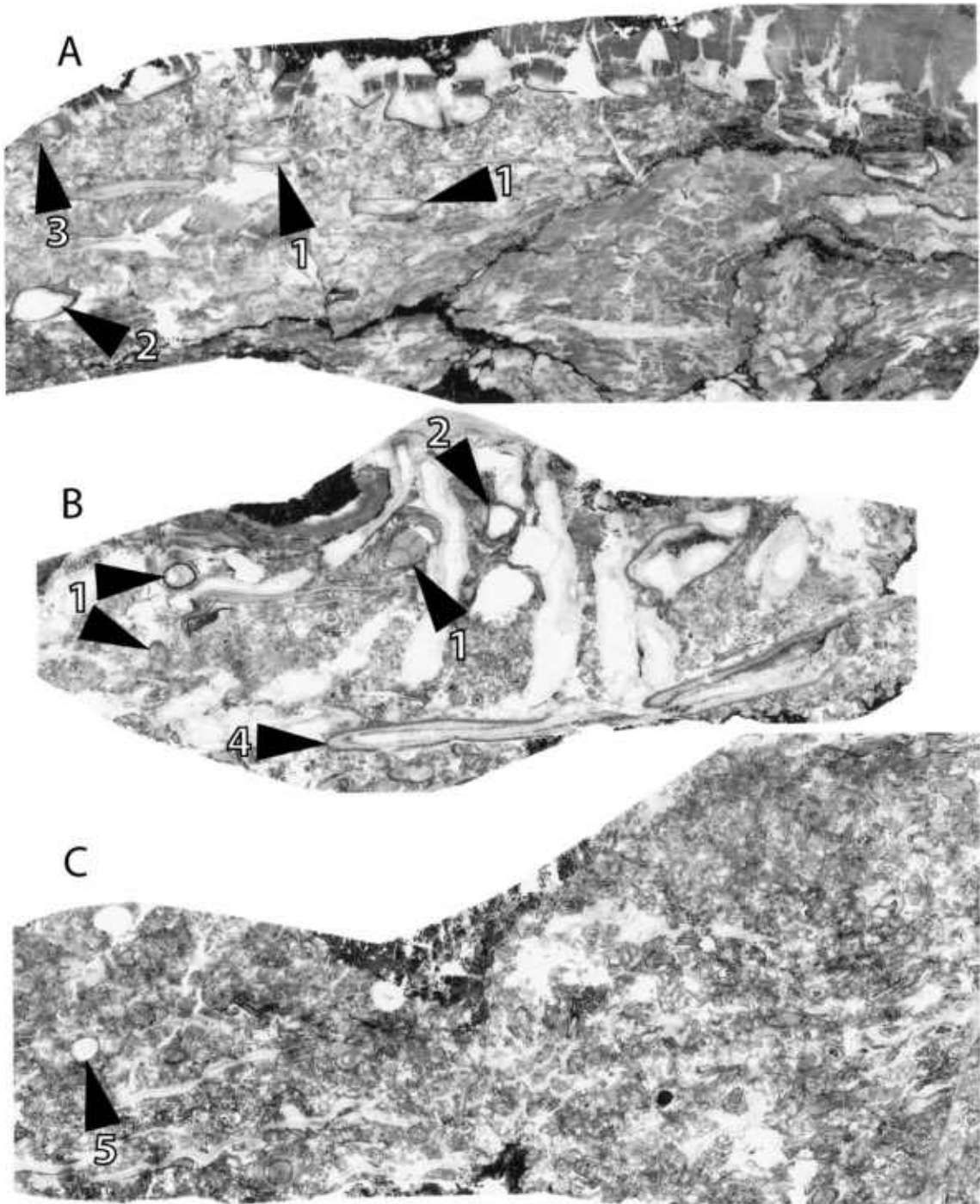
4.3. Baker coal

Fossil peats from the Baker coal are variable in character, suggesting that coal-balls from different

Fig. 9. Coal balls from the Baker coal. (A) Mass of ground cover, consisting mostly of *S. plurifoliatum* (1), with the small fern *Anachoropteris involuta* (3), sandwiched between *L. hallii* periderm fragments. The upper periderm fragment has leaf cushions attached. A specimen of *Lepidocarpon* (2) is also present. Magnified $\times 1$. UI 36644 B bot. (B) Peat composed of *Sphenophyllum* axes (1), penetrated by stigmarian rootlets. Other elements include *Stipitopteris* (4), the rachis of *Psaronius* tree ferns, and *Lepidocarpon* (2). Magnified $\times 1$. UI 36687 A. (C) Mass of *Sphenophyllum* stems. (5) *Callospermarion* ovule. Magnified $\times 1.5$. UI 36647 F bot.

layers, had we been able to collect them, would have varied considerably in character. Fig. 9 illustrates a layer of peat penetrated by a single generation of

lycopsid roots and a stigmarian axis, probably from *Lepidophloios* given its massive character. The degree of flattening in this specimen, or in any of the others



from Baker (Figs. 8–10) is minor. Masses of *Sphenophyllum* and *Chaloneria*, weakly flattened and sparsely root-penetrated (Fig. 9A–C; Fig. 10A–B), and the scarcity of large pieces of periderm, suggest relatively rapid rates of peat accumulation and burial. Such coal balls also indicate vegetation types with different accumulation and burial histories from the more typical lycopsid–medullosan–tree fern-rich assemblages. The rarity of layers of lycopsid periderm (bark) is significant; this material is highly resistant to decay and can be the only cellularly identifiable material in an otherwise highly rotted mass of peat. Note the typical lack of penetration of this tissue type by stigmarian rootlets (Fig. 8). Thus, its rarity in the Baker sample argues for limited surface rotting and relatively rapid peat accumulation compared to the other coals examined in this study.

4.4. Danville coal

Rooting and re-rooting are common in the Danville peats from this study. Roots, as the last organs of self-burial, frequently are the best preserved elements in a matrix of poorly preserved detrital material (Fig. 11A and C). Such roots, those of *Psaronius* in Fig. 11A, for example, can be barely flattened. Although Danville is a Middle Pennsylvanian coal, large masses of *Psaronius* outer roots resemble those of Late Pennsylvanian coals (compare with Fig. 4B of DiMichele and Phillips, 1994). Danville peats also commonly contain chunks of poorly preserved lycopsid bark (Fig. 12C). These factors point to intense rotting of the peat and slow accumulation rates.

4.5. Taphonomy summary

The Danville and Baker coals are the preservational extremes among the four coals examined. Danville peats appear to have accumulated slowly, indicated by periderm lags and heavy rooting. Baker

peats appear to have accumulated quickly, indicated by masses of sparsely rooted to unrooted ground cover and uncommonness of lycopsid bark lags. Springfield peats also appear to have accumulated rapidly, but flattening obscures many of the roots of tree ferns and lycopsids, and may have inflated the aerial component in quantitative analyses. In general, rooting in the four coals, on average, is not widely different. Shoot/root ratios for the four coals can be calculated in two ways. If aerial debris is treated as including all *Psaronius* inner roots and 1/2 of the *Psaronius* outer roots, and all unidentified tissues are removed from the calculation, the shoot/root ratios are as follows: 69.1% for the Springfield, 62.3% for the Herrin, 65.9% for the Baker, and 58.9% for the Danville.

5. Plant compositional patterns

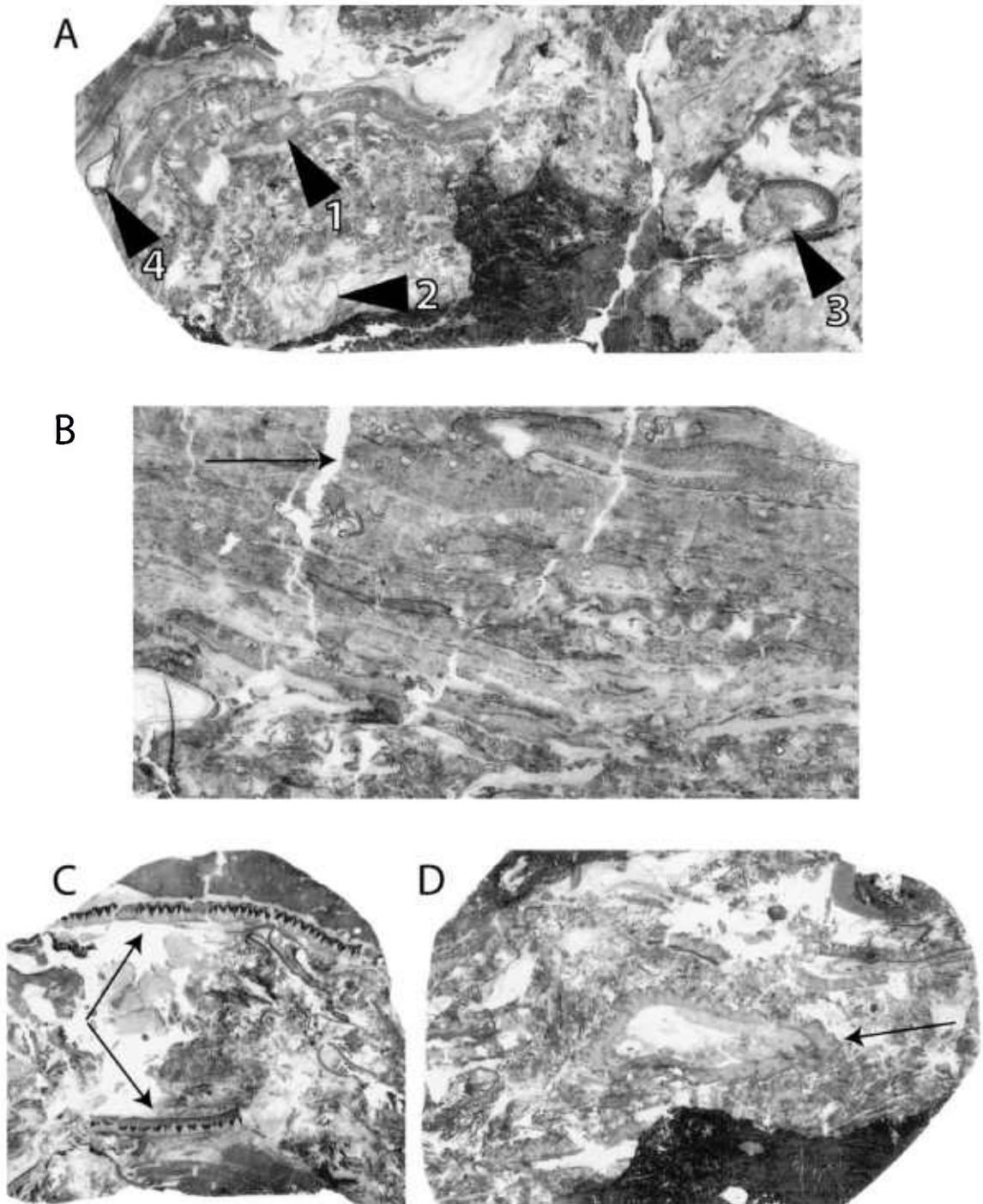
5.1. General floristic patterns

The floras of the four coals represented in this study arguably are drawn from the same species pool. A summary of taxonomic presence–absence by coal (Fig. 13) demonstrates that most of the common taxa are shared. Taxa in Fig. 13 are ranked so that the 10 most common and abundant forms are listed at the top; the top nine most abundant taxa are listed in Table 1, based on their rank order importance averaged across the four coals. All but one of these, *Sphenophyllum plurifoliatum*, were trees. Of the remaining 22 taxa, 15 are ground cover or small, upright, shrubs. The many taxa missing from the Danville Coal likely reflect the small size of the Danville random sample. There are only three taxa restricted to one of the four coals; in fact, two of these, *Lepidodendron mannabachense* and *Sublepidodendron sp.*, reported here from the Baker and Herrin coals, respectively, also are known from the Spring-

Fig. 10. Coal balls from the Baker coal. (A) Association of *Chaloneria* (*Polysporia*) (1) and *Sphenophyllum* (2), including *Myeloxylon* (3) and *Lepidocarpon* (4). Magnified $\times 1$. UI 36673 E top. (B) Mass of *Chaloneria* stems. Arrow points to dispersed *Valvisporites* megaspores of *Chaloneria*. Magnified $\times 2$. UI 36665 B top. (C) *S. resinosum* periderm fragments (arrows). The outer periderm (phellem) shows distinctive areas of expansion between leaf cushions, including cells filled with a resin-like substance. Inner periderm (phellogen) is present at the top of the specimen. Magnified $\times 1$. UI 36680 C top. (D) *S. resinosum* stems in detrital peat. Arrow points to largest specimen. These specimens lack resin-like material in cortical cells, pith cells, and in leaf-cushions interareas, which is generally present and helps facilitate recognition of this species. Magnified $\times 1$. UI 36662 C top.

field coal at other localities (DiMichele and Phillips, 1996a), demonstrating the broadly regional nature of this flora as well as its temporal persistence.

The four coals also have similar patterns of quantitative distribution of the component taxa, illustrated by dominance–diversity curves (Fig. 14), which are



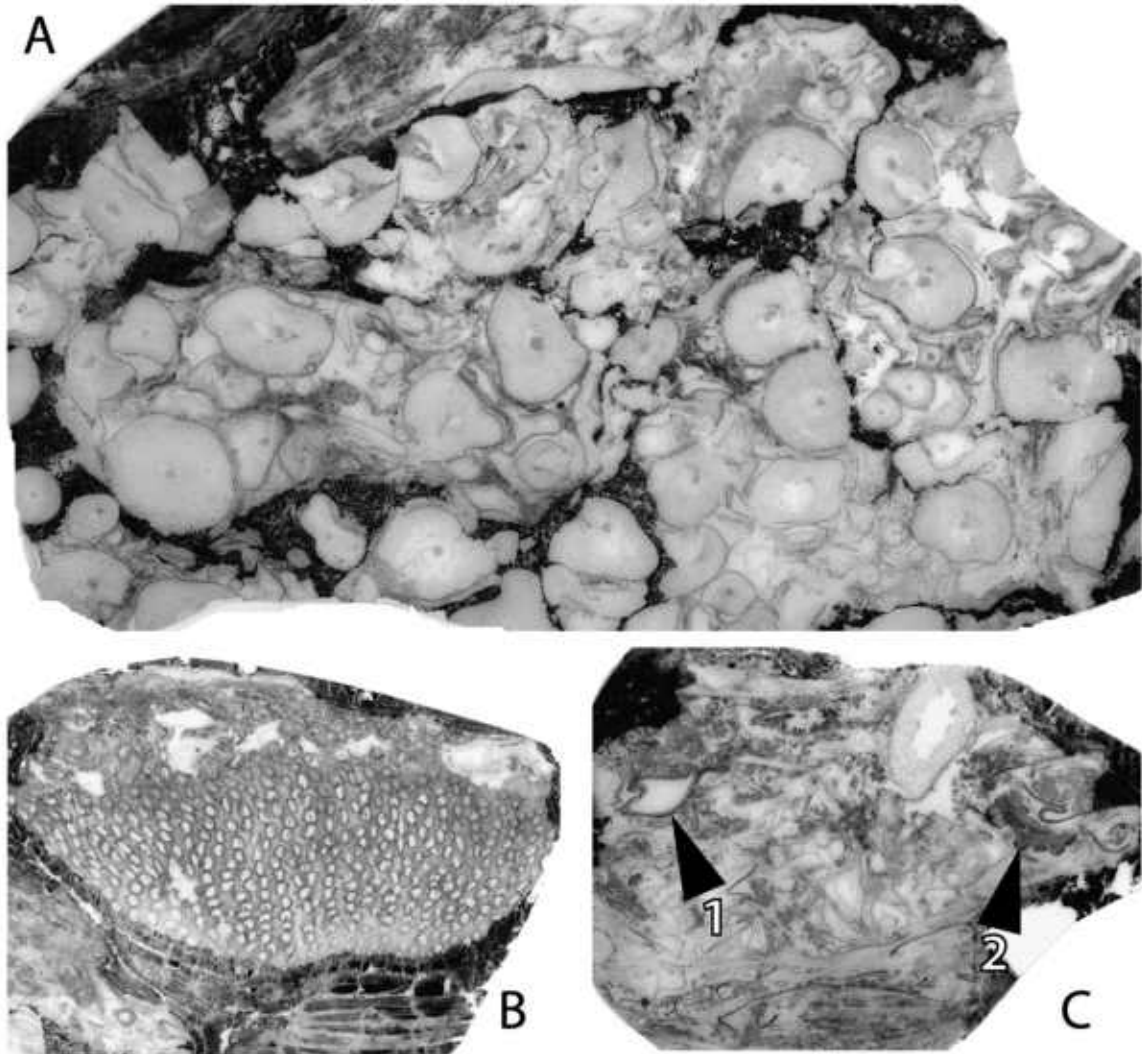


Fig. 11. Coal balls from the Danville coal. All magnified $\times 1$. (A) Mass of *Psaronius* outer roots. The size and minimal compression of these roots is most similar to those found in coal balls from Late Pennsylvanian coals and differs from coal balls of other coals examined in this study. UI 37135 B. (B) Fragment of the inner root mantle of *Psaronius*. UI 37137 D top. (C) *Psaronius* outer roots with *Lepidocarpon* (1) and a fragment of lycopsid stem, most likely *D. scleroticum*. UI 37132 C top.

basically similar in form. The large fraction of taxa with abundance percentages less than 1.0% indicates that sampling captured many of the rarer elements and thus likely reflects the basic rank-order dominance of taxa within each coal at the sample site.

On a quantitative level, the Danville stands out as distinct from the three other coals. A Pearson product moment correlation comparing the quantitative composition of all coals to each other (Table 2) shows

similarities among the Baker, Herrin, and Springfield coals of between 0.7 and 0.8, whereas similarities of any of these floras to those of the Danville ranges from about 0.4 to 0.5. The vegetation of the Danville differs from the other coals in terms of the taxa that are most abundant. Inspection of Table 3 shows that the dominant elements of the Baker, Herrin, and Springfield coals are *Lepidophloios hallii*, *Psaronius* spp., *Medullosa* spp., and either *Diaphorodendron*

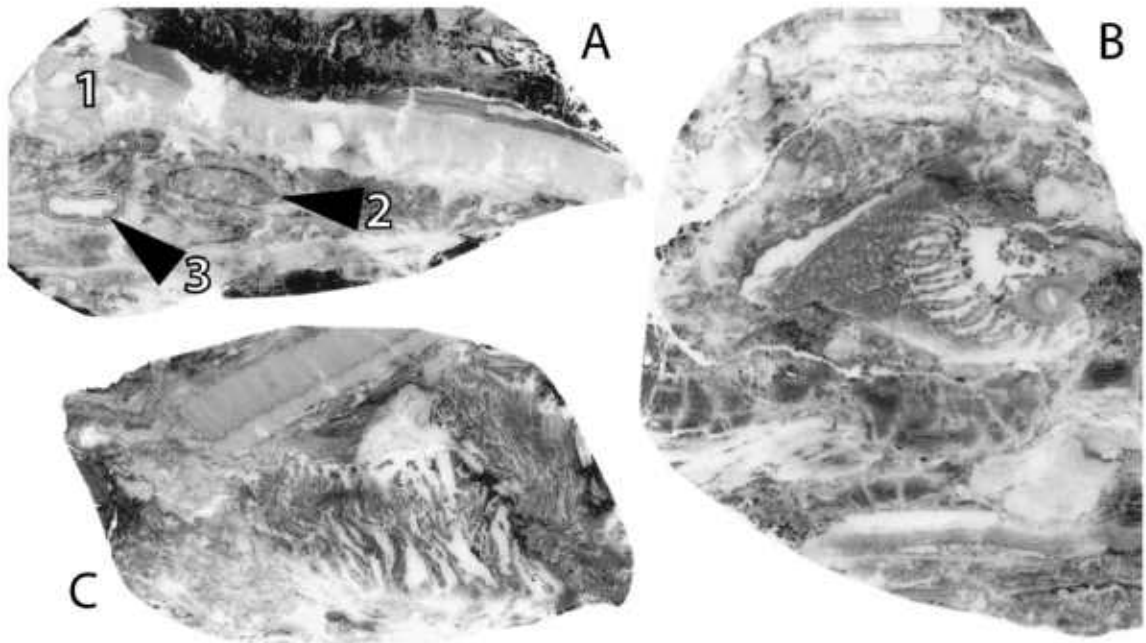


Fig. 12. Coal balls from the Danville coal. (A) Mixed assemblage. (1) Periderm of stigmarian axis. (2) *S. resinosum* stem. (3) Medullosan pteridosperm ovule. Magnified $\times 1$. UI 37149 C. (B) *D. scleroticum* axis, showing characteristic mixed pith protosteles, sclerotic nests in cortical parenchyma, and inner periderm with distinct bands of holes. Magnified $\times 1$. UI 37150 B top. (C) *Sigillaria* primary and secondary xylem, and periderm. Magnified $\times 1.5$. UI 37155 B top.

scleroticum or *Synchysidendron resinosum*. In contrast, the Danville coal is dominated by *Psaronius* spp., with subdominant *Sigillaria* and possibly *S. resinosum*. This flora resembles that found in several zones of the mid-seam portion of the Springfield vertical profile, and is more similar, in the dominance of *Psaronius* and *Sigillaria*, to coals of Late Pennsylvanian age in the American midcontinent (Willard and Phillips, 1993; Pryor, 1993). Nonetheless, in details of species composition the Danville coal is clearly allied with other late Middle Pennsylvanian coals of the midcontinent (DiMichele et al., 1996).

5.2. Compositional peculiarities

Each of the coals has certain compositional peculiarities that set it apart from the others. These are variations on a general pattern of broadly similar taxonomic composition and similar patterns of rank-order abundance, especially among the Springfield, Herrin, and Baker coals. The distinctive qualities likely reflect environmental differences related to the

frequency of disturbances and their intensity (fires, blow downs of trees, catastrophic flooding), and perhaps to distinctive physical conditions within some of the mires.

5.2.1. Springfield coal

The Springfield coal in general is quite similar to the Herrin Coal in composition. It is characterized, however, both in the western Kentucky samples and in samples from western Indiana by a high diversity of *Psaronius* species, indicated by identified reproductive organs or by palynological studies (Mahaffy, 1988; Willard, 1993; Willard et al., 1995; Phillips and DiMichele, 1998). In samples from Indiana, the Springfield coal also contains a notable representation of rarely encountered lycopsids, such as *Sublepidophloios* sp., *L. mannabachense*, and *Lepidodendron hickii*, often in abundances that indicate local dominance. There are clear regional patterns of compositional variation that have been identified palynologically and appear to be related to the influence of fresh-water channels on the edaphic characteristics of the peat (Willard, 1993).

SPECIES	DANVILLE	BAKER	HERRIN	SPRINGFIELD
<i>Lepidophloios hallii</i>	X	X	X	X
<i>Psaronius</i> spp.	X	X	X	X
<i>Medullosa</i> spp.	X	X	X	X
<i>Synchysidendron resinosum</i>	X	X	X	X
<i>Diaphorodendron scleroticum</i>	X	X	X	X
<i>Sphenophyllum plurifoliatum</i>	X	X	X	X
<i>Lepidophloios johnsonii</i>		X	X	X
<i>Sigillaria</i> spp.	X	X	X	X
<i>Arthropitys</i> spp.	X	X	X	X
<i>Pennsylvanioxylon</i> spp.	X	X	X	X
<i>Anachropteris</i> sp.		X	X	X
<i>Anachropteris gillotii</i>			X	
<i>Anachropteris involuta</i>		X	X	X
<i>Anachropteris mediatena</i>	X	X	X	
<i>Botryopteris</i> sp.	X		X	X
<i>Botryopteris "pseudoantiqua"</i>	X		X	
<i>Botryopteris cratis</i>			X	X
<i>Botryopteris forensis</i>	X	X	X	X
<i>Zygopteris illinoiensis</i>	X	X	X	X
<i>Ankyropteris brongnartii</i>			X	X
<i>Hizemodendron serratum</i>		X	X	X
<i>Paralycopodites brevifolius</i>		X	X	X
<i>Lepidodendron hickii</i>		X		X
<i>Sublepidophloios</i> sp.			X	
<i>Lepidodendron manabachense</i>		X		
<i>Chaloneria periodica</i>	X	X	X	X
<i>Paurodendron fraipontii</i>		X	X	X
<i>Sutcliffia insignis</i>		X	X	X
<i>Heterangium</i> spp.		X	X	X
<i>Schopfiastrum decussatum</i>		X	X	
<i>Callistophyton boysssetii</i>	X	X	X	X
<i>Calamodendron</i> sp.		X	X	X

Fig. 13. Stratigraphic distribution of taxa in the four coals analyzed in this study (see also Table 2). The Danville coal is at the top of the stratigraphic section. The 10 most common taxa are listed first and all but one, *L. johnsonii*, occurs in all coals.

5.2.2. Herrin coal

The Herrin coal is consistently diverse at all localities sampled throughout the southern part of the Illinois Basin (Phillips et al., 1977; Phillips and DiMichele, 1981; Winston, 1986; DiMichele and Phillips, 1988), and is the most species-rich sample in this study. However, at all localities the flora is similar in its composition and species richness and appears to have been homogeneous over a vast area. The coal consists of several recurrent species associations that appear at each site. Low diversity assemblages dominated by *L. hallii* are more abundant in the Herrin than in other

coals, probably indicative of large tracts of standing water. Assemblages enriched in *Medullosa* spp. and *Paralycopodites brevifolius* occur in association with mineral matter or charcoal enrichment of the coal seam. Mixed assemblages of *S. resinosum*, *D. scleroticum*, *Medullosa* spp., *Psaronius* spp., and a diverse array of ground cover and vines appear to have occupied periodically exposed peats.

5.2.3. Baker coal

Coals balls with distinctive composition indicate vegetational differentiation within the Baker mire.

Table 1
Ten most abundant taxa, on average, in the five samples

Taxon rank	Danville	Baker 2	Baker 1	Herrin	Springfield	Mean rank	Standard deviation
<i>Lepidophloios hallii</i>	8	1	1	1	1	2.4	3.130495
<i>Psaronius</i> spp.	1	4	4	3	2	2.8	1.30384
<i>Medullosa</i> spp.	6	3	2	2	4	3.4	1.67332
<i>Synchysidendron resinotum</i>	5	2	3	5	11	5.2	3.49285
<i>Diaphorodendron scleroticum</i>	7	9	8	4	3	6.2	2.588436
<i>Sigillaria</i> spp.	2	10	11	10	5	7.6	3.911521
<i>Sphenophyllum plurifoliatum</i>	9	5	5	11	9	7.8	2.683282
<i>Lepidophloios johnsonii</i>	×	6	7	12	7	8	2.708013
<i>Arthropitys</i> spp.	10	12	12	7	13	10.8	2.387467

Taxon rank is listed for each sample.

Most noteworthy are coal balls enriched in *S. plurifoliatum* and *Chaloneria (Polysporia) periodica*. This assemblage appears to have had few trees; coal balls rich in these two species suggest dense masses of low scrub, which may be considered to be the Pennsylvanian equivalent of modern marshes (DiMichele et al., 1979). The Baker is also peculiar in the abundance of monocarpic lycopsid trees, including *L. hallii*, *S. resinotum*, and *L. hickii* (a pattern confirmed by palynological analyses, C. Eble, personal communication, 2001). The commonness of a monocarpic reproductive strategy, only one cone-forming interval late in the life of any single tree (“all eggs in one

basket”), is consistent with two quite distinct, alternative environmental scenarios. Long periods with low levels of destructive disturbance permit the reproductive risk inherent in monocarpy; trees can come to maturity without being killed by random disturbances during development. On the other hand, if monocarpic lycopsids grew rapidly and effectively “bolted,” like many modern biennial herbs (Phillips and DiMichele, 1992), then abundant monocarpics could indicate high disturbance and ephemeral habits favoring plants with rapid completion of the life cycle, essentially a weedy, opportunistic life history pattern adapted to exploiting patchy disturbed sites.

Dominance-Diversity Whole Seam Averages

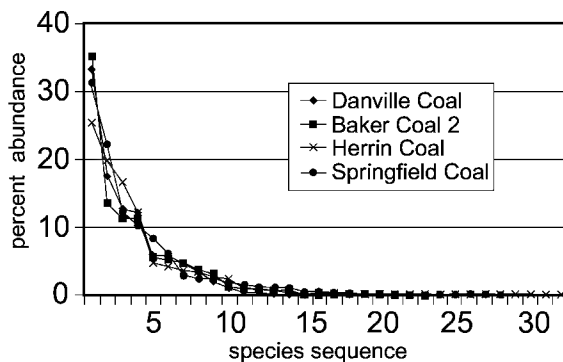


Fig. 14. Dominance–diversity patterns in the four coals (see also Table 3). The basic shapes of the curves are the same for all coals. The Baker, Herrin and Springfield coals all have large proportions of taxa at 1% or less normalized relative abundance, suggesting that sampling has captured many of the less common to rare elements of these floras. The Danville coal sample is small and clearly has under-sampled the flora, while capturing the dominant elements.

5.2.4. Danville coal

The Danville coal sample is too small to reveal many generalities, especially considering that not enough coal balls from this seam have been collected or reported in the literature to provide much of a basis for comparison. The dominance of *Psaronius* presages patterns that will appear in the Late Pennsylvanian. Even some of the coal balls, rich in large, uncompressed roots of the *Psaronius* outer root mantle, resemble specimens from Late Pennsylvanian coals. The abundance of *Sigillaria* in the Danville sample is

Table 2
Pearson product moment correlations among whole-seam samples
Pearson correlation matrix

	Danville	Baker 2	Baker 1	Herrin	Springfield
Danville	1.000				
Baker 2	0.363	1.000			
Baker 1	0.374	0.896	1.000		
Herrin	0.530	0.792	0.797	1.000	
Springfield	0.486	0.735	0.526	0.757	1.000

Table 3
Whole-seam average rank order abundances of taxa in whole-seam random samples

Rank order modified data									
Danville	Baker 1		Baker 2		Herrin		Springfield		
(1) P.	33.3965	(1) LP.1	35.2605	(1) LP.1	31.109	(1) LP.1	25.436	(1) LP.1	31.4167
(2) SI.	17.6109	(2) LD.1	13.583	(2) M.	13.703	(2) M.	19.8942	(2) P.	22.2222
(3) LD.	12.7747	(3) M.	11.3277	(3) LD.1	11.2325	(3) P.	16.6477	(3) LD.5	12.4298
(4) LE/LM.	12.142	(4) P.	11.1961	(4) P.	10.7506	(4) LD.5	12.1811	(4) M.	10.292
(5) LD.1	5.8935	(5) SP.	5.656	(5) SP.	7.0276	(5) LD.1	4.7752	(5) SI.	8.39129
(6) M.	5.8225	(6) LP.W	5.3362	(6) LP.3	4.4981	(6) LE/LM.	4.2299	(6) LD.2	6.1933
(7) LD.5	4.6864	(7) LD.	4.688	(7) LP.W	4.1328	(7) AP.	3.6493	(7) LE/LM.	2.8642
(8) LP.	3.3444	(8) LE/LM.	3.611	(8) LD.5	4.0267	(8) K.	3.4245	(8) LP.W	2.4472
(9) SP.	1.9882	(9) LD.5	3.1299	(9) LD.	3.8852	(9) LD.	2.4526	(9) LF.	2.1835
(10) AP.	1.065	(10) SI.	1.297	(10) PO.	2.9208	(10) SI.	2.3694	(10) SP.	2.0154
(11) Z.	0.426	(11) CD.	0.9875	(11) SI.	2.1402	(11) SP.	1.1019	(11) LD.	1.5832
(12) K.	0.284	(12) AP.	0.9778	(12) AP.	0.8477	(12) LP.W	0.9715	(12) LD.1	1.2709
(13) B.F	0.213	(13) PO.	0.7182	(13) LP.M	0.8475	(13) SF.	0.4739	(13) CD.	1.1772
(14) A.M	0.142	(14) SU.	0.6982	(14) PX.	0.7174	(14) LF.	0.2368	(14) AP.	1.0579
(15) PX.	0.071	(15) A.M	0.2593	(15) SU.	0.5869	(15) A.I	0.2269	(15) K.	0.519
(16) B.4	0.071	(16) A.	0.2395	(16) LE/LM.	0.4171	(16) SU.	0.1547	(16) A.I	0.5013
(17) B.	0.071	(17) LD.2	0.1596	(17) A.M	0.3129	(17) LP.5	0.1541	(17) Z.	0.4559
(18) PO.	0.071	(18) PX.	0.1298	(18) LD.2	0.1958	(18) A.	0.1541	(18) SE.	0.2477
		(19) Z.	0.1098	(19) A.	0.1434	(19) B.5	0.1422	(19) PO.	0.0896
		(20) SF.	0.06	(20) SF.	0.1304	(20) A.4	0.1184	(20) H.	0.0788
		(21) B.F	0.03	(21) A.I	0.0392	(21) SE.	0.1067	(21) PX.	0.0777
		(22) H.	0.02	(22) SE.	0.026	(22) A.M	0.0829	(22) LP.3	0.0749
		(23) LF.	0.01	(23) Z.	0.0131	(23) AT.	0.0829	(23) B.5	0.0727
				(24) K.	0.0131	(24) PX.	0.0474	(24) B.F	0.0451
						(25) B.4	0.0474	(25) B.	0.035
						(26) LD.2	0.0474	(26) A.	0.0291
						(27) CD.	0.0474	(27) SU.	0.0287
						(28) B.	0.0355	(28) AT.	0.0103
						(29) H.	0.0355		
						(30) B.F	0.0118		
						(31) Z.	0.0118		
						(32) PO.	0.0118		

LP.1—*Lepidophloios hallii*, LP.W—*L. johnsonii*, LP.5—*Sublepidophloios* sp., LD.5—*D. scleroticum*, LD.1—*S. resinosum*, LD.—tissues attributable to *Diaphorodendron* and *Synchysidendron*, LD.2—*Hizemodendron serratum*, SI.—*Sigillaria* spp., SE.—*Paurodendron fraipontii*, PO.—*Chaloneria periodica*, LF.1—*Paralycopodites brevifolius*, LE/LM.—unattributable lycopsid tissues and leaves, P.—*Psaronius* spp., PX.—*Pennsylvanioxylon* spp., AP.—*Arthropitys* spp., CD.—*Calamodendron* sp., SP.—*Sphenophyllum plurifoliatum*, M.—*Medullosa* spp., SU.—*Sutcliffia insignis*, K.—*Callistophyton boysssetii*, H.—*Heterangium* spp., SF.—*Schopfiastrum decussatum*, A.—*Anachoropteris*, A.I—*A. involuta*, A.4—*A. gillottii*, A.M—*A. mediatana*, B.—*Botryopteris* spp., B.F—*B. forensis*, B.4—*B. "pseudoantiqua"*, B.5—*B. cratis*, AT.—*Ankyropteris bronngartii*, Z.—*Zygopteris illinoiensis*.

unusual for Middle Pennsylvanian coals, although it has been noted in the Springfield at the western Kentucky Island Creek mine and in samples from western Indiana, including roof shales (DiMichele and Nelson, 1989). *Sigillaria* tends to be more common in clastic swamp deposits than in peats (Gastaldo, 1987). The Danville is the only one of the four samples to lack *Lepidophloios johnsonii*, which is among the

more common species in the Springfield, Herrin and Baker coals.

5.3. Sampling, scale and diversity

This study affords the opportunity to examine the effects of sample size and scale of resolution on our understanding of the plant composition of Pennsylvanian

Table 4
Springfield coal quantitative plant composition by zone

Springfield coal Island Creek VS1—normalized														
Species	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6	Zone 7	Zone 8	Zone 9	Zone 10	Zone 11	Zone 12	Zone 13	Average
PX.	0	0	0	0	0.433296	0	0.169533	0	0	0.108032	0	0	0	0.05468162
A.	0	0	0.097726	0	0	0.146784	0	0	0	0.108032	0	0	0	0.02711862
A.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A.1	0.717647	0.749981	0.879927	0	0.108324	0.293568	1.164191	0.460062	0.762228	0.756096	0	0	0	0.45323262
A.J	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A.M	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B.	0	0	0	0	0	0	0.332626	0.092049	0	0	0	0	0	0.03266731
B.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B.5	0	0	0	0	0	0	0.166313	0.092049	0.508152	0	0	0	0	0.05896262
B.F	0	0	0	0	0	0	0	0	0	0	0.582612	0	0	0.04481631
Z.	0	0	0	0	0	0.146784	0.332626	2.576091	0	1.620224	0	0	0	0.35967115
AT.	0	0	0	0	0	0	0	0	0	0.108032	0	0	0	0.00831015
P.	17.900198	6.125504	34.376496	23.0572	3.683016	45.410112	52.807195	35.376462	16.516552	14.63872	4.36959	10.735896	1.409616	20.4928121
FE	0.372875	0.249956	0.293309	0	0	0.293568	0.665252	0.643977	0.254076	0.108032	0	0	0	0.22161885
LD.	1.119096	6.240086	2.248615	0	2.38842	0.146784	0.665252	0.460062	1.016428	0.756096	0.582612	0	2.819232	1.41866792
LD.1	0	0	16.521589	0	0	0	0	0	0	0	0	0	0	1.27089146
LD.5	0	17.499971	0	0	0	0	24.282986	17.113428	36.082016	30.676864	12.235416	0	0	10.6069755
LD.2	0	0	0	15.609512	36.722052	1.615284	0.332626	1.379637	0.254076	0.761216	0	0	0	4.35956946
LF.	1.864532	0	6.452143	20.068496	0	0	0	0	0	0	0	0	0	2.18347469
LP.1	71.227917	63.790647	5.083586	8.548392	7.257708	41.699592	1.66313	3.864411	2.79496	6.156928	19.809795	85.052706	83.166291	30.7781587
LP.3	0	0	0	0.347864	0	0	0	0	0	0	0	0.625392	0	0.07486585
LP.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LP.W	0	0	24.929038	0	4.224636	0	0	0	0	0	0	0	0	2.24259031
LPM	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LP.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LE/LM.	1.090522	0.749981	0.390904	5.57432	0.216648	0	0.322966	0.552294	3.811388	9.180928	0	0.416928	11.277162	2.58338777
PO.	0	0	0	0	0	0	1.164191	0	0	0	0	0	0	0.08955315
SI.	0	0	0	1.114864	38.88864	0	0	25.301763	23.1229	19.659136	0.582612	0.416928	0	8.39129562
SE.	0	0	0	1.114864	0	0	0	0.092049	1.016428	0.54016	0	0	0	0.212577
M.	4.102096	1.499962	4.496968	10.777648	3.683016	4.404576	10.977302	6.624783	12.196764	7.232128	56.330064	1.250784	0	9.50585315
SU.	0.372875	0	0	0	0	0	0	0	0	0	0	1	0	0.02868269
H.	0	0	0	0.7434	0	0.146784	0	0	0	0.108032	0	0	0	0.07678585
SF.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
K.	0	0	0.293309	2.601192	0	0.587136	0.831565	0.920124	0	0.97216	0	0	0	0.47734508
AP.	0	0	0.391035	0	0.216648	1.468104	1.164191	2.668506	0.508152	4.320768	0.582612	0.208464	0	0.88680615
CD.	0	1.499962	1.759723	2.229728	1.408212	0	0.997878	0.275964	0	0	4.661178	1.459248	0	1.09937638
SP.	1.118625	1.499962	1.759723	8.175984	0.974916	3.376956	1.66313	1.656333	0.762352	1.944448	0	0	1.409616	1.872465
Total ID	99.886383	99.906012	99.974091	99.963464	100.205532	99.736032	99.702953	100.150044	99.606472	99.756032	99.736491	100.166346	100.08192	99.913213

See Table 3 for the key to taxonomic abbreviations.

nian-age coals. The Danville sample was quantified as individual coal balls rather than as a single sample, which permits examination of the effects of very small sample size on diversity. The Springfield coal was sampled at the level of individual coal-ball zones of known position relative to each other and to the thickness of the coal bed. Such analysis permits study of floristic changes accompanying peat accumulation, as well as the chance to study intra-mire community composition. Samples from the Herrin and Baker coals are random collections of coal balls from spoils; equivalent whole-seam random samples were created for the Springfield and Danville coals as discussed earlier. In collecting random samples all relative positional information is lost, reducing resolution to “whole-seam” composition, effectively a spatio-temporal average of a mire landscape.

5.3.1. Springfield coal profile analysis

The Springfield coal sample consisted of 13 zones. Zones were analyzed using exploratory statistics to determine the existence of recurrent patterns of taxonomic composition. Zone-by-zone composition and normalized relative abundance is summarized in Table 4. Cluster analysis (Fig. 15) and factor analysis (Fig. 16) reveal similar patterns. A small

number of zones are dominated by *L. hallii*, with subdominant *Psaronius* and little ground cover, probably representing areas with prolonged intervals of standing water. These zones occur at the base and top of the profile; in the center is a zone co-dominated by *L. hallii* and *Psaronius*. Most of the remaining zones are dominated by *Psaronius* or by *D. scleroticum*, and include *Sigillaria* and *Medullosa* as subdominants. Such assemblages are enriched in ground cover and vines and are the highest in species richness of the profile. Two zones are singularly distinct: one is dominated by *Sigillaria* with subdominant *Hizemodendron serratum*, a ground cover lycopsid, and includes other ground cover plants. The other is dominated by *Medullosa* with subdominant *L. hallii* and *D. scleroticum* and is low in species richness and diversity of growth forms. Fusain is not differentially associated with any of the assemblages in the profile.

This profile analysis reveals considerably greater internal heterogeneity than could be detected with a whole-seam random sample. The Springfield coal swamp apparently was edaphically variable, which led to marked spatial variation in plant assemblages throughout the mire. The most common assemblages, those dominated by *L. hallii*, or by a mixture of tree

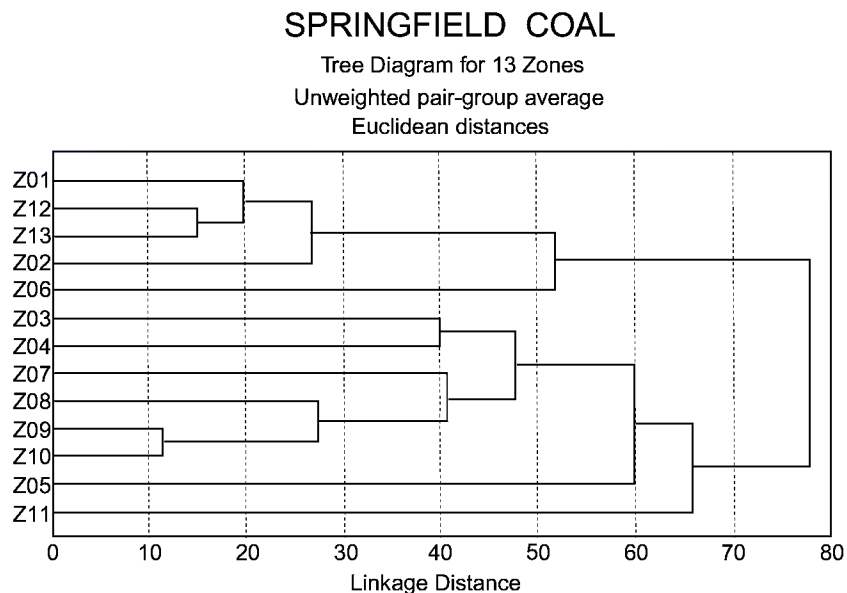


Fig. 15. Unweighted Pair Group Cluster Analysis of 13 zones in the Springfield coal coal-ball profile.

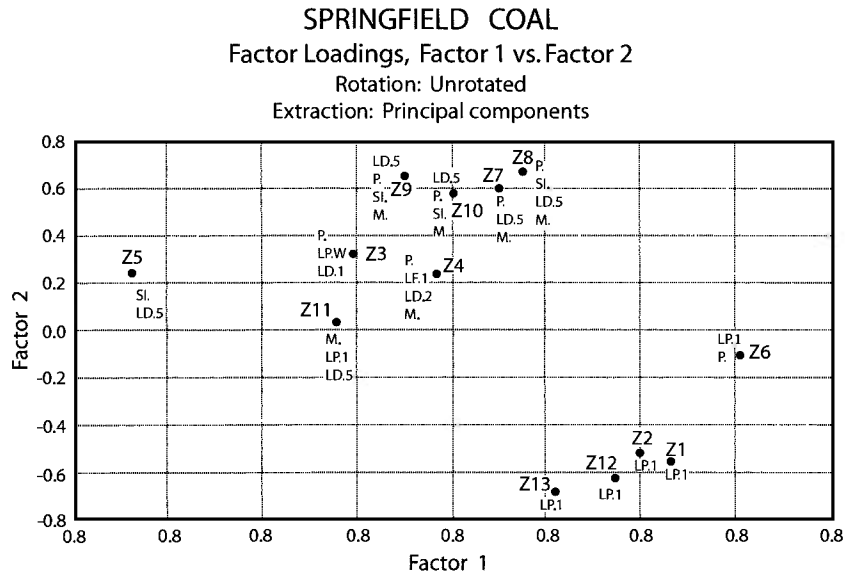


Fig. 16. Factor analysis of 13 zones in the Springfield coal coal-ball profile.

ferns, medullosans, and lycopsids, have been identified in other late Middle Pennsylvanian coals and elsewhere in the Springfield, which, as mentioned above, had a high degree of original landscape heterogeneity. In western Indiana, in particular, the Springfield peat accumulated laterally to a system of drainage channels (Eggert, 1994). In this area, plant composition of the coal can vary greatly within and among profiles suggesting extensive edaphic variation temporally at a site and spatially on the local and regional scales (Willard, 1993; Willard et al., 1995; Phillips and DiMichele, 1998).

5.3.2. Estimates of taxon richness on different scales of resolution

Taxon richness, the number of species or genera identified, was examined for each of the different levels of sample size: by coal ball for the Danville coal, by coal-ball zone for the Springfield coal, and by whole-seam compositional average for all four coals. Results are shown in Fig. 17. In each case, as expected, taxon richness goes up with sample size. Calculations were based both on raw “information units” (number of cm² sampled) and “normalized” sample sizes in which roots were not counted and sample size was recalculated based on sampling of

aerial plant parts only; the results were not substantially different and only the normalized data sets are presented. Pearson product moment correlations (Table 5) were calculated for each of the three data sets using both raw data and log-transformed data (percentages converted to natural logarithms); again, results were not substantially different and graphs show raw data only.

The graphical data indicate a high variance in the individual coal-ball sample with no indication that a plateau in diversity was reached at a particular sample size (Fig. 17A). Clearly, individual coal balls, unless huge, are unlikely to capture a significant fraction of whole-seam diversity, and larger coal balls are generally more diverse than smaller ones. Coal-ball zones (Fig. 17B) also show a clear relationship of sample size to species richness, reaching a plateau at about 900–1000 cm², when normalized for aerial sampling only. As with individual coal balls, zone by zone analysis will be affected by the intrinsic diversity of the parent plant assemblage and no one zone can be expected to capture the diversity of the full mire landscape. Adequate whole-seam random samples appear to have been reached by the samples greater than 7000 normalized information units (cm² of coal-ball

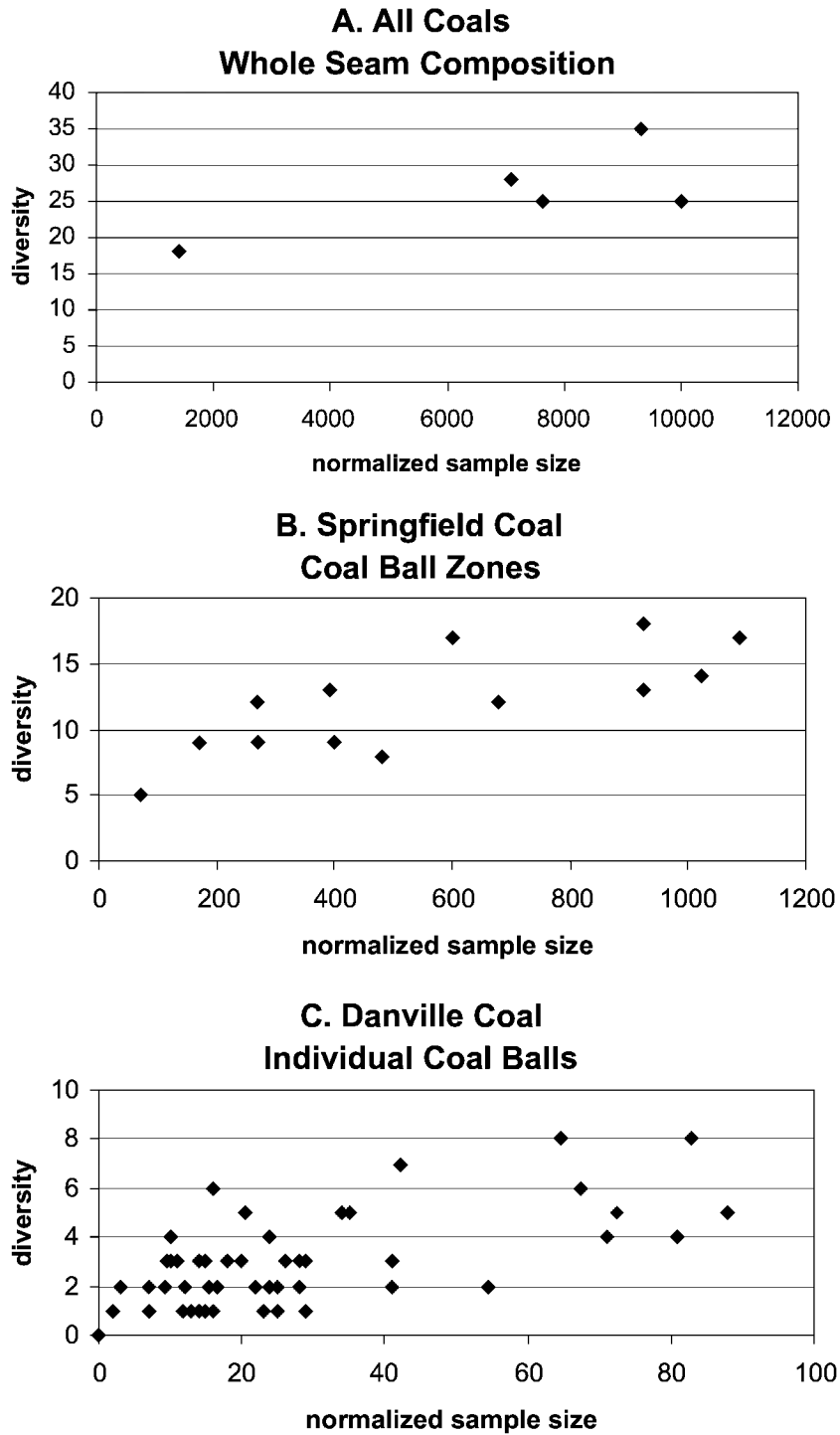


Table 5

Pearson product moment correlations of plots of diversity by sample size based on raw data counts (IUs—information units) and on normalized sample sizes (corrected for aerial, identified material only)

Correlation: diversity by sample size		
Log-transformed data sample	IUs r^2	Normalized r^2
All coals—whole-seam average	0.67	0.64
Springfield coal—coal-ball zones	0.68	0.66
Danville coal—individual coal balls	0.28	0.29

Normalized sample sizes are illustrated in Fig. 17.

peel surface area) (Fig. 17C). The Danville sample, consisting of less than 2000 information units compares closely in its species richness with that of the larger zones from the Springfield profile sample, although the Danville coal balls came from more than one layer in the coal bed. The inadequacy of the Danville sample is similarly reflected in the relatively low number of taxa represented by <1% biomass.

6. Discussion

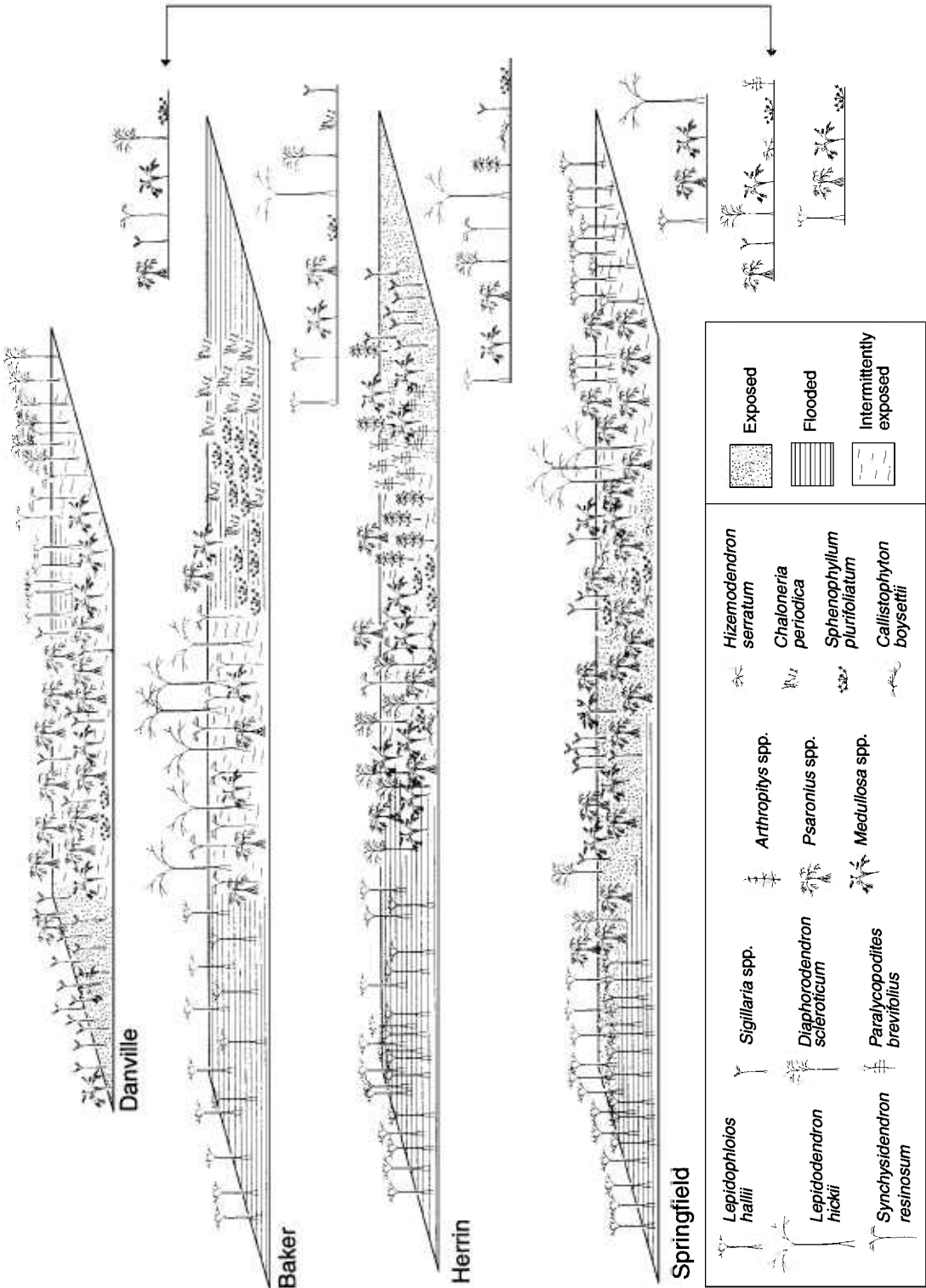
The samples from the four coals that comprise this study represent essentially the same flora or species pool, one that has been identified throughout the midcontinent United States from the upper Middle Pennsylvanian (Phillips et al., 1985; DiMichele et al., 1996; DiMichele and Phillips, 1996a). Three of the coals, the Springfield, Herrin, and Danville, extend across large areas of the Illinois Basin. Coal balls from the Springfield and Herrin coals have been sampled in many places, and the composition of the samples reported in this study is consistent with assemblages from elsewhere in the basin. Reports on the plants from Danville coal balls are limited to some of the earliest American studies of coal balls (see Phillips et al., 1973), and this is the first detailed

record of a macroflora from that coal. The Baker coal is the most restricted of the four coals, attaining a mineable thickness only in small areas of western Kentucky (Eble et al., 2001). Its composition, however, is similar to that of the more widespread, older coals.

Separation of the coals by a complex of rocks, including marine shales and limestones, terrestrial fluvial clastics and paleosols, indicates that significant changes in base level occurred between each episode of peat formation. It is most likely that these changes in base level were glacioeustatic, driven by changes in ice volume at the south pole (Frakes et al., 1992). However, other causes of base-level changes, such as tectonic activity, have been documented in the area of our three Kentucky samples, as discussed earlier. Base-level changes also probably were accompanied by climatic changes (Cecil, 1990); paleosols in the rocks between the coals often have characteristics indicating formation under seasonally dry climates. Consequently, the plants that comprised the successive mires were forced to migrate spatially and were subjected to changing climatic conditions within the tropics. It is, therefore, worthy of note that the basic species pool and the landscape-average, dominance–diversity structure of these mires were persistent throughout the late Middle Pennsylvanian, a time interval that could represent as little as 125,000 years or as much as 650,000 years, using the estimates in DiMichele et al. (1996).

The concept of floral or faunal “persistence” is relative rather than absolute, a matter of degree and of comparison between successive, temporally separated samples, rather than of reference to some absolute standard of similarity (Ivany, 1999; Pfefferkorn et al., 2000). This is particularly true when examining assemblages over long spans of geologic time. The assemblages documented here clearly are drawn from a common species pool, a pattern that becomes more apparent if the coals in question are

Fig. 17. Relationship of sample size to taxon diversity at different sampling scales (see also Table 1). (A) Diversity averaged over an entire coal seam at a single collecting site. Except for one small sample of the Danville coal, there appears to be no correlation between sample size and diversity as long as samples are larger than about 7000 cm². (B) Diversity within coal-ball zones collected in a single profile at one site in the Springfield coal. There is a clear correlation between sample size and the number of taxa encountered. (C) Diversity of individual coal balls. Variance at this scale is high because of the vagaries of peat taphonomy and preservation; coal balls can be close to point samples if small and so can sample single or limited numbers of organs if detrital sizes are large, or many bits if detritus size is small.



examined over a broader aerial extent than sampled in this study (e.g., DiMichele and Phillips, 1996a). Few new species originated during the interval, and the dominant taxa are common to all coals in the late Middle Pennsylvanian throughout the eastern United States, including the Appalachian Basin as well as the Illinois Basin.

Examination of patterns on a landscape average, however, can mask significant differences between successive assemblages. In this study, the analysis of the Springfield coal on a zone-by-zone basis, indicates considerable internal variation in vegetational composition across the landscape. Such variation within a mire is paralleled by nearly all profile-based studies done to date of coals from many different times during the Pennsylvanian. Detailed examination of individual coal balls suggests unique vegetational patterns in each of the coals studied herein. The Baker coal sample, for example, contains a significant number of specimens that are composed purely of *S. plurifoliatum* or of a mixture of *S. plurifoliatum* and *C. periodica*. This kind of vegetation has not been identified elsewhere in coal-ball macrofossil assemblages, but is hinted at by palynological analysis of coals in the early Late Pennsylvanian, immediately following major extinctions during the Middle–Late Pennsylvanian transition (Phillips et al., 1974; Peppers, 1985; Kosanke and Cecil, 1996).

When examined in the context of vegetational persistence, similar assemblages can be identified in the Springfield, Herrin and Baker coals. Most common are those dominated by the monocarpic lycopsid *L. hallii*. These assemblages are of low diversity, contain minimal ground cover and vines, and likely grew in standing water. *Lepidophloios* has many reproductive and vegetative features consistent with this inference (Phillips, 1979; Gastaldo, 1987; DiMichele and Phillips, 1988). Also shared are mixed dominance assemblages rich in medullosans, tree ferns and the lycopsid trees *Diaphorodendron* and

Synchysidendron, assemblages that contain a diversity of ground cover, including ferns, sphenopsids, pteridosperms and lycopsids.

Even the small sample of Danville coal vegetation, reflective in its dominance–diversity patterns of Late Pennsylvanian assemblages, is similar in many ways to assemblage zones identified in the Springfield coal analysis. It appears that conditions favorable to tree–fern dominance and *Sigillaria* abundance existed throughout the later Middle Pennsylvanian.

Fig. 18 schematically represents the changes in peat-forming vegetation found in this study. Each of the coals has distinct landscape elements, but the basic dominant components persist.

The fate of peat-forming vegetation during intermire intervals remains an open question. It is quite possible that vegetation survived in refugial pockets, wet areas within a generally drier landscape, or even that it survived intact in regions outside of the basins, in extrabasinal lowlands. Because of the gaps in sampling, it is not possible to differentiate reassembly from persistence of a narrow kind, namely the migration of vegetation as intact units. Peat-forming vegetation is peculiar in its edaphic (substrate physical characteristics, including chemistry) isolation from surrounding mineral–soil environments (Knoll, 1985; DiMichele et al., 1987). Species overlap between these habitats is limited and the basic patterns of dominance and diversity are different (Pfefferkorn and Thomson, 1982; Gastaldo et al., 1996). Thus, it is likely that peat-substrate specialist plants must have survived in swampy areas with rigorous substrate conditions that could have reduced competition from the broader flora, including preventing the acclimation of invading forms during time intervals between widespread peat accumulation. Were this vegetation reduced to small, isolated pockets, the opportunity for acclimation of new species to such environments would be greatly enhanced by edge effects alone, increasing the opportunity for stochastic entry of

Fig. 18. Diagrammatic reconstructions of the vegetation of the four coal seams. Symbols indicate major plant taxa, the assemblages they comprise, and the inferred environments they occupied based on taphonomic indicators. The plants shown to the right of each landscape reconstruction represent the rank order abundance of the major taxa in each coal bed. Three assemblages are indicated for the Springfield coal, showing their vertical relationships. The assemblages from the middle portion of the Springfield coal are similar to the flora of the Danville coal. The Danville coal is shown as smaller than the others, reflecting its distinctly smaller sample size.

new forms. Yet, there are few instances of new species appearing in mires during the late Middle Pennsylvanian.

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