

Paleoecology of the Late Pennsylvanian-age Calhoun coal bed and implications for long-term dynamics of wetland ecosystems

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Received 1 January 2005; accepted 11 March 2006

Available online 28 July 2006

Abstract

Quantitative plant assemblage data from coal balls, miospores, megaspores, and compression floras from the Calhoun coal bed (Missourian) of the Illinois Basin (USA) are used to interpret spatial and temporal changes in plant communities in the paleo-peat swamp. Coal-ball and miospore floras from the Calhoun coal bed are dominated strongly by tree ferns, and pteridosperms and sigillarian lycopsids are subdominant, depending on geographic location within the coal bed. Although the overall composition of Calhoun peat-swamp assemblages is consistent both temporally and spatially, site-to-site differences and short-term shifts in species dominance indicate local topographic and hydrologic control on species composition within the broader context of the swamp. Statistical comparison of the Calhoun miospore assemblages with those from other Late Pennsylvanian coal beds suggests that the same basic species pool was represented in each peat-swamp landscape and that the relative patterns of dominance and diversity were persistent from site to site. Therefore, it appears that the relative patterns of proportional dominance stayed roughly the same from one coal bed to the next during Late Pennsylvanian glacially-driven climatic oscillations.

Published by Elsevier B.V.

Keywords: Late Pennsylvanian; Coal; Coal-ball; Paleoecology; Palynology; Ecosystem stability

1. Introduction

The Late Pennsylvanian (Missourian) Calhoun coal bed of the Illinois Basin contains a coal-ball paleoflora that has been intensively studied for over 50 years. In fact, most taxa of Late Pennsylvanian anatomically preserved plants were originally described from this coal bed (Phillips, 1980). The result has been the elaboration of a benchmark flora rich in tree ferns, primitive seed plants,

ground cover plants, and distinctive lycopsids. The palynology of the coal, however, has been only cursorily described, primarily in service of stratigraphic studies (Peppers, 1996).

The objective of this paper is to provide a paleoecological interpretation of this Late Pennsylvanian ecosystem using coal balls, palynology, and compression–impression fossils. Such a study is possible because of the unusually high degree to which the paleoflora has been sampled from multiple sites in the coal, both by the authors and previous researchers (e.g., Noé, 1934; Graham, 1934; Arnold and Steidtmann, 1937; Schopf, 1941; Stewart, 1951;

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Delevoryas, 1957; Taylor, 1965; Rothwell, 1980). In this paper, the paleoflora of the Calhoun coal bed is compared with other Late Pennsylvanian floras previously described from the Illinois Basin, including the Bristol Hill and Friendsville coal beds, which are exposed in the same general area as the Calhoun coal bed and have similar floras (Willard and Phillips, 1993). In addition, the Calhoun paleoflora is compared with that of the Duquesne coal bed of Ohio, which has been studied intensively both from a floristic and paleoecological perspective (Rothwell, 1988; Pryor, 1993,1996).

This paper combines palynological and coal-ball analyses, which allow tree-fern biomass estimates to be resolved to species or species-group (Lesnikowska, 1989). This integration permits tree-fern ecological patterns to be understood at much finer resolution than is possible based solely on analysis of plant remains in coal-balls. These longer-term, Late Pennsylvanian ecological patterns are compared with patterns described for Middle Pennsylvanian coals, which had considerably different floristic composition and patterns of dominance (DiMichele et al., 2002).

2. Geologic setting

The Calhoun Coal Member is in the Missourian Series of the Upper Pennsylvanian, part of the Mattoon Formation of the McLeansboro Group (Kosanke et al., 1960) (Fig. 1). In its type area, the coal is overlain by the Bonpas Limestone Member (Mattoon Formation) of Missourian age (Nance and Treworgy, 1981). The coal was named by Noé (1934), who first collected coal balls from exposures in Richland County, Illinois (USA). In the study area, the Calhoun coal bed occurs primarily in Richland County, with smaller exposures in southwestern Lawrence County, Illinois (Fig. 2). Further north in Marion, Clay, Effingham, and Shelby Counties (Illinois) (Nance and Treworgy, 1981), the Bonpas Limestone is correlated with the Late Pennsylvanian (Missourian) Omega Limestone Member (Nance and Treworgy, 1981). Likewise, a coal bed beneath the Omega Limestone is correlated with the Calhoun coal bed, which lies beneath the Bonpas Limestone.

Palynological and coal-ball samples from the Calhoun coal bed are compared with samples from the Bristol Hill and Friendsville coal beds. The Bristol Hill Coal Member

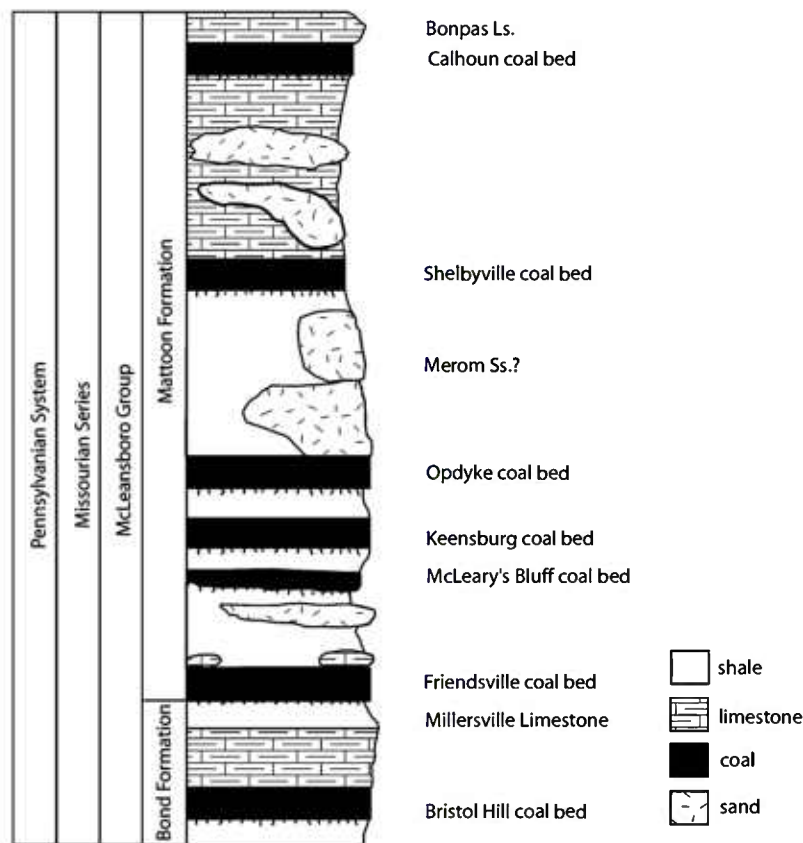


Fig. 1. Generalized geologic section showing stratigraphic relations among Late Pennsylvanian (Missourian) coals and limestones, southeastern Illinois, USA.

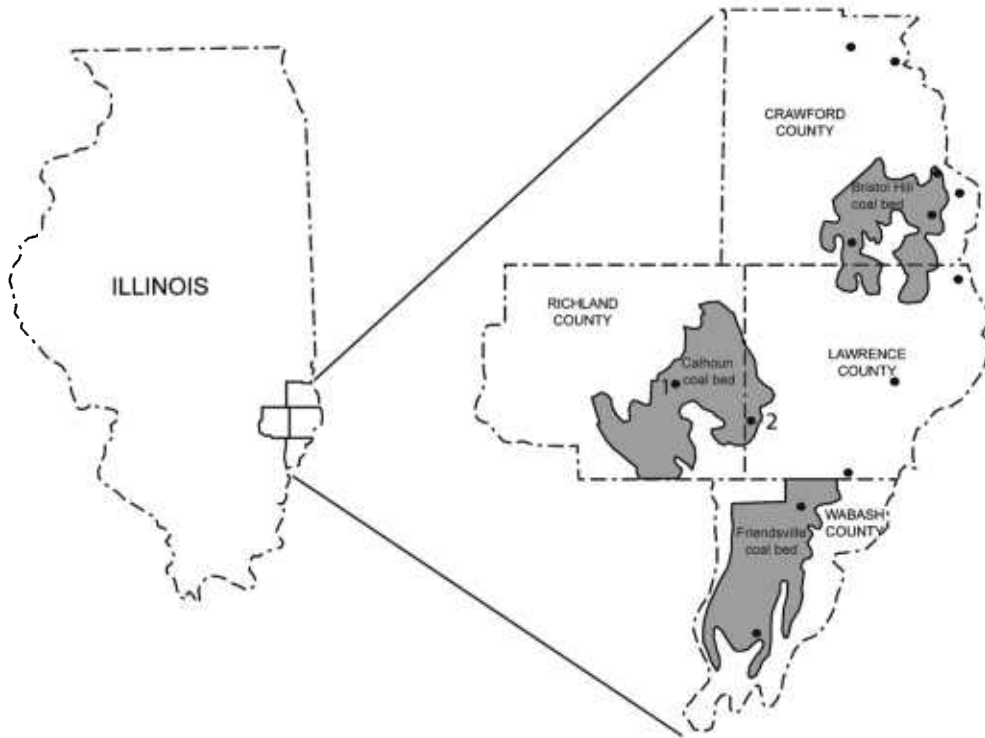


Fig. 2. Map of the Late Pennsylvanian Calhoun, Friendsville, and Bristol Hill coal beds in Richland, Lawrence, Wabash, and Crawford Counties, southeastern Illinois. 1 = Location of the New Calhoun locality, 2 = Location of the Berryville locality.

is in the Bond Formation; the Friendsville Coal Member is within the Mattoon Formation at the Bond-Mattoon Formation boundary, both in the McLeansboro Group, part of the Missourian Series (Fig. 1). Willard and Phillips (1993) described the paleobotany, palynology, and local geology of these coal beds.

3. Collection sites, sample preparation, and analysis

3.1. Collection sites

This study focuses on plant fossils of the Calhoun coal bed and the rocks immediately below and above it,

collected at two sites in southern Richland and southwestern Lawrence counties. The Richland County locality (site 1 on Fig. 2) is known in the paleobotanical literature as “New Calhoun.” It is located on Bonpas Creek in the Claremont 7 1/2” Quadrangle, along the SE, SE, NW quarters and SW, SW, NE quarters of Section 32, Township 3 North, Range 14 West. This site is described and the local outcrop geology illustrated as “Stop 14” in Weibel et al. (1989). At this site, ten coal-ball profiles were collected in a linear transect along Bonpas Creek (Fig. 3). Six of these samples form the following three sets of replicates collected from approximately the same coal-ball exposure: 1) samples 3 and 10A (Fig. 4A), 2) samples 1 and 10B, and 3)

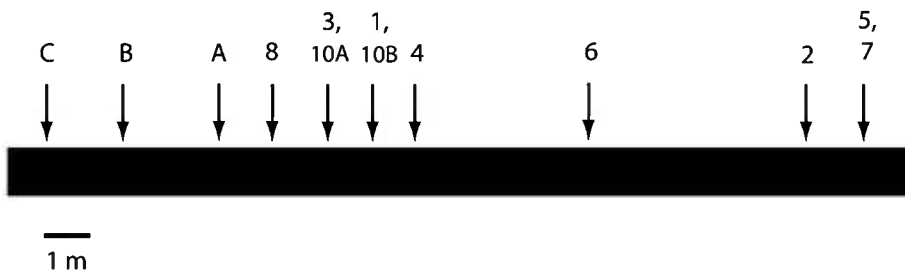


Fig. 3. New Calhoun locality. Spatial distribution of coal-ball (numbers) and palynological (letters) samples from exposure of the Calhoun coal bed on northeast facing exposure of Bonpas Creek, Richland County, Illinois. See text for further description.

samples 5 and 7. All profile zones were numbered with zone 1 at the top of the profile, closest to the roof shale. Samples of coal for palynological analysis were collected at four locations along Bonpas Creek. Site A was collected as four zones and a full seam channel sample. Sites B and C were collected as full seam channel samples. Samples of the mudstone roof and underclay also were collected at site B. Three palynological samples were collected from coal separating the coal-ball layers at Coal-Ball Site 4, and the

numbers of these samples correspond to the nearest coal-ball zone. Three random samples of the underclay were collected from the mudstone exposed below the coal at the level of Bonpas Creek, and thus serve as replicates. Two of these samples contained identifiable macrofossil foliage, and the other sample contained only decayed axes that were probably derived from pteridosperm fronds.

The Lawrence County site (site 2 on Fig. 2) is known in the paleobotanical literature as “Berryville.” It occurs



Fig. 4. Coal balls in place in the Calhoun coal bed at two sampling localities. Colors delimit coal-ball zones at both localities. a. New Calhoun locality, coal-ball profile 10 A, Bonpas Creek bank. b. Berryville locality, coal-ball profiles in place in stream bank. Vertical Section 1 comprises small masses to left in photo; vertical Section 2 comprises large coal-ball mass to right.

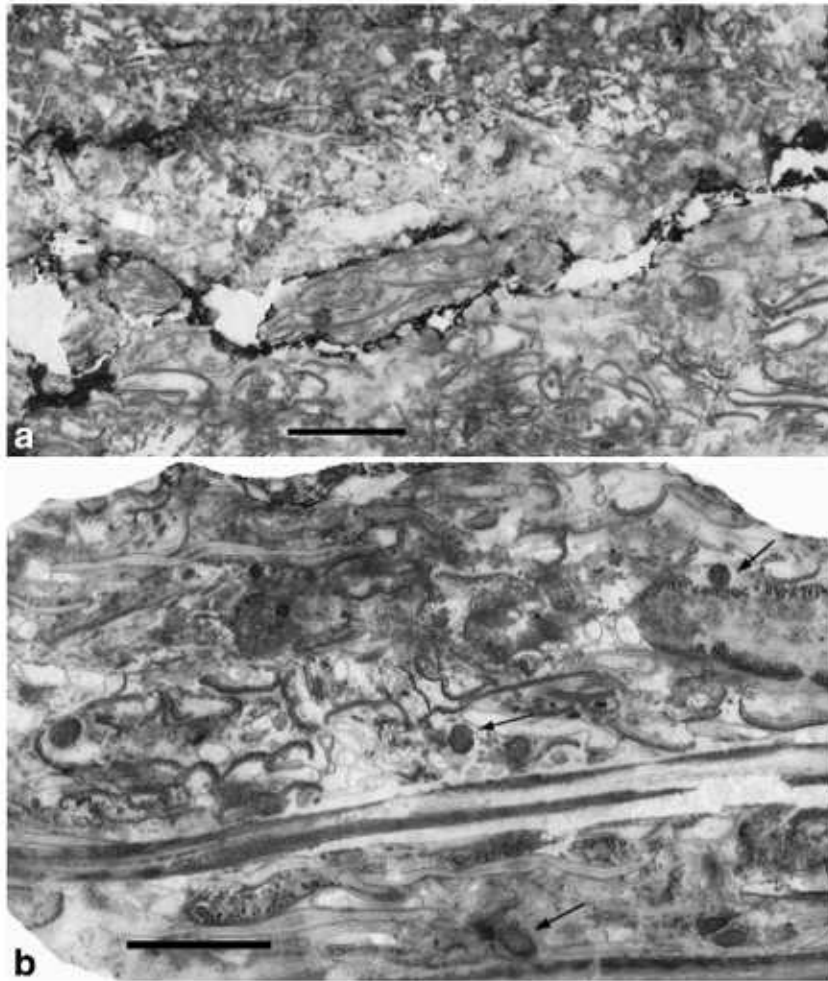


Fig. 5. a. Mixed marine-peat coal-ball from the top coal-ball zone at the New Calhoun site. Marine invertebrate fossils, possibly deposited in a burrow into the peat from the overlying marine limestone, occupy upper half of coal-ball. b. Coprolites (arrows), probably from detritivorous arthropods, in a mixed assemblage of aerial plant debris, primarily medullosan foliage. Scale bars = 1 cm.

along Sugar Creek in the Claremont 7 1/2 " Quadrangle, in the NE of the NW quarter, Section 7, Township 2 North, Range 13 West. The details of the geology at this site are described as "Stop 15" in Weibel et al. (1989). At each of these locations, multiple samples were collected, including coal-ball macrofossils and coal samples for palynological analysis. Samples of the underclay also were collected at each site for analysis of compression–impression macrofossil remains and palynology. Two adjacent coal-ball profiles were collected from a coal exposure at the base of a slope along Sugar Creek (Fig. 4b). The Berryville profiles were numbered such that the lowest numbers are at the bottom of the profile, closest to the underclay (note that this numbering scheme is opposite that used in the New Calhoun samples). Samples for palynological analysis were collected from coal separating coal-ball zones in both Berryville Vertical

Sections 1 and 2. The numbers of the palynological samples correspond to the coal-ball zones closest to the coal samples. One random sample of the underclay was collected for compression–impression macrofossil analysis.

3.2. Sample preparation and quantification

Coal balls are calcium-carbonate concretions that entomb permineralized peat, the parent plant material of the coal bed; they occur in situ and reveal the plant taxa and botanical organs that comprise the peat. Coal also preserves pollen and spores produced by the peat-swamp vegetation. Compression–impression fossils, formed in mudstones, are coalified remains of plants deposited in muds that accumulated in standing water deposits, generally swamps of floodbasin lakes, in settings associated with peat formation.

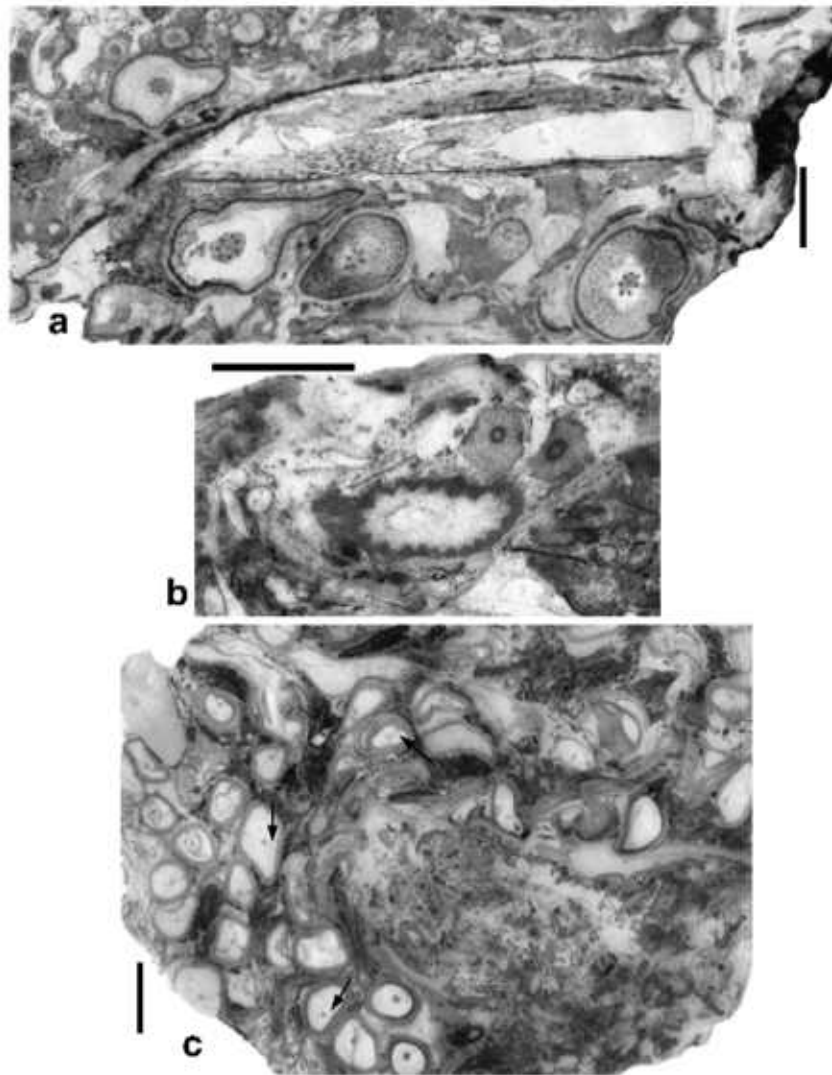


Fig. 6. Roots of major trees. a. *Psaronius* outer roots of several generations, apparently penetrating the peat substrate. b. *Arthroxyylon* roots of calamites. c. Stigmarian rootlets of *Sigillaria*; arrows point to connectives between the vascular bundle and rootlet outer cortex. Scale bars=1 cm.

3.2.1. Coal balls

This study of the Calhoun coal bed used 3,488 coal-ball specimens. The coal balls bear the following University of Illinois accession numbers: 30,003–31,659; 31,825–31,959, 32,560–32,715; 34,675–35,259; 35,587–35,602; and 38,430–38,798. Coal balls were cut and acid etched, and cellulose acetate peels were prepared of the cut surfaces, as outlined by Phillips et al. (1976). Using methods outlined by Phillips et al. (1977), a clear plastic sheet ruled with centimeter square grids was placed over the middle peel from each coal-ball; taxonomic and tissue–organ composition were recorded for each square centimeter along with preservational details. These quantitative analyses were performed on 82,411 cm² of surface area derived from peels of the

sliced coal-ball surfaces. Specimens, voucher peels, and quantitative grid-sheet records are housed in the Paleobotanical Collections, Department of Plant Biology, University of Illinois at Champaign-Urbana.

In statistical analyses of coal-ball data, only datasets with at least 1000 cm² were included. Unless specified otherwise, coal-ball data are presented as normalized data with all unidentifiable material omitted. Excluded unidentifiable material includes marine invertebrate remains (Fig. 5a) and coprolites (Fig. 5b). Data referred to as root-free have had all root material subtracted (e.g., calamite roots, Fig. 6b, and stigmarian root systems, Fig. 6c) except for one-half of *Psaronius* outer roots (Fig. 6a), which are included as aerial material (Phillips and DiMichele, 1981). Coal balls from all profiles and random samples were on

average 67% aerial material once the *Psaronius* root correction was made.

3.2.2. Palynological assemblages

Coal samples for miospore analysis (including all pollen and spores smaller than 210 μm (Guennel, 1952)) were processed using procedures outlined by Kosanke (1950). Samples were oxidized with Schulze's solution before being treated with 5% KOH to remove humic material. A float-sink technique using zinc chloride was used to separate organics from mineral matter before staining miospores with Safranin O and mounting grains on microscope slides in glycerin jelly. Roof shale and underclay samples were processed by treating with HCl and HF to remove carbonates and silicates. No oxidation

or alkaline treatment was necessary for these samples, and residue was sieved through 150 μm mesh to separate miospore and megaspore fractions. The miospore fraction was further sieved through 10 μm mesh to remove the clay-sized fraction, before swirling in a watch glass to separate mineral from organic matter. The residue was stained with Bismarck Brown and mounted on microscope slides using glycerin jelly.

Three hundred miospores per sample were counted to establish relative abundance. Where miospore preservation was poor, however, only 200 miospores were counted. Megaspores were picked from dried residue using a small paintbrush and dissecting microscope. Miospore and megaspore slides are stored in collections at the U.S. Geological Survey, Reston, Virginia (USA).

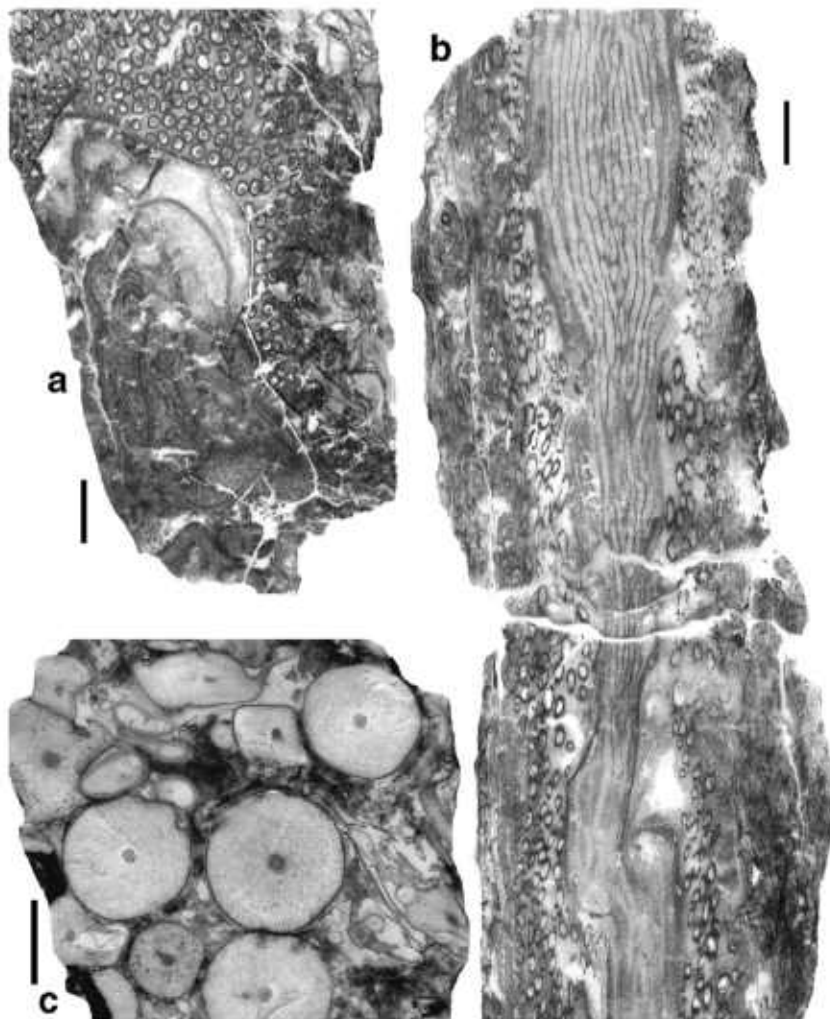


Fig. 7. *Psaronius* organs. a. Stem of *Psaronius chasei* showing crushed primary body with vascular tissue and inner root mantle. b. Stem of *Psaronius blicklei*, strongly flattened, showing vascular bundles and inner root mantle. c. *Psaronius* outer roots. The lack of flattening of these roots suggests that they were borne on the aerial part of the stem and did not penetrate the peat substrate. Scale bars=1 cm.

3.2.3. Compression fossils

Underclay samples of approximately hand size were collected by excavation and without bias regarding the presence or absence of plant fossils or particular taxa. These samples were examined visually and quantified according to the techniques of Pfefferkorn et al. (1975), in which each hand sample is treated as a quadrat, and the occurrences of taxa are noted once for each quadrat, regardless of the number of specimens on the sample. The result is a frequency distribution for each taxon, independent of the abundances of the other taxa. These samples are housed in the Paleobotanical Collections of the National Museum of Natural History in Washington, DC (USA).

3.3. Quantitative analysis of data

Coal-ball data collected in zones or layers from the coal bed are temporally distinct samples from different parts of the coal bed and they represent temporally different plant litter zones from the parent peat body. Nonetheless, the samples can be analyzed as a group of assemblages via ordination and cluster analysis, which group the samples according to similarity in taxonomic quantitative composition. From such analyses, the degree to which there are recurrent species assemblages in the peat-forming landscape can be determined. Samples from the Calhoun coal bed were compared with detrended correspondence

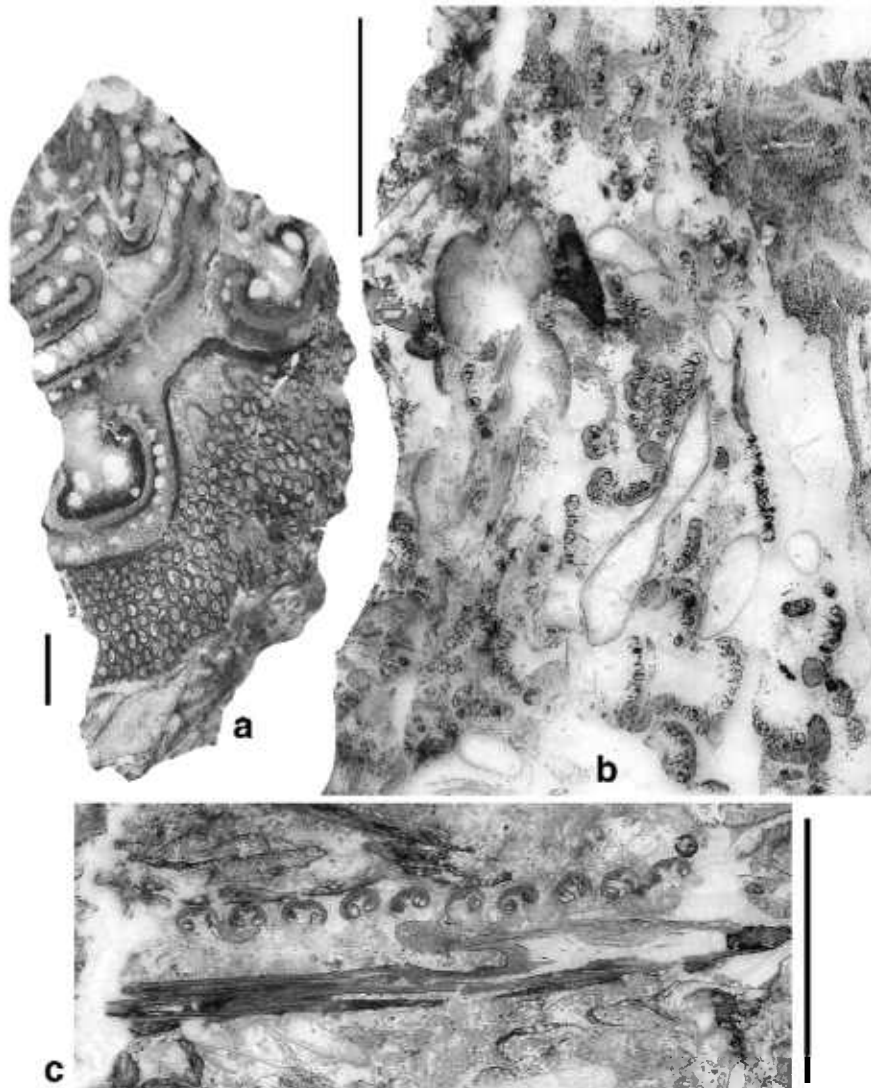


Fig. 8. *Psaronius* organs. a. *Psaronius blicklei* stem, showing vascular bundles, distinctive mucilage cavities in the primary cortex, and inner root mantle. b. Synangia attributable to *Scolecopteris* borne on laminate foliage. c. Synangia attributable to *Scolecopteris* borne on laminate foliage; associated petiolar remains (*Stipitopteris*) can be seen in the middle of the photograph, with highly flattened, sterile *Pecopteris* foliage in the lower left quadrant. Scale bars=1 cm.

analysis ordination and both r-mode (samples) and q-mode (taxa) UPGMA cluster analysis, using procedures in the program MVSP (Kovach, 1999).

Palynological analyses were conducted on forty-four samples from the Calhoun, Bristol Hill, and Friendsville coal beds, one sample from the roof shale, and five samples of the underclay of the Calhoun coal bed. Samples analyzed include both channel samples of the entire coal bed at a sampling site and zones sampled as part of the profile analysis of the coal. As with the coal-ball zones, a joint analysis of all palynological samples effectively treats the samples as if they coexisted in space, allowing recurrent patterns of species association to be identified. Because of the way in which palynological samples are prepared (Guennel, 1952), large pollen grains

of medullosan pteridosperms are not represented in miospore analyses. Detrended correspondence analysis ordinations and r-mode and q-mode UPGMA cluster analyses were performed using MVSP (Kovach, 1999).

4. Results

4.1. The paleoflora of the calhoun coal bed

The Calhoun coal paleoflora comprises coal balls (permineralized peat which is anatomically preserved), spores and pollen (dispersed reproductive organs of the peat-forming plants), and compression–impression fossils (from the clastic swamp that preceded onset of peat formation).

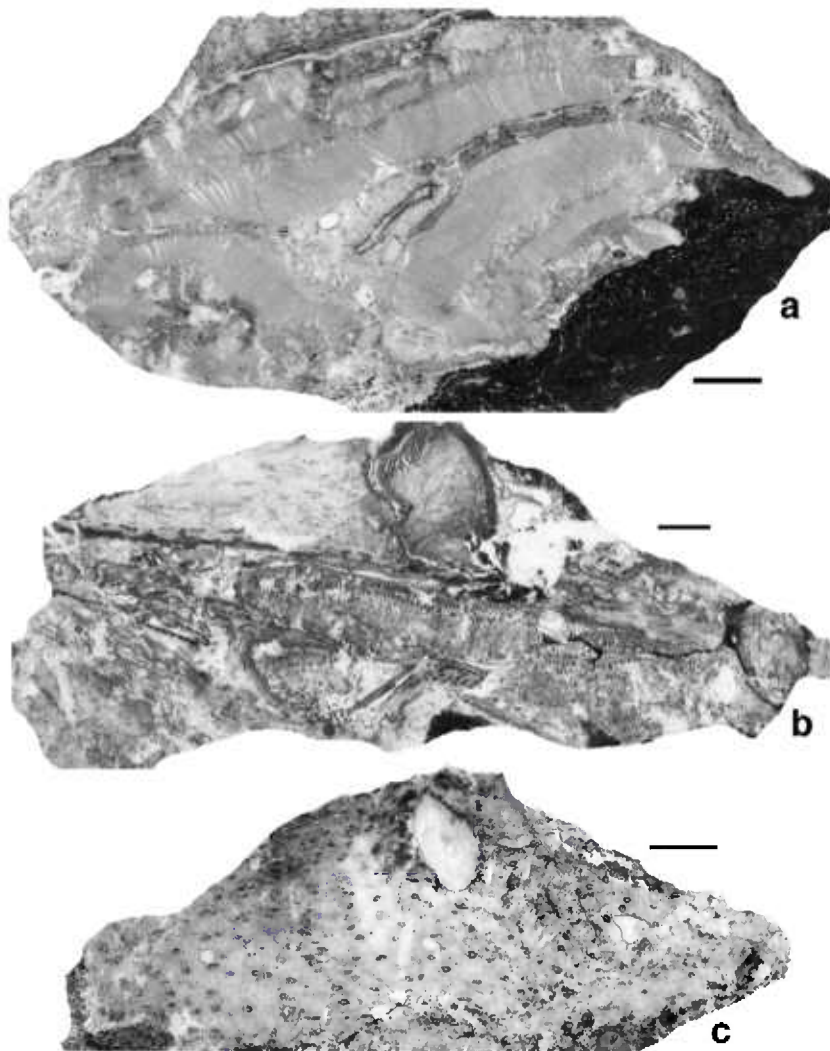


Fig. 9. *Medullosa* organs. a. *Medullosa* stem with multiple vascular bundles, each surrounded by secondary xylem. b. *Myeloxylon*, the rachial organ of *Medullosa*, intermixed with laminate foliage. c. *Myeloxylon* parenchyma with embedded vascular bundles. Scale bars=1 cm.

4.1.1. Coal-ball flora

Sixty-two species have been described from Calhoun coal-ball assemblages (Phillips, 1980), excluding root taxa. Many of these are organ taxa, particularly reproductive organs, some of which cannot be incorporated into unique whole-plant taxa. Using various means to infer the number of biological species, the total number of species present in the peat flora may lie somewhere in the mid-30s, which is a low diversity compared to modern tropical rain forests but comparable to subtropical peat-accumulating swamps. Most of the species known from the Calhoun coal bed were identified in the current analysis, which represents the largest set of coal-ball replicates ever sampled from one site. There are a number of species that have been previously described

from the Calhoun coal bed but are not represented in our current dataset; this reflects the intensity with which earlier workers focused on discovery of new species, many of which are extremely rare. In our quantitative analyses, most taxa are represented by stems with which reproductive organs and leaves can be associated. Exceptions are *Psaronius* and *Medullosa*, which are the most abundant taxa and are represented primarily by roots and foliage, respectively. Reproductive organs (fern synangia, seeds, and pollen organs) and foliage (*Pecopteris*, *Alethopteris*, and *Neuropteris* species) are relatively rare and cannot be associated uniquely with particular stem taxa. Consequently, these important sources of biomass (reproductive organ and foliage) have to be treated at the generic level.

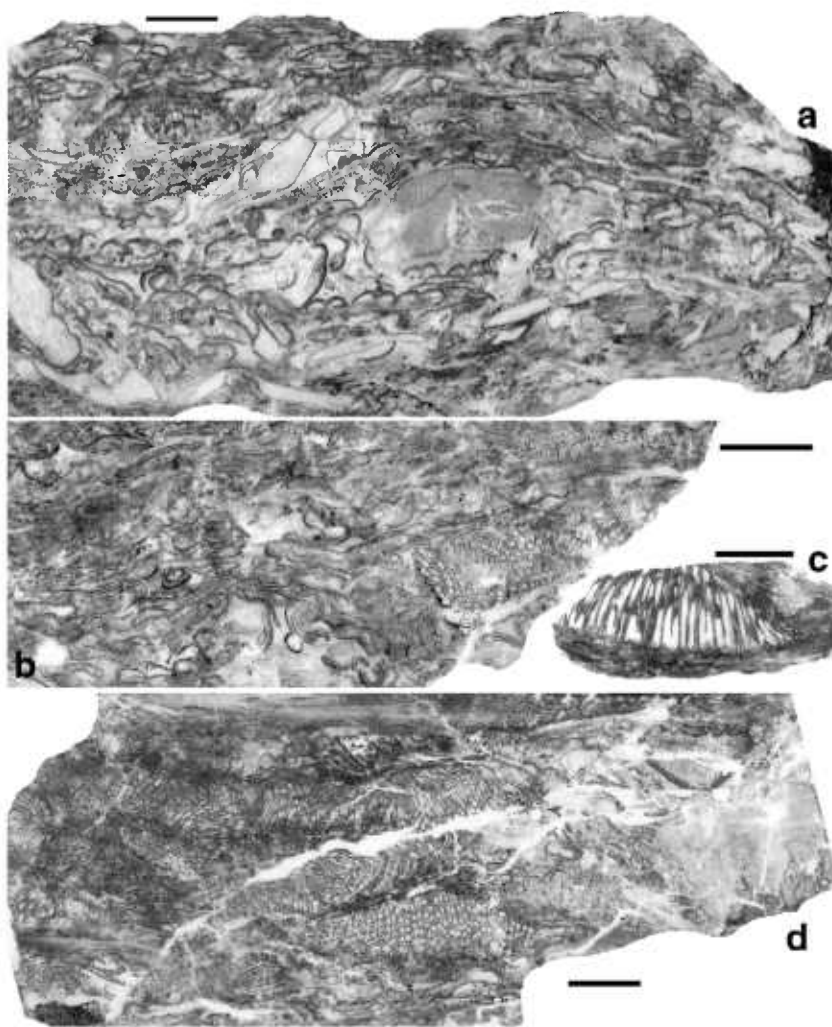


Fig. 10. *Medullosa* organs. a. Foliage of the *Alethopteris* type. Note penetrating *Psaronius* outer roots. b. Foliage of the *Alethopteris* type intermixed with the pollen organ medullosan *Dolerotheca*. c. Oblique longitudinal section of *Dolerotheca*. d. Several *Dolerotheca* intermixed with vegetative foliage. Scale bars=1 cm.

Tree ferns of the genus *Psaronius* comprise the most abundant component of the Calhoun coal-ball flora. In this study, the following three species of *Psaronius* stems were identified: (1) *P. chasei* (Fig. 7a), (2) *P. blicklei* (Figs. 7b, 8a), and (3) *P. magnificus*. The most common organs of these plants are roots, particularly those from the outer parts of the stem root mantle (Figs. 6a, 8c), which are composed mostly of air spaces. Less common are roots from the inner part of the root mantle, generally found closely investing stems (Fig. 7a, b). Quantitative analysis of the carbon content of these organs indicates that the inner root mantle is a high biomass tissue, whereas the outer root mantle has the lowest carbon per cubic centimeter than any tissue pro-

duced by trees in the Calhoun peat forest (Baker and DiMichele, 1997). Fertile foliage, largely assignable to *Scolecoperis*, is uncommon, although it occasionally occurs in great abundance (Fig. 8b, c).

Medullosan pteridosperms are of secondary importance to *Psaronius*, although they dominate some zones of coal-ball profiles and are more abundant at the Berryville locality than at New Calhoun. Stems of *Medullosa* (Fig. 9a) are rare and not differentiable to the many species suggested by the diversity of ovules identified in the flora. Foliage accounts for most of the medullosan vegetative debris. The most common foliar parts are rachis and petiolar axes assignable to the organ taxon *Myeloxylon* (Fig. 9b, c). Leaf laminae, particularly

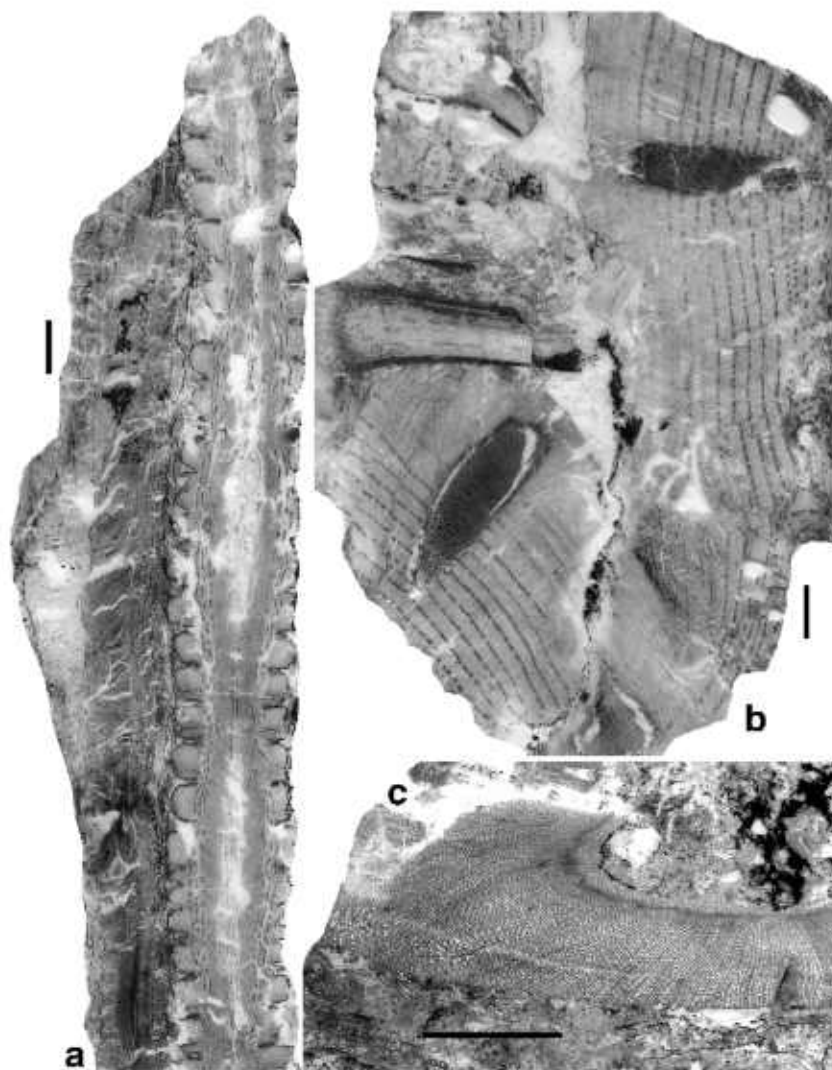


Fig. 11. *Sigillaria* organs. a. Oblique cross section of *Sigillaria elegans* stem with attached leaf cushions. *Sigillaria* periderm is appressed against the left side of the stem. b. *Sigillaria* stem periderm. Dark secretory bands alternate with thick-walled cells. Large parichnos aerating strands run obliquely through the periderm. c. *Sigillaria* stele and wood. Note undulatory outer margin of stele, a characteristic of the genus. Scale bars=1 cm.

Alethopteris and *Neuropteris*, sometimes occur in dense layers (Fig. 10a, b). Mixed in with the foliage, sometimes in unusual abundance, are pollen organs assignable to the organ genus *Dolerototheca* (Fig. 10b, c, d).

Sigillaria elegans (= *Sigillaria brardii* in compression preservation) shares subdominance with *Medullosa* on a landscape basis, but like *Medullosa*, dominates some coal-ball zones, particularly at the New Calhoun locality. *Sigillaria* vegetative remains consist of stems, many of which still bear leaf cushions (Fig. 11a) and pieces of periderm, often with the banding and large parichnos strands characteristic of some species in this genus (Fig. 11b). *Sigillaria* stelar morphology is dis-

tinctive, characterized by an undulatory outer surface (Fig. 11c). Anatomically, sigillarian leaves are characterized by a v-shaped vascular strand, sometimes separated into two distinct strands (Fig. 12c). The stigmarian root systems of *Sigillaria* bore distinctive rootlets, generally much smaller than those of other arborescent lycopsids and characterized by the presence of connectives (columns of tissue joining the small vascular strands to the outer cortex: Fig. 6c). *Sigillaria* reproductive organs are assignable to the species *Mazocarpon oedipternum* and can be either microsporangiatic (Fig. 12a) or megasporangiatic (Fig. 12b), bearing multiple megaspores per sporangium.

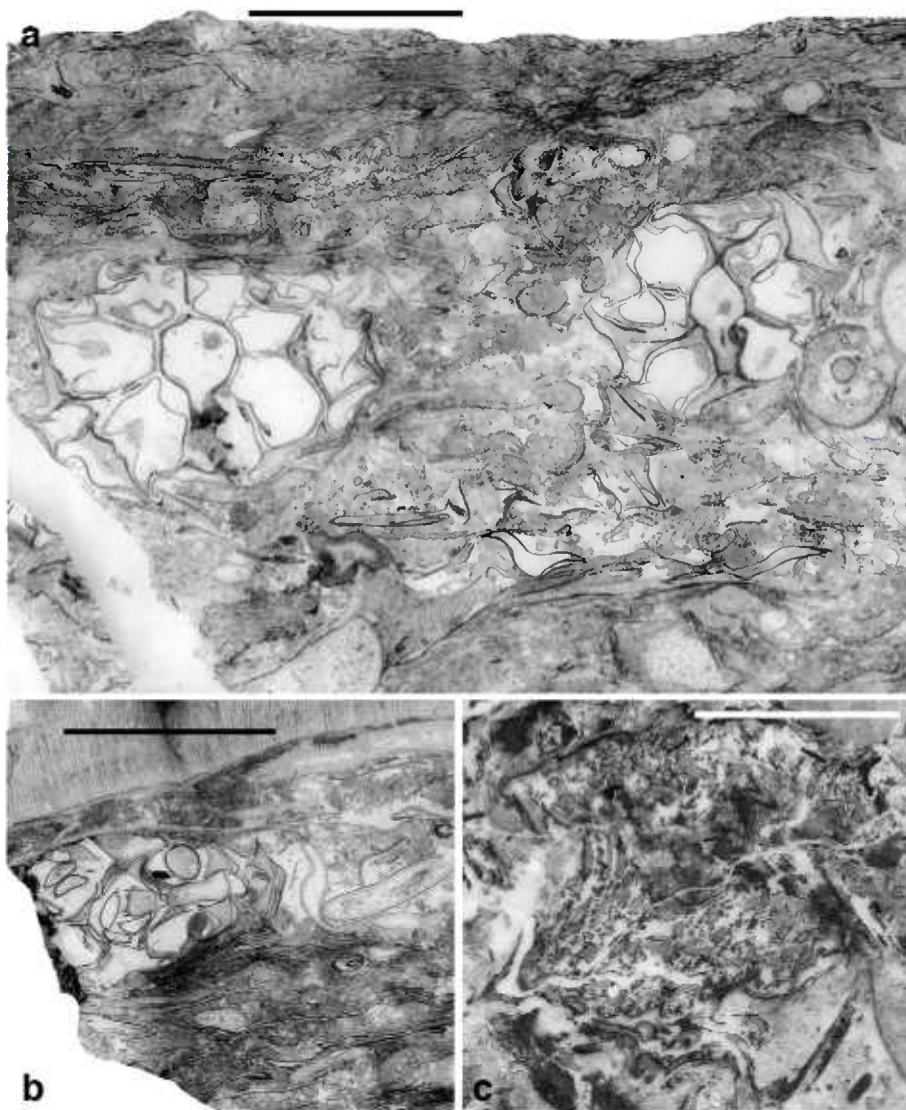


Fig. 12. *Sigillaria* organs. a. Two microsporangiatic cones, *Mazocarpon oedipternum*, from which spores have been released. b. Megasporangiatic *Mazocarpon oedipternum* with megaspores remaining in the sporangia. c. *Sigillaria* leaves. These leaves are partially decayed, but even in this condition they are identifiable by their v-shaped or paired vascular strands. Scale bars=1 cm.

Calamites of the genera *Arthropitys* and *Calamodendron* have been identified in the Calhoun flora, although only *Arthropitys* was encountered in this study. Stems of *Arthropitys* can be quite large and woody (Fig. 13a). In the Friendsville coal bed, at the Allendale locality, a calamite stem was found nearly 45 cm in diameter (Willard and Phillips, 1993). Large cones attributable to the genus *Calamostachys* (Fig. 13b) are found rarely. Calamite roots (Fig. 6b) are assignable to the organ genus *Arthroxyton*.

A diversity of small plants is found in the flora, drawn from each of the major evolutionary lineages: sphenopsids, ferns, lycopsids, and pteridosperms. Sphenopsids

belonging to the species *Sphenophyllum plurifoliatum* (Fig. 14a, b) frequently are found in mixed assemblages or evidence growth in litter. Reproductive organs assignable to *Bowmanites bifurcatus* (Fig. 14b) occur rarely. Next to *Sphenophyllum*, small ferns are most common, mostly the genera *Zygopteris* (Fig. 15a), *Anachoropteris* (Fig. 15b), *Botryopteris* (Fig. 15c), *Zygopteris* (Fig. 16a), and *Ankyropteris*. Small lycopsids are represented by *Paurodendron fraipontii* (Fig. 15d), a centrally rooted plant similar in morphology to some of the primitive forms of *Selaginella*. The most common ground-cover and liana growth forms of pteridosperms are *Callistophyton poroxyloides* (Fig. 15e) and *Heterangium americanum*.

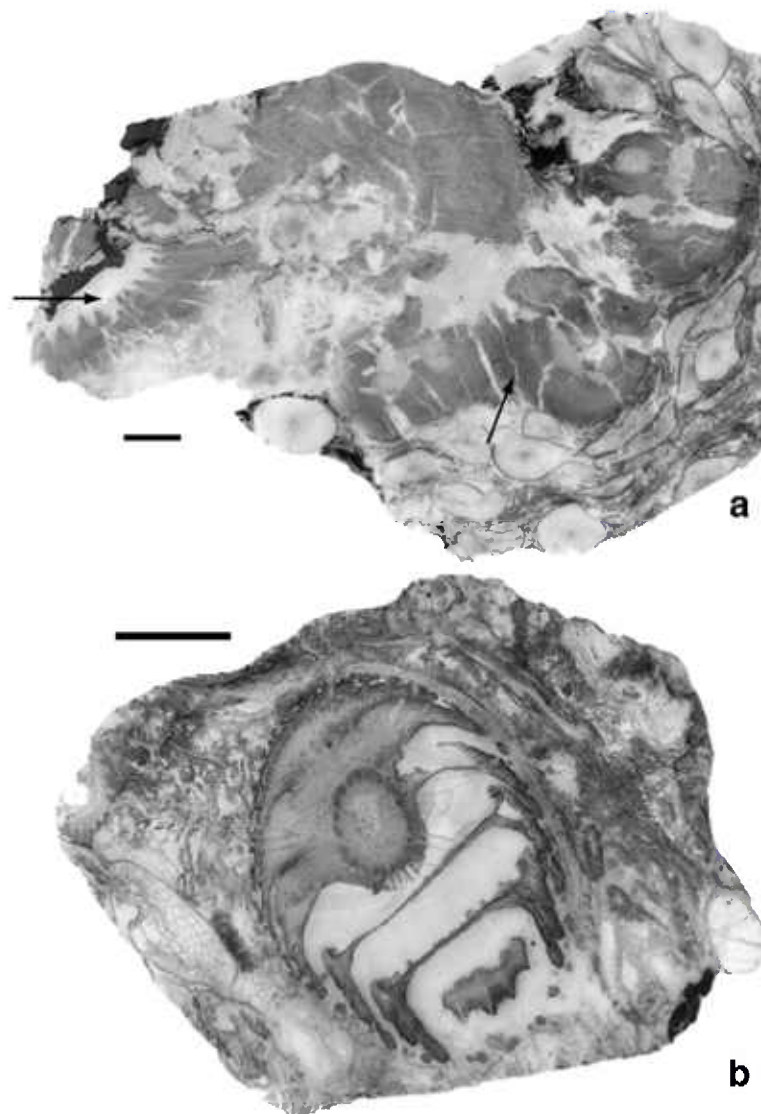


Fig. 13. Calamitean organs. a. Stem of *Arthropitys* bearing small lateral branch. Pith and stele of main axis at arrow 1. Lateral branch at arrow 2. b. *Calamostachys* cone in oblique section. Scale bars = 1 cm.

Seeds of *Callistophyton*, assignable to *Callospermarion* (Fig. 15f) are commonly encountered. These small plants often occur together in mixed assemblages (Fig. 16a).

Cordaites are rarely encountered in the Calhoun coal-ball flora but are worthy of mention because they are so prominent in many Middle Pennsylvanian floras. Cordaites generally occur as isolated stems in assemblages dominated by other kinds of plants. Fig. 16b illustrates a mixed assemblage dominated by medullosan foliar debris, including sigillarian reproductive organs, calamite stems, and a fragmentary cordaitalean stem, that is clearly recognizable by its septate pith.

4.1.2. Miospore flora

In this study, sixty-eight miospore taxa were identified from samples of the Calhoun coal bed. Forty-three taxa were identified from the roof shale, with twelve species exclusive to the roof. Thirty-three miospore taxa were identified from the underclay, with only three exclusive to it. The apparent difference in biodiversity among the three depositional environments most likely reflects the much more intensive sampling of the coal, which was the focus of

the study. Nearly all the miospore taxa have been correlated with source to at least the major plant group level, and the majority of taxa have been correlated with source fructifications and whole plant assemblages. Therefore, the taxa provide a biodiversity estimate of 34 species for the coal, comparable to calculations based on coal-ball assemblages.

Ferns, primarily tree ferns, are the most abundant component of palynofloras of the Calhoun coal bed and associated strata (Table 4). The most common species is *Speciososporites minor* (Fig. 17d,e), which dominates most miospore assemblages. *Apiculatisporis saetiger* (Fig. 17c) ranks second in most samples, followed by species of *Cyclogranisporites* (Figs. 17l) and *Punctatisporites minutus* (Fig. 17a). All of these miospore assemblages were produced by species of *Psaronius* and indicate dominance of *Psaronius* “minor”, *P. blicklei*, and *P. magnificus* (Lesnikowska, 1989).

Medullosan pteridosperms are poorly represented in miospore assemblages because medullosan prepollen typically is too large to be included on miospore slides. *Monoletes*, produced by *Medullosa*, is present rarely throughout these assemblages. *Vesicaspora wilsonii*,

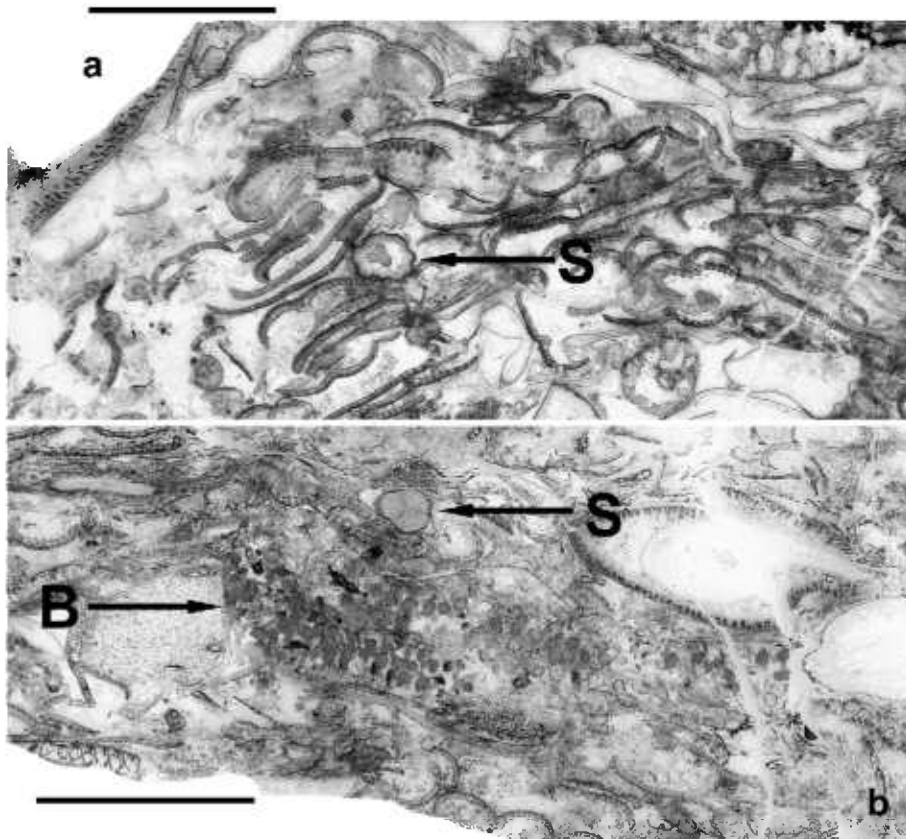


Fig. 14. *Sphenophyllum* organs. a. *Sphenophyllum* stem (S at arrow) in a ground mass of medullosan foliar material. b. *Bowmanites* cone (B at arrow) and *Sphenophyllum* stem (S at arrow) intermixed with medullosan foliar remains. Scale bars = 1 cm.

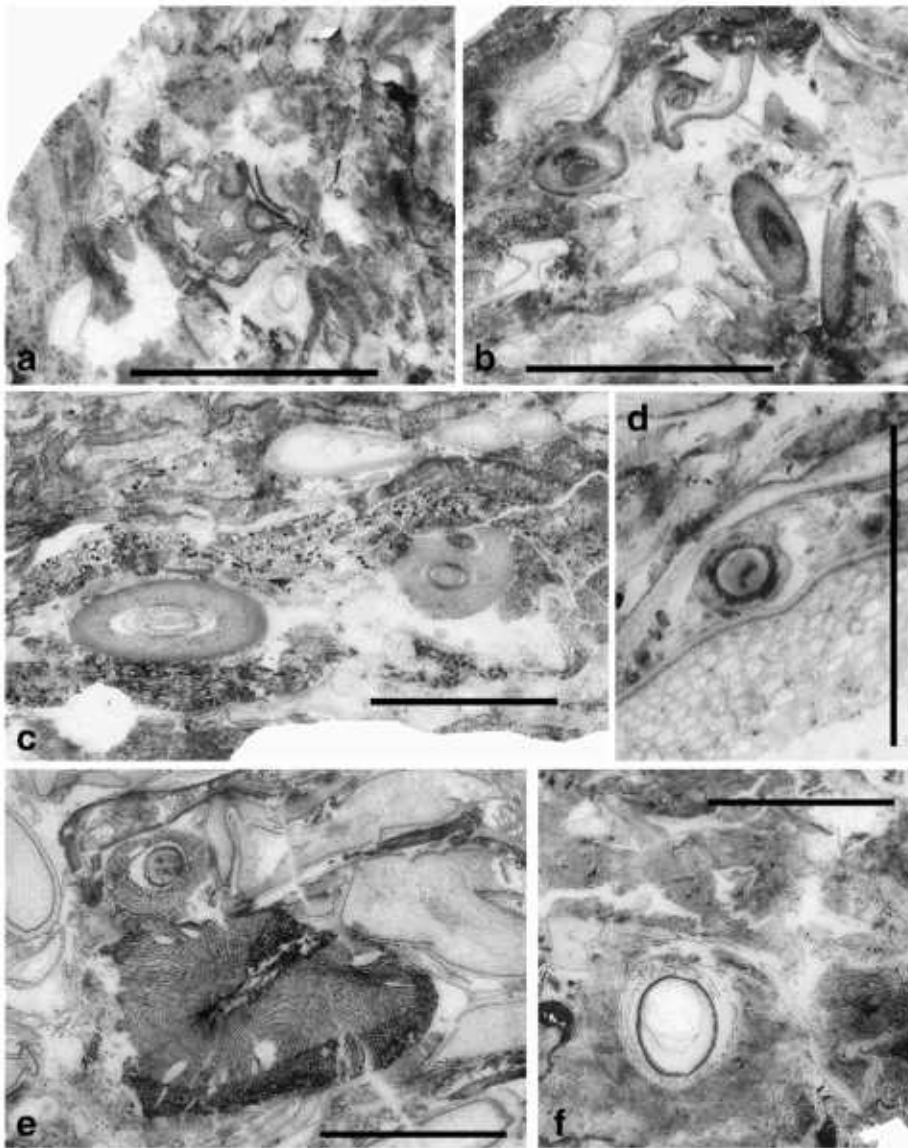


Fig. 15. Ground cover plants. 1. Fern, *Zygopteris*. b. Fern, *Anachoropteris involuta*. c. Fern, *Botyopteris forensis*. d. Sellaginalean lycopsid, *Paurodendron fraipontii*. e. Pteridosperm, *Callistophyton poroxyloides*. f. Ovule of *Callistophyton*, *Callospermarion pusillum*. Scale bars=1 cm.

produced by the Callistophytaceae, also is present occasionally.

Both sigillarian and small lycopsids are represented in the miospore record from the Calhoun coal bed. *Crassispora* (Fig. 17m), produced by *Sigillaria*, is an abundant component of some profiles at the New Calhoun site, although *Crassispora* is relatively rare at the Berryville locality. *Endosporites*, produced by *Chaloneria*, is present occasionally in low abundance at both localities. Other lycopsid species present rarely include rare *Cirratriradites saturnii* and *Cadiospora magna*.

Calamites are represented primarily by species of *Calamospora*, which are present consistently in all samples.

Laevigatosporites vulgaris was also produced by calamites and is present rarely in miospore assemblages of the Calhoun coal bed. Cordaitean pollen, primarily species of *Florinites* (Fig. 17n, o, p), is present at both localities, but cordaitean pollen is slightly more abundant at the Berryville site than at the New Calhoun site.

The greatest diversity of understory plants consists of small ferns. Forty-four species and twenty genera of fern miospores were identified in the Calhoun coal bed and associated strata. The most abundant taxa include *Laevigatosporites minor* (Fig. 17f), *Deltoidospora* spp. (Fig. 17i), *Granulatisporites* spp. (Fig. 17g), and *Triquitrites* spp. Other taxa present in the assemblages are

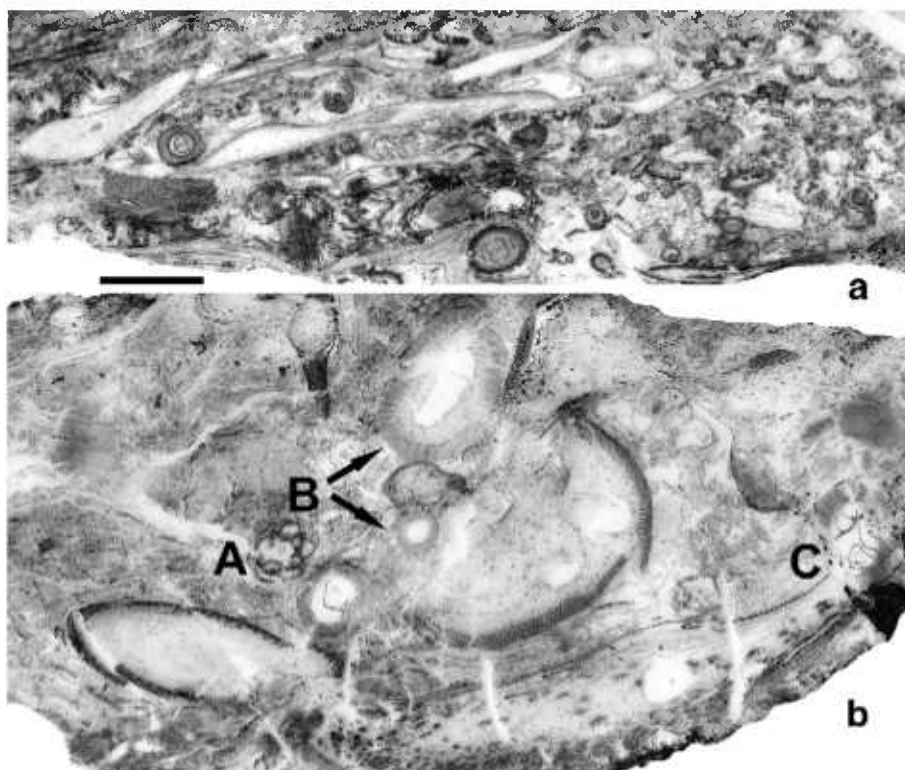


Fig. 16. Mixed assemblages. a. Mixed assemblage of ground cover plants, including *Zygopteris* and *Botryopteris*. b. Mixed assemblage of medullosan organs, *Mazocarpon* (sigillarian) peduncle (A), calamite stems (B at arrows), and cordaite stem (C). Scale bars=1 cm.

Microreticulatisporites nobilis (Fig. 17h), *Ahrensisporites guerickei* (Fig. 17j), and *Reinschospora triangularis* (Fig. 17k).

4.1.3. Compression floras

The underclay of the Calhoun coal bed at both the New Calhoun and Berryville sites contains a macroflora preserved as carbonized compressions and impressions in a medium gray claystone with little distinct bedding. In places, the plant remains are abundant and give the claystone a dark gray color and finely laminated bedding. All compression collections are dominated overwhelmingly by pteridosperms. This underclay appears to have formed in a swamp setting, inferred from the rich organic composition and the lack of physical features typical of paleosols (bioturbation, evidence of extensive rooting, or horizonation and pedogenic fabric).

Three compression collections were made at the New Calhoun site, only two of which had identifiable foliar plant remains (Table 1). In each collection, the most abundant species are the pteridosperms *Neuropteris scheuchzeri* and *Neuropteris ovata*. Other elements include calamite stems, *Asterophyllites equisetiformis*, *Sphenopteris* sp., leaves of *Sigillaria*, *Pecopteris* sp.,

fine roots, and pteridosperm axes. No reproductive remains were identified, and no charcoal was noted. The third collection was made from a dark gray, highly organic claystone in which pteridosperm axes were abundant and often highly decayed.

One collection was made at the Berryville site (Table 1) from claystones within 5 cm beneath the bottom of the coal bed. Pteridosperm axes are the most frequently encountered plant organs in this collection. The most common foliage type is again *Neuropteris scheuchzeri*, associated with *N. ovata*, *Pecopteris* sp., *Cordaite* sp., possible leaves of *Sigillaria* (which may be stigmarian rootlets), fine roots, and charcoal.

4.2. Spatio-temporal patterns: coal balls

The coal-ball profiles and their respective taxonomic compositions by zone are shown in Table 2. Results of the ordination of samples (Fig. 18) and r-mode cluster analysis (Fig. 19) reveal four principal assemblages. The most common assemblage is dominated by *Psaronius* tree ferns. Several assemblages are dominated by or rich in either *Sigillaria* lycopsids or *Medullosa* pteridosperms, and rare assemblages have high percentages of the

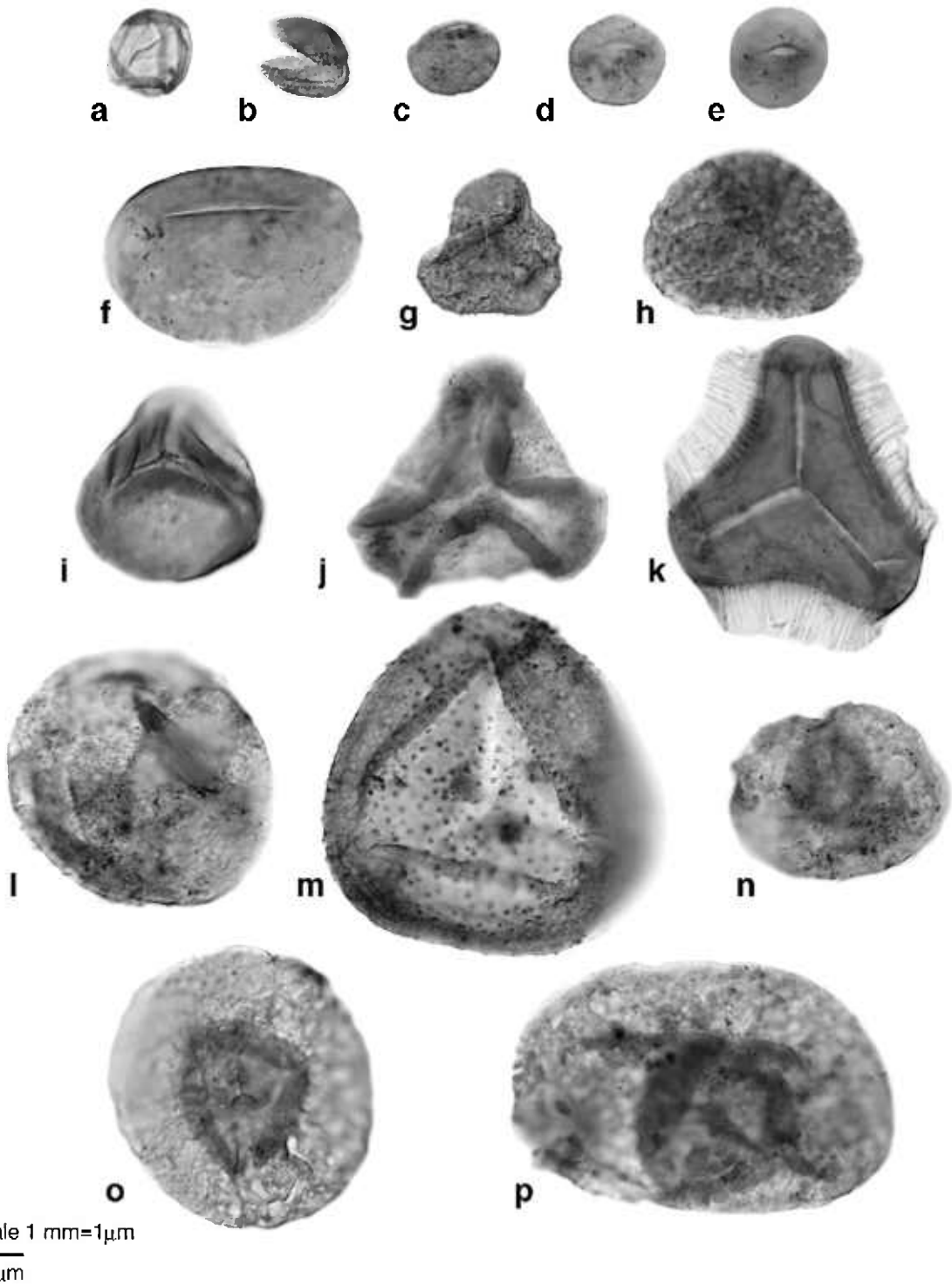


Fig. 17. Miospores from the Calhoun coal bed. a. *Punctatisporites minutus*. b. *Spinospirites exiguus*. c. *Apiculatisporis saetiger*. d and e. *Speciosporites minutus*, different focal planes. f. *Laevigatosporites minor*. g. *Granulatisporites minutus*. h. *Microreticulatisporites nobilis*. i. *Deltoidospora* sp. j. *Ahrensisporites guerickii*. k. *Reinschospira triangularis*. l. *Cyclogranisporites* sp. m. *Crassispora kosankei*. n. *Florinites millottii*. o. *Florinites volans*. p. *Florinites mediapudens*.

Table 1
Relative abundance of compression impression fossils in underclays from New Calhoun and Berryville sites, southeastern Illinois, USA

	NC USNM38324	NC USNM 38883	BV 1990-24
Sample Size (quadrats)	61	56	106
<i>Neuropteris scheuchzeri</i>	51	51	20
<i>Neuropteris ovata</i>	36	7	2
<i>Pecopteris</i> spp.	0	1	7
<i>Calamites</i> spp.	5	0	0
<i>Asterophyllites equisetiformis</i>	1	0	0
<i>Sphenopteris</i> sp.	1	0	0
<i>Cordaites</i> sp.	0	0	4
<i>Sigillaria</i> leaves	0	1	2
Pteridosperm axes	Not counted	25	78
Fine roots	5	8	3
Charcoal	0	0	3

calamitean *Arthropityx*. Gradational assemblages are common, generally with mixtures of tree ferns, lycopsids, and pteridosperms. Assemblages heavily dominated by tree ferns form the core of the ordination, surrounded by samples with progressively higher levels of sigillarian lycopsids and medullosan pteridosperms.

A UPGMA q-mode cluster analysis of taxa found four major groups (Fig. 19), each including only one of the four end-point dominants (*Psaronius*, *Medullosa*, *Sigillaria*, or *Arthropityx*). Each of the clusters also included a variety of smaller, ground cover plants and vines. However, no patterns were identifiable among the minor plants associated with the dominant tree forms.

Two major gradients are detectable from the ordination analysis (Fig. 18). The first gradient has *Psaronius* and *Medullosa* as end points, with mixed floras in-between. The second gradient has *Psaronius* and *Sigillaria* as end points, with a few intermediate assemblages enriched in *Medullosa*. These gradients differ in their importance at the Berryville and New Calhoun sites. Coal-ball profiles from Berryville are preferentially enriched in medullosans, and the *Psaronius-Medullosa* gradient is well developed in samples from that profile, with no occurrences of *Sigillaria*-dominated samples. In contrast, the New Calhoun profiles contain significant occurrences of sigillarians, and thus the *Psaronius-Sigillaria* gradient is most prominent in profiles at this site (there are no *Medullosa*-dominated samples from New Calhoun).

The differences in profiles do not appear to represent temporal changes at either site (i.e., there are no systematic trends in dominance patterns from the bottom to

the top of coal-ball profiles). The data patterns suggest that *Psaronius* was widespread and a consistently abundant element in this peat-forming swamp, yet there are few samples exclusively dominated by *Psaronius*. It appears that *Medullosa*, *Sigillaria*, and even *Arthropityx* occupied essentially the same kinds of subhabitats as the tree ferns. Occasional dominance by one of the non-fern groups could simply be a happenstance of sampling or of local populational abundance. Furthermore, the spatio-temporal distribution of charcoal does not reveal a relation between fire-frequency and taxonomic composition in this swamp. Thus, there are no clear indicators of strong physical control of plant distribution among these samples.

4.3. Spatio-temporal patterns: miospores

Miospore assemblages in the Calhoun coal bed and associated strata (roof shale and underclay) are shown in Table 3. These samples are dominated uniformly by fern spores. Typically, these are tree-fern spores, which exceed 60% of the assemblage in eleven of seventeen samples (Table 4). In the remaining five coal samples, spores of small ferns are dominant or co-dominant. In the roof shale from the New Calhoun site, however, lycopsid spores are subdominant to tree ferns. Lycopsid spores typically are present in small quantities in coal samples, but they are common (3–13%) in profile A at the New Calhoun site. Sphenopsid spores typically are present in low abundances, only exceeding 10% in the underclay sample. Cordaite pollen comprises <5% of assemblages, and pteridosperm prepollen is rare because its size normally exceeds the mesh size on sieves used to isolate palynomorphs from coal.

The dominant tree-fern species usually is *Speciososporites minutus*. One exception is New Calhoun Profile A, in which *S. minutus* dominates only the underclay and basal coal sample, whereas *Cyclogranisporites* spp. dominate the upper three zones (Table 3). Other common tree-fern spores are *Punctatisporites minutus*, *Apiculatisporis saetiger*, and *Spinisporites exiguus*. The most common small-fern spores are *Laevigatosporites* spp. and *Deltoidospora* spp. The sigillarian miospore *Crassispora kosankei* is dominant only in the roof shale from New Calhoun Site B and is abundant in all zones from New Calhoun Site A. Cordaitean pollen is represented by *Florinites* spp., and *Calamospora parva* is the most abundant sphenopsid miospore.

Two major patterns are recognizable in the first two axes of the palynological-sample ordination. Most notable is the strong sorting of samples by parent coal bed, and the strong sorting of Calhoun samples in particular by profile

(Fig. 20). Calhoun coal bed samples form three clusters attributable to profiles Calhoun A and Calhoun 4 from the New Calhoun site, and Berryville 1 and 2 from the Berryville site. Samples of the Calhoun underclay and roof shale from the New Calhoun site and Calhoun channel samples B and C also occur near other samples from the coal. Samples from the Bristol Hill and Friendsville coal beds cluster separately from each other and from those of the Calhoun coal bed. An ordination of samples taken exclusively from the Calhoun coal bed produced an identical pattern of sample distribution as that found in the ordination of samples from all three coals. When patterns of species distribution are superimposed on these sample distribution patterns it is clear that there are overlaps among the coal beds and that the differences in clusters reflect patterns of proportional representation of the dominant tree-fern species, and in the commonness of the less abundant (but occasionally dominant) sigillarian lycopid trees and open forms of vegetation.

The second major pattern is reflected by plant distribution (Fig. 21). The largest number of samples, including representatives from all three coal beds and both sites in the Calhoun coal bed, are dominated by *Speciosporites minutus*, ranging from about 25–50% of spore count data. In a subset of samples from the Friendsville coal bed, *Punctatisporites minutus* is approximately codominant with *Speciosporites minutus* and/or *Apiculatisporis saetiger*. Only a small number of samples from the Friendsville coal bed are dominated by *A. saetiger*. However, this species is important in many samples from the Calhoun and Friendsville coal beds, where it strongly overlaps with *Speciosporites minutus* in abundance distribution. This group of samples accounts for 34 of the 46 samples analyzed. Using the groupings established by Lesnikowska (1989), the two dominant spore types (*Speciosporites minutus* and *Punctatisporites minutus*) were both produced by the tree-fern reproductive organ taxon *Scolecoperis illinoense*-group, which was borne on plants of *Psaronius chasei*. *Apiculatisporis saetiger* was produced by *Scolecoperis monothrix*, which was borne on plants of *Psaronius blicklei*.

Smaller groups of samples were dominated by lycopids or enriched in various kinds of ground-cover plants or less common tree-fern species. Calhoun profile A from the New Calhoun site, and several samples from the Berryville profiles show very equable patterns of dominance with codominance of the tree-fern spore *Cyclogranisporites* (produced by the *Scolecoperis latifolia*-group) borne on the tree ferns *Psaronius magnificus* and *Psaronius* “sclerotic bands” morphotype (Lesnikowska, 1989). The *Cyclogranisporites*-rich assemblages also have abundant *Crassispora* sp.,

produced by sigillarian lycopids and a variety of ground-cover ferns. Several samples from the Bristol Hill and Friendsville coal beds contain high percentages of calamitean spores and *Endosporites* spores, the latter produced by the small, sub-arborescent lycopid *Chaloneria*. In all of these cases, the spore composition points to open vegetation, possibly with exposed substrates that were conducive to the development of a rich array of ground cover or small shrubs. Such vegetation also was identified in the coal-ball samples, both quantitatively and also by inspection of etched surfaces. In the coal balls, layers enriched in small, ground cover plants tended to be thin and often were masked by later root penetration or burial by organs of the canopy plants, and so had to be picked out by detailed examination (Fig. 16a).

Special note should be made of the samples from the Calhoun underclay and roof shale, sampled at the Berryville and New Calhoun sites. The New Calhoun underclay sample falls squarely in the group of samples dominated by *Speciosporites minutus*. However, the compression macroflora of the underclay is overwhelmingly dominated by the pteridosperm *Neuropteris scheuchzeri* (a typical clastic-swamp species), and large pteridosperm pollen is not included in the palynological analysis. Furthermore, tree-fern foliage is uncommon in the underclay compression flora. The miospore assemblage from the Berryville underclay is dominated strongly by *Cyclogranisporites*, and cordaitan pollen (*Florinites*, *Wilsonites*) is subdominant (15%). *Calamospora* is common (7%), and the rest of the assemblage is comprised of small-fern spores. The megaspore flora includes two *Monoletes* specimens and three lycopid megaspores. Although the representation of pteridosperms remains poor even with inclusion of the megaspore fraction, the abundance of cordaitan and tree-fern miospores is consistent with their presence in the Berryville underclay megaf flora. The roof shale flora is the only sample from the Calhoun coal bed that is dominated by *Crassispora*, produced by sigillarian lycopids. *Crassispora* appears to have been produced in relatively small numbers and thus under-represents the importance of the parent plants (Willard and Phillips, 1993), perhaps accounting for the rarity of *Crassispora* dominance in the palynological profiles, compared to its more frequent, but still uncommon, dominance of some coal-ball zones.

5. Discussion

A reconstruction of the original vegetation of the Calhoun coal swamp is illustrated in Fig. 22, based on

Table 2

The taxonomic composition and relative abundance of taxa in ED BTcoal-ball samples used in the statistical analyses

Collection Site and Zone	<i>Pennsylvanioxylon</i>	<i>Mesoxylon</i>	<i>Anachoropteris</i>	<i>Anachoropteris clavata</i>	<i>Anachoropteris involuta</i>	<i>Anachoropteris gillotii</i>	<i>Botryopteris</i>	<i>Botryopteris forensis</i>
C RS1	0.29	0.07	0.02	0.05	0.04		0.06	0.31
C RS2	0.31	0.27	0.04		0.04		0.04	0.35
B RS 2	0.35		0.03	0.29	0.97		0.06	1.50
P RS1	0.49		0.39		0.10		0.10	0.20
B VS1-1				0.75	3.75	50		
B V1-2				0.15	0.15	0.1		0.30
B VS1-3					0.74			1.24
B VS1-4					0.66	0.09	0.09	3.31
B VS1-5								
B VS1-6								
B VS1-7	0.76		0.07	0.28				0.97
B VS2-1	0.08				0.60			0.76
B VS2-2				0.41				
B VS2-3				1.36				
B VS2-4					1.20		0.08	1.12
B VS2-5				0.14	0.14			0.27
C VS1-1								0.51
C VS1-2	0.60							
C VS1-3								
C VS1-4								0.37
C VS1-5								0.78
C VS2-1	0.73			0.24				0.24
C VS2-2								0.56
C VS2-3								0.90
C VS2-4								0.22
C VS2-5								0.32
C VS2-6								
C VS3-1								
C VS3-2		0.91						
C VS3-3		9.09						1.82
C VS3-4								1.93
C VS4-1								
C VS4-2		0.38						
C VS4-3	0.17							0.84
C VS4-4								0.25
C VS5-1			0.37					
C VS5-2	3.09	0.81					0.07	0.14
C VS5-3	0.12		0.12				0.24	
C VS5-4				0.12			0.23	0.57
C VS5-5	0.35	0.66						0.15
C VS5-6	1.14							0.10
C VS5-7								
C VS5-8							0.09	0.09
C VS6-1								
C VS6-2								
C VS6-3	0.24			0.24				0.24
CVS6-4				0.17				0.67
CVS6-5	0.15							0.31
C VS7-1								
C VS7-2	0.63							
C VS7-3	2.86						0.32	0.32
C VS7-4								
C VS7-5								
C VS7-6	0.26						0.26	1.79
C VS7-7	0.99		0.11					0.44
C VS10-1	1.52			0.76				0.76
C VS10-2	2.01							0.50
C VS10-3								
C VS10-4	0.71							0.36

<i>Botryopteris</i> sp. "pseudoantiqua"	<i>Botryopteris</i> <i>cratis</i>	<i>Zygopteris</i>	<i>Rhabdoxylon</i> <i>americanum</i>	<i>Ankyropteris</i>	Ferns	<i>Psaronius</i>	<i>Medullosa</i>	<i>Sutcliffia</i>	<i>Heterangium</i> <i>americanum</i>
		0.17			0.12	45.27	11.13	0.00	0.25
		1.58			0.12	44.59	18.17		0.59
		0.15			0.38	57.87	31.76		0.88
		0.59			0.59	82.67	12.80		0.49
.25	0.12				0.00	0.75	46.08	37.94	
					1.05	7.11	42.68		0.21
		0.50				30.11	56.26		
0.46		0.57			2.14	76.86	3.50		1.23
0.73		0.46				58.79	18.98		0.93
					0.36	65.07	14.94		
		0.41		0.28	0.28	19.25	63.37		0.83
0.08					0.53	21.50	65.86		0.08
		0.41			0.83	45.77	43.89		0.41
					0.68	72.81	15.63		2.72
		0.24	0.08		0.24	42.06	52.35		0.16
					0.55	92.10	5.31		
	0.12					73.55	16.29		
						9.44	14.91		
						32.33	2.76		
						87.09	0.74		
						88.54	0.58		0.19
						88.81	8.27		0.24
						52.27	4.82		0.56
		0.22				91.44	1.58		0.68
		0.11				24.11	7.92		0.11
		0.16				77.41	17.69		
						48.15	46.91		
						57.18	36.95		0.59
					0.73	31.70	18.35		1.82
						63.65	5.46		1.82
						90.34	4.83		0.97
						19.46	18.44		
					0.38	56.49	11.30		0.38
						76.61	4.04		0.34
					0.12	74.45	1.37		
					0.37	79.06	11.96	0.37	0.37
	0.24	0.14			0.48	31.92	13.68	0.27	0.21
					0.12	28.29	4.69		0.12
						78.35	4.47		0.23
					0.15	32.69	3.40		0.31
		0.25			0.18	20.32	27.42		0.15
						68.66	20.22		0.00
		0.62			0.09	68.86	26.08		0.09
						16.56	33.13		
		0.28				27.10	15.92		0.56
						90.63	4.76		0.00
						94.84	0.50		0.17
						29.92	1.07		0.31
						51.07	14.89		
						55.97	13.84		
						59.17	8.57		
						32.13	5.66		
						14.86	3.28		0.16
						76.22	4.35		0.51
		0.22				48.83	2.71		0.43
		0.76			0.76	81.82	9.85		
						46.37	38.10		1.50
						21.35	6.87		
				0.71		62.92	3.57		

(continued on next page)

Table 2 (continued)

Collection Site and Zone	<i>Callistophyton poroxyloides</i>	<i>Schopfiastrum</i>	<i>Arthropitys</i>	<i>Sphenophyllum</i>	<i>Sigillaria</i>	<i>Chaloneria</i>	<i>Paurodendron</i>	<i>Idanothekion</i>	Fern sp. 3
C RS1	0.18	0.01	1.73	0.48	39.78	0.05	0.01		
C RS2	0.40				33.94				
B RS 2	0.65		2.97	0.47	1.64		0.03		
P RS1	0.40		0.40	0.20	0.30	0.30			
B VS1-1		2.75		1.75	0.62	4.74			
B V1-2	0.90		33.83		13.47				
B VS1-3	0.50		0.25		10.41				
B VS1-4	4.45		4.63	2.36			0.09		
B VS1-5			2.32		16.66	1.39			
B VS1-6	0.73		3.63		11.26	2.18			
B VS1-7	0.55		0.83	1.80	10.32				
B VS2-1	0.53		0.30		9.54	0.15			
B VS2-2	1.24		1.66	0.41	4.97				
B VS2-3	2.72				3.40		0.68		
B VS2-4	0.80		1.04	0.24	0.40				
B VS2-5	0.68		0.55						
C VS1-1				1.01	8.65				
C VS1-2			0.24	0.36	74.08	0.24			
C VS1-3			2.26		62.41	0.25			
C VS1-4			2.58	0.37	8.86				
C VS1-5	0.78		0.19		8.93				
C VS2-1				0.24	0.49	0.73			
C VS2-2	0.22			0.22	41.12	0.22			
C VS2-3	0.22		2.03	1.13	1.35	0.22		0.22	
C VS2-4	0.11			0.56	66.85				
C VS2-5	0.63			0.79	3.00				
C VS2-6	1.65			0.82	2.47				
C VS3-1	0.29		2.05	0.88	2.05				
C VS3-2			1.82		44.69				
C VS3-3			7.27		9.07			1.82	
C VS3-4				1.93	0.00				
C VS4-1			3.34		58.75				
C VS4-2			2.42		27.92	0.75			
C VS4-3	0.17			1.01	16.66			0.17	
C VS4-4			7.10		16.70				
C VS5-1			2.24	0.37	4.86				
C VS5-2	0.21		0.96	0.27	46.94	0.82			
C VS5-3	0.35		0.59		65.14				
C VS5-4	0.34		0.46	0.57	14.66				
C VS5-5	0.08		0.69	0.23	61.28				
C VS5-6	0.30		1.29	0.70	48.10				
C VS5-7	0.00		7.75	0.51	2.86				
C VS5-8	0.18		0.27	0.27	3.37				
C VS6-1	1.23		49.08						
C VS6-2	1.40		0.28	0.56	53.91				
C VS6-3	0.95		0.24	0.48	2.14				
CVS6-4	0.50		0.17	1.50	1.50				
CVS6-5	0.00		4.73	1.07	62.29				0.15
C VS7-1	4.26		4.26		25.53				
C VS7-2					29.56				
C VS7-3	0.32		0.92	0.32	26.65	0.64			
C VS7-4	0.00				62.21				
C VS7-5	0.00				81.69				
C VS7-6	0.26		0.26	0.26	15.86				
C VS7-7			3.96	1.87	40.46				
C VS10-1	0.76		1.52	0.76	0.76				
C VS10-2			1.00	1.50	8.52	0.50			
C VS10-3				0.00	71.11	0.67			
C VS10-4	1.07		7.84	0.36	22.46				

the quantitative findings of this study. In this reconstruction, the habitat is depicted as a planar peat swamp, as defined by Cecil et al. (1985). The forest is dominated by a framework of *Psaronius* canopy trees with patches of *Medullosa* and *Sigillaria* dominance. *Calamites* are depicted as rare components, and primarily as large trees rather than as dense thickets of undergrowth, which may have been more common in Middle Pennsylvanian swamps. Patches of ground-cover ferns, sphenopsids, and pteridosperms primarily occupy light gaps created by tree falls or by disturbances such as fire. High rates of litter degradation, prior to burial or water coverage, are reflected by only small amounts of surface litter in exposed areas.

The flora of the Calhoun coal bed (Table 5) is exceptionally well known, a consequence of years of detailed studies by numerous paleobotanists who focused on describing new plants and their morphological and systematic significance. Quantitatively, the flora is dominated by tree ferns with subdominant pteridosperms and sigillarian lycopsids. The dominant tree ferns, based on correlation of spores and macrofossils (Lesnikowska, 1989), are *Psaronius chasei* (*Speciososporites* and *Punctatisporites minutus*), *P. blicklei* (*Apiculatisporis saetiger*), and *P. magnificus*/*Psaronius* n. sp. (*Cyclogranisporites* sp.). The vegetation comprised of these plants is spatially heterogeneous at several scales. At the coarsest level, that of the landscape average, the Berryville and New Calhoun sites have persistent differences in composition. Both miospore and coal-ball analyses indicate that the New Calhoun samples are differentially enriched in *Sigillaria*. At the Berryville site, coal-ball assemblages are enriched in pteridosperms. In miospore analyses, this enrichment is manifested as a greater abundance of *Spinospores exiguus* and some small-fern taxa. The abundance of pteridosperms in the Berryville flora may enhance the apparent relative abundance of subdominant forms in the palynological analysis, because pteridosperm pollen is generally excluded from palynological samples by its large size (accounting for patterns of low dominance and high diversity in spore-pollen counts).

At the scale of zones within coal-ball profiles, the differential enrichment in pteridosperms vs. *Sigillaria* persists irregularly throughout the thickness of the coal at the two sites. However, this compositional difference is manifested quantitatively rather than qualitatively within the profiles, indicating that there was local “drift” (in the sense of Hubbell and Foster, 1986) of the dominant tree taxa at a site through time. Additionally, both palynological and coal-ball analyses document

compositional variance among individual samples/profiles, which may reflect local topographic/hydrologic differences within the swamp landscape. These differences may be analogous to variability within the subtropical Everglades wetland, where a topographic change of a few centimeters and the associated difference in hydroperiod is sufficient to alter community composition and the characteristic pollen signature, all within a distance of <50 m (Willard et al., 2001, 2002).

At the most finely resolved scales (i.e., centimeter by centimeter examination of individual coal-ball faces), it is possible to identify fire horizons marked by layers of fusain (fossil charcoal). These taxonomically diverse assemblages of sprawling ground-cover plants probably are indicative of disturbance and high light exposure. Layers enriched in seeds also have been identified, possibly reflecting seasonal patterns of reproduction and seed dispersal.

These different spatial and temporal scales reveal a landscape in which there were persistent local plant populations that shifted over the landscape, in effect demonstrating slow but oscillatory changes in composition at any given sampling site (coal-ball or palynological profile site). Within this background were local patches of disturbance, local topographic and hydrologic variability, and probably limited fires, creating the spatial heterogeneity that drove local shifts in the plants on the smaller scale. The most common pattern, revealed both by palynology and coal balls, is the long-term persistence of stands of tree ferns, lycopsids, and pteridosperms in more or less constant proportions.

5.1. Underclay to coal transition

At both the New Calhoun and Berryville localities, the underclay of the Calhoun coal bed is organic rich and contains a compression flora. The underclay at these sites does not appear to have a pedogenic overprint, which may occur in some circumstances, indicating clear differences between conditions of underclay formation and peat deposition (Cecil, 2003; Cecil et al., 2003). Rather, it seems that organic accumulation began on wet floodplains, possibly in low areas, such as shallow lakes, accounting for the accumulation of organic material at first within muds and then later as peat.

There is a marked contrast between the palynology and macroflora from underclay sediments. The macroflora at the three sites sampled is dominated by pteridosperms, particularly the neuropterids, *Neuropteris scheuchzeri*, and *N. ovata*. The palynological samples, however, are highly dominated by tree-fern spores.

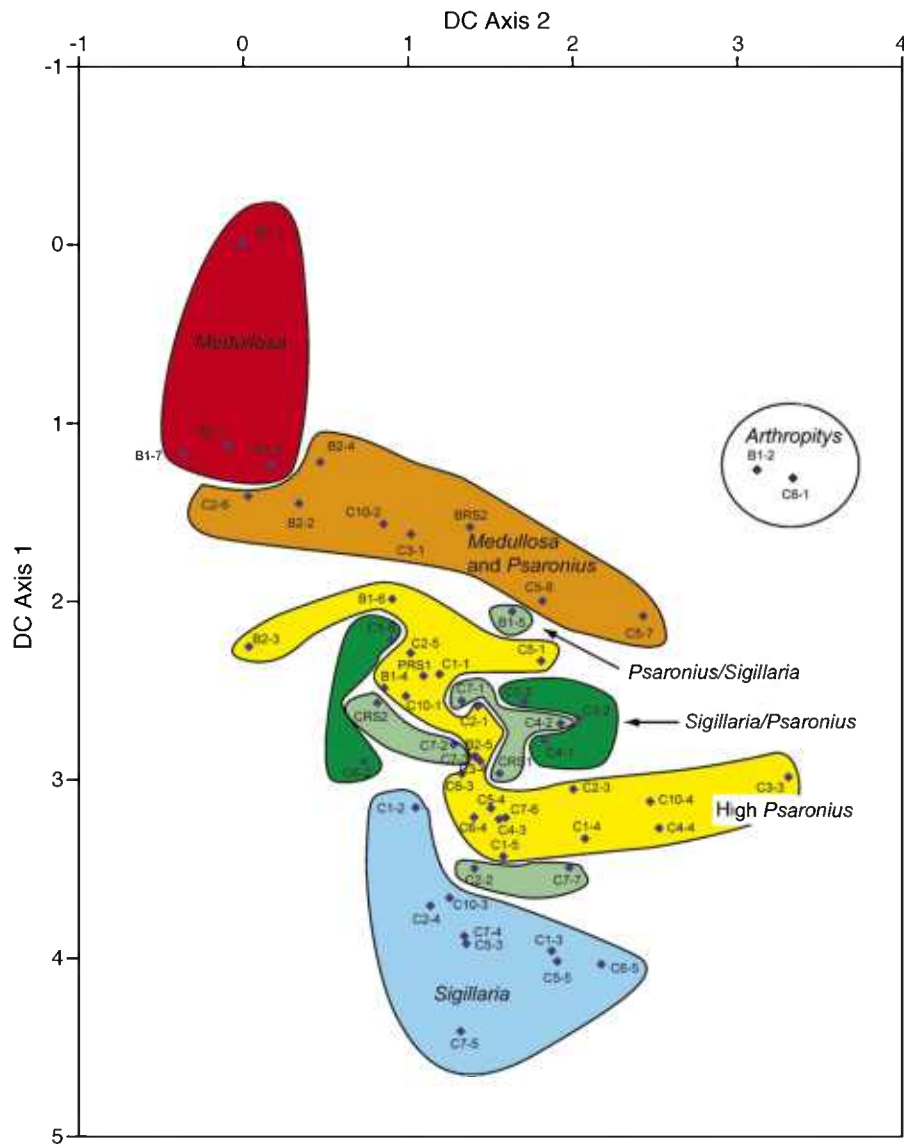


Fig. 18. Detrended correspondence analysis (DCA) of coal-ball zones and random samples from the New Calhoun and Berryville localities of the Calhoun coal bed, plus a single random sample from the Palestine locality of the Bristol Hill coal bed. Samples are labeled by locality (C = New Calhoun; B = Berryville; P = Palestine). Numbers indicate profile and zone. Random samples are labeled 'RS.' Colors distinguish samples with similar dominance-diversity composition. Yellow = *Psaronius* dominance. Light green = *Psaronius* with subdominant *Sigillaria*. Dark green = *Sigillaria* with subdominant *Psaronius*. Gray = *Sigillaria* dominance. Red = *Medullosa* dominance. Orange = *Medullosa* and *Psaronius* in approximately equal abundances. Two samples with abundant *Arthropitys* are shown in white. Note the predominance of Berryville samples enriched in *Medullosa* and the predominance of New Calhoun samples enriched in *Sigillaria*.

Although bits of tree-fern foliage occur in the compression assemblages, indicating that plants were present, this foliage is only a minor component. Again, the explanation may lie in the exclusion of pteridosperm pollen from palynological preparations, in combination with the massive spore output of tree ferns. In coal-ball analyses, however, the correlation of tree-fern abundance in peat and in palynology is high. Additionally, the tree-fern

spores correlate well with tree-fern reproductive organs and with vegetative remains in profile zones, conforming to the “whole-plant” models established by Lesnikowska (1989).

Spatial heterogeneity in the onset of peat formation is another possible explanation for the discordance between macroflora and microflora in the underclay samples analyzed. It is possible that peat accumulation

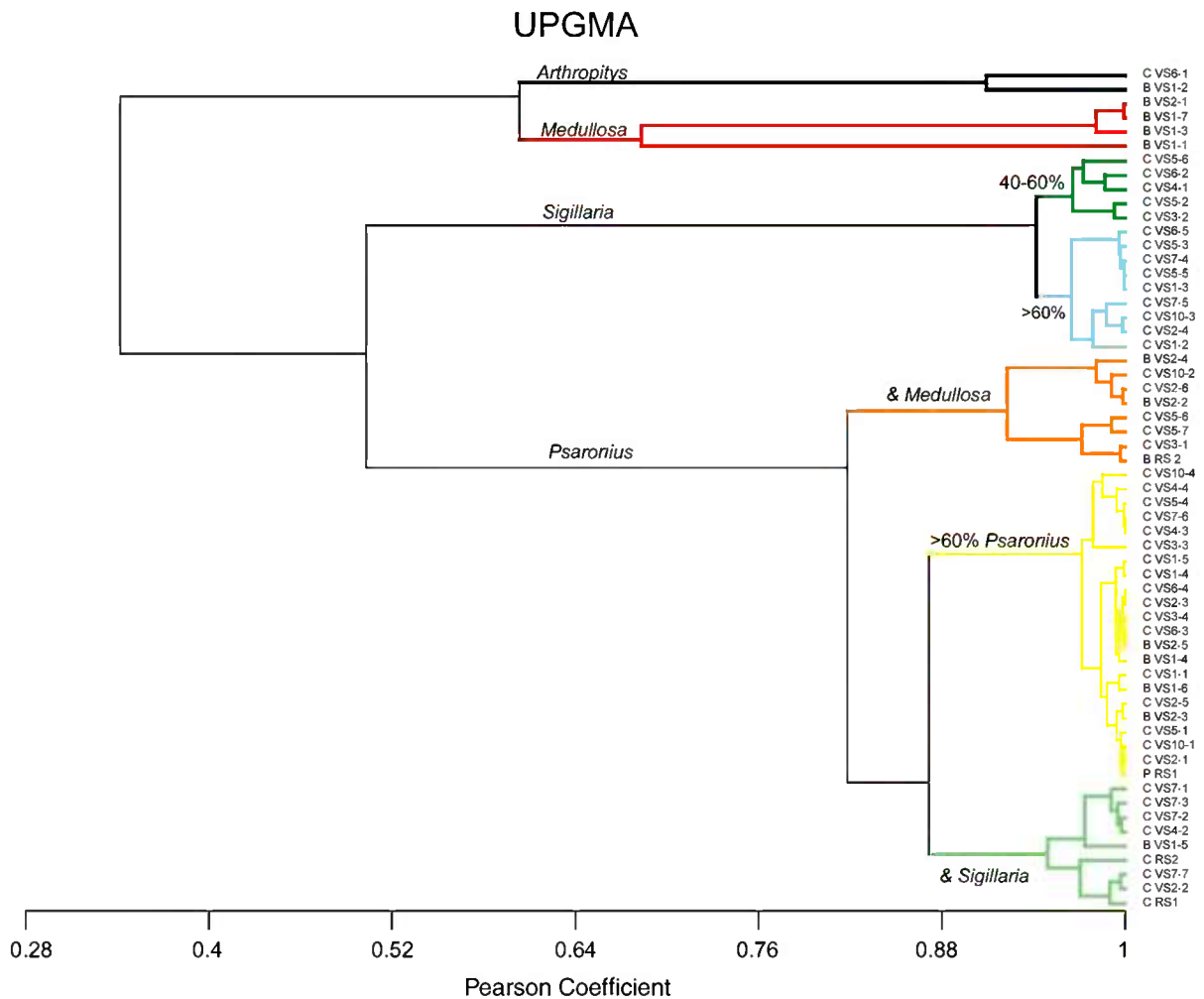


Fig. 19. Cluster analysis (unweighted pair groups method) of coal-ball samples from the Calhoun and Bristol Hill coal beds. Same sample suite analyzed by DCA in Fig. 18. Colors correspond to colors used in the ordination. Each of the major taxa (*Psaronius*, *Sigillaria*, *Medullosa*, and *Arthropitys*) is dominant in one of the major groups. As in the ordination, *Medullosa* and *Sigillaria* occur in mixed assemblages dominated by or rich in *Psaronius*.

began in patches on the landscape, perhaps in response to increasingly wet climate and consequent reduced clastic transport as plant roots covered and bound mineral soils (Cecil, 1990). As a result, the base of the Calhoun coal bed would be asynchronous. It appears from the analysis of Late Pennsylvanian floras that tree ferns were favored on organic-rich peat substrates, whereas pteridosperms were favored in clastic to organic-enriched clastic substrates. Thus, tree-fern spores, produced in vast quantities and widely dispersed, would have left a strong signature even in those portions of the landscape dominated by pteridosperms. Although rare, fossils of tree-fern foliage were found in the compression floras indicating the presence of these plants somewhere on the landscape locally.

5.2. Late Pennsylvanian coal beds: vegetational comparisons

In addition to the Calhoun coal bed described in this paper, the Late Pennsylvanian (Missourian) Friendsville and Bristol Hill coal beds of Illinois (Willard and Phillips, 1993) and Duquesne coal bed of Ohio (Pryor, 1993, 1996) have been examined extensively for macrofossils. All of these coal beds have similar floristic composition and vegetation. Assemblages dominated by tree ferns, primarily *Psaronius blicklei* and *P. chasei*, are most common. Other assemblages are dominated by medullosan pteridosperms and by sigillarian lycopsids. In the Duquesne coal bed, the sigillarian assemblages also include cordaites and calamites. In addition, assemblages dominated by the small lycopsid *Chaloneria* were identified in the

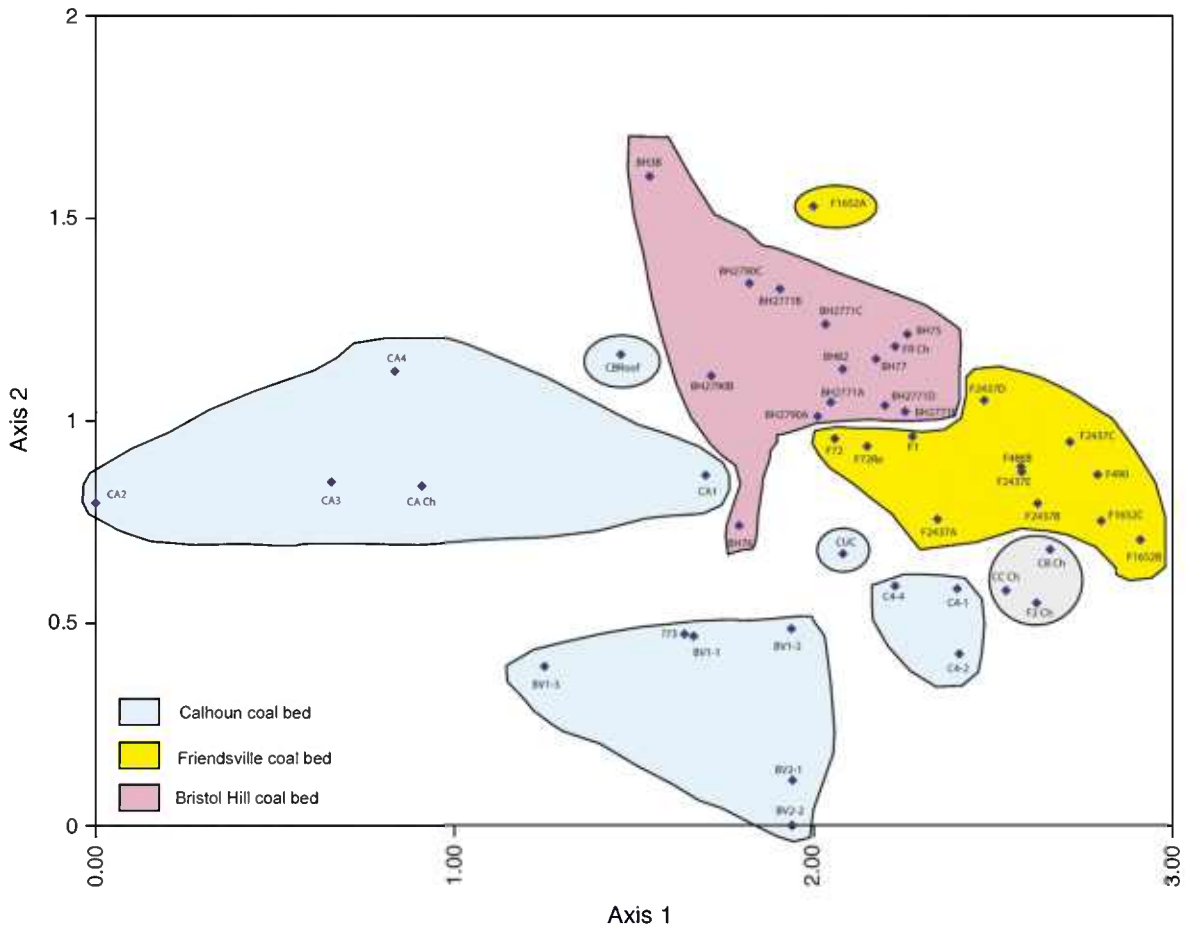


Fig. 20. Detrended correspondence analysis (DCA) of palynological samples from the Calhoun, Bristol Hill and Friendsville coal beds. Samples are labeled by coal bed, and samples from the Calhoun coal bed are labeled by locality (C = New Calhoun and B = Berryville locality from the Calhoun coal bed; BH = Bristol Hill coal bed; F = Friendsville coal bed). Samples are numbered either by profile number/letter and zone number/letter, or by the designation 'CH' if whole seam channel samples. The roof shale sample from the New Calhoun site is labeled 'roof' and the sample from the New Calhoun underclay is labeled 'UC.' In this plot, colors indicate the sample source; gray = Calhoun coal bed, yellow = Friendsville coal bed, pink = Bristol Hill coal bed. Note that most coal beds cluster separately from one another. See text for details.

Duquesne coal bed. Similar assemblages have been found in late Middle Pennsylvanian (Desmoinesian) coal beds of the Illinois Basin (DiMichele et al., 2002) and have been identified palynologically from several Late Pennsylvanian coal beds of the Illinois Basin (Peppers, 1996).

For the Late Pennsylvanian Duquesne coal bed of Ohio, Pryor (1993) used root penetration analysis to assess patterns of succession and determined that sigillarians were most common in the lower parts of the coal bed, medullosans in various admixtures with *Psaronius* in the middle parts of the coal bed, and heavily *Psaronius*-dominated assemblages in the upper parts of the coal bed. In addition, she noted that ground cover, shrubs, and vines were most common in the *Psaronius-Medullosa* mixed assemblages. As in the Calhoun coal bed, analysis of coal

balls revealed a prominent component of ground cover and vines in some phases of peat swamp development.

The studies by Pryor (1993,1996) suggest distinct changes in the physical character of the Duquesne swamp during peat accumulation. Palynological analysis of the Bristol Hill coal bed (Willard and Phillips, 1993) also suggests similar changes in the composition of the swamp forest during peat accumulation, with an increase in the abundance of tree ferns. Palynological studies of other Late Pennsylvanian coal beds (Helfrich and Hower, 1989; Grady and Eble, 1990) also suggest changes in composition during peat accumulation and complex vegetational responses, perhaps related to the changes in ground-water regime or regional climate. Macrofossil studies of coal-ball profiles from the Calhoun coal bed, however, do not reveal any particularly noteworthy temporal changes in vegetation

Table 3

Percent abundance of miospore taxa present in coal and underclay samples from New Calhoun and Berryville sites, Calhoun coal bed southeastern Illinois

Sample Code	<i>Punctatisporites minutus</i>	<i>Speciososporites minutus</i>	<i>Apiculatisporis saetiger</i>	<i>Punctatosporites minutus</i>	<i>Spinosporites exiguus</i>	<i>Cyclogranisporites</i> spp.	<i>Acanthotriletes echinatus</i>	<i>Ahrensiasporites guerrickii</i>	<i>Apiculatisporites spinulistratus</i>	<i>Apiculatisporites lappites</i>	<i>Calamospora</i> spp.	<i>Camptotriletes</i> sp.	<i>Convolutispora</i> spp.	<i>Crassispora kosankei</i>	<i>Deltoidospora</i> spp.
BV11	3.3	23.0	7.0	4.7	9.3	12.7	1.3	2.3	0.3	0.0	3.0	0.0	0.0	0.7	0.0
BV12	13.0	28.8	7.4	4.0	5.4	11.7	0.7	2.3	0.3	0.0	0.0	0.0	0.0	0.0	0.7
BV13	3.0	13.3	7.3	1.3	11.0	8.3	1.3	9.3	0.0	0.0	0.0	0.0	2.0	0.3	4.0
CalVS2	7.7	41.7	0.7	6.7	15.0	4.7	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.7	0.7
CalVS2Yel	4.8	49.0	2.4	8.6	12.1	4.1	0.0	2.1	0.0	0.0	0.0	0.0	1.4	0.0	1.4
CalProfB	23.0	47.0	23.7	0.0	1.7	0.7	0.3	0.0	0.3	0.0	0.7	0.0	0.0	0.0	0.0
CalRoofB	6.3	15.0	10.3	0.0	1.3	11.7	0.3	0.3	0.0	2.0	4.3	0.0	0.3	17.3	4.3
CalChanC	14.0	39.3	27.7	0.0	7.7	0.3	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0
CalUC	9.4	34.8	8.4	0.0	9.7	6.0	0.7	1.3	0.0	0.0	12.4	0.0	0.3	0.7	0.3
CalA1	4.3	33.4	14.4	0.0	0.3	8.0	2.0	1.7	0.0	0.0	9.4	0.3	0.3	3.3	4.0
CalA2	0.0	4.0	1.0	0.0	0.0	9.4	0.0	8.7	0.0	0.0	2.3	2.0	4.7	5.7	11.4
CalA3	0.3	11.7	3.3	0.0	0.0	14.3	0.0	5.7	0.0	0.0	6.0	2.3	3.7	5.0	14.3
CalA4	0.7	11.0	3.3	0.0	0.3	18.4	0.0	2.3	0.0	0.0	9.0	2.7	1.0	13.4	2.3
CalChanA	0.7	13.5	7.1	0.0	1.4	12.2	0.0	6.1	0.0	0.0	3.7	0.0	4.7	3.7	7.1
Cal41	11.7	52.2	17.7	0.0	5.4	2.3	0.0	0.0	0.0	0.0	4.0	0.0	0.3	0.0	0.0
Cal42	7.0	48.5	20.1	0.0	10.4	4.3	0.3	0.0	0.0	0.0	1.0	0.0	0.0	0.3	0.0
Cal44	9.0	41.0	17.7	0.0	5.7	4.3	0.0	0.3	0.0	0.0	4.7	0.0	0.0	0.0	0.0
BH-	23.7	23.0	7.7	0.0	0.0	4.7	3.3	0.0	0.0	1.3	19.3	0.0	0.0	0.0	0.3
FlatRock															
BHMac75	25.0	23.7	14.0	0.0	0.0	7.3	0.0	0.0	0.0	0.0	12.3	0.0	1.0	0.0	0.3
BHMac76	15.3	15.7	10.3	0.0	0.0	16.0	0.0	0.0	0.0	0.0	16.3	0.0	0.3	0.0	0.7
BHMac77	27.0	28.3	6.7	0.0	0.0	6.0	0.0	0.0	0.0	0.3	13.3	0.0	0.7	0.0	0.7
BHMac3B	2.5	15.5	2.5	0.0	0.0	5.0	1.5	0.0	1.0	0.0	31.5	0.0	0.0	0.5	1.5
BHMac82	24.0	23.3	7.7	0.0	0.7	20.7	1.7	0.0	0.0	1.3	7.7	0.0	0.0	0.0	0.7
BH2771A	16.7	37.4	4.9	0.0	0.0	12.8	0.0	0.0	0.0	0.0	10.8	0.0	0.0	2.3	0.0
BH2771B	13.8	25.6	4.5	0.0	0.0	12.8	0.0	0.0	0.0	0.0	6.6	0.0	0.3	3.1	0.3
BH2771C	17.0	36.0	2.7	0.0	0.0	13.0	0.0	0.0	0.0	0.0	11.7	0.0	0.3	1.7	0.7
BH2771D	23.0	42.3	1.6	0.0	0.3	6.2	0.0	0.0	0.0	0.0	12.1	0.0	0.0	0.0	1.0
BH2771E	22.3	45.0	3.3	0.0	0.0	7.0	0.0	0.0	0.0	0.0	10.0	0.0	0.0	0.0	0.0
BH2790A	15.7	40.7	2.7	0.0	0.0	12.3	0.0	0.3	0.0	0.0	7.7	0.0	0.0	0.3	1.0
BH2790B	8.3	31.7	2.3	0.0	1.0	26.7	0.0	0.0	0.7	0.7	10.7	0.0	0.0	0.3	0.0
BH2790C	3.7	37.5	9.3	0.0	0.0	33.5	0.0	0.0	0.0	0.7	4.0	0.0	0.0	0.4	0.4
Mac73	2.0	13.7	4.7	0.0	1.7	17.7	1.0	0.0	1.7	3.3	4.3	0.0	0.0	0.0	1.7
FR1652AR	4.3	10.7	11.3	0.0	10.0	5.3	0.0	0.0	0.3	4.0	8.7	0.0	0.0	0.0	0.7
FR1652B	21.7	15.3	31.3	0.0	14.7	1.7	3.3	0.0	0.0	9.3	0.3	0.0	0.0	0.0	0.0
FR1652C	24.3	22.3	28.7	0.0	12.0	1.0	1.0	0.0	0.0	4.3	2.3	0.0	0.0	0.0	0.0
FR72	10.7	27.3	12.7	0.0	2.3	11.3	1.0	0.0	1.7	2.3	6.0	0.0	0.3	0.0	0.3
FR72Re	17.7	30.3	13.3	0.0	1.3	11.3	1.0	0.0	1.7	0.0	2.0	0.0	0.3	0.3	0.3
FR490DRR	31.7	26.7	19.0	0.0	6.7	3.7	0.3	0.0	0.3	6.0	1.3	0.0	0.0	0.0	0.0
FRMac1	19.5	17.1	12.3	0.0	7.2	6.5	7.2	0.0	0.0	0.0	13.0	0.0	0.3	0.3	0.0
FRHill486B	28.7	23.3	19.7	0.0	3.7	5.7	3.0	0.0	0.0	3.7	2.0	0.0	0.0	0.0	0.0
FR2Chan	20.7	20.7	20.3	0.0	22.3	1.7	3.0	0.0	0.0	0.0	1.7	0.0	0.3	0.0	1.0
FR2437A	16.7	44.3	12.3	0.0	5.0	4.0	1.3	0.0	0.0	0.0	4.3	0.0	0.3	0.0	0.7
FR2437B	25.0	27.7	24.0	0.0	5.7	1.0	1.3	0.0	0.0	0.0	2.3	0.0	0.0	0.3	0.3
FR2437C	36.1	26.1	18.7	0.0	5.4	1.3	0.3	0.0	0.0	0.0	3.0	0.0	0.0	0.7	0.3
FR2437D	33.6	29.8	10.2	0.0	3.1	1.7	0.3	0.0	0.0	0.0	6.8	0.0	0.0	0.0	1.7
FR2437E	36.0	35.0	10.0	0.0	3.3	0.3	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0

(continued on next page)

Table 3 (continued)

Sample Code	<i>Endosporites</i> spp.	<i>Florinites</i> spp.	<i>Gillespiesporites venustus</i>	<i>Granulatisporites</i> spp.	<i>Laevigatosporites</i> spp.	<i>Lophotriletes</i> spp.	<i>Microreticulatisporites</i> spp.	<i>Punctatisporites</i> spp.	<i>Cordaitean pollen*</i>	<i>Raistrickia</i> spp.	<i>Reticulatisporites carnosus</i>	<i>Reinschospora</i> spp.	<i>Schopfipollenites</i>	<i>Triquitrites</i> spp.	<i>Verrucosiporites</i> spp.
BV11	0.3	0.3	0.7	4.7	13.7	0.7	0.3	1.0	1.0	0.0	0.0	0.0	0.0	5.0	5.0
BV12	0.0	3.0	1.3	2.3	9.0	1.0	1.0	1.3	3.7	0.0	0.0	0.0	0.0	0.7	1.0
BV13	0.3	0.7	0.0	1.0	15.9	3.0	0.3	9.6	0.7	0.3	0.0	1.7	0.0	4.0	0.3
CalVS2	0.7	0.7	0.0	1.7	7.3	3.7	0.0	0.3	1.0	0.0	0.0	0.0	0.0	0.0	1.0
CalVS2Yel	0.0	0.7	0.3	2.8	6.6	2.1	0.0	1.4	1.0	0.0	0.0	0.0	0.0	0.0	0.0
CalProfB	0.0	1.0	0.3	0.3	0.7	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.3
CalRoofB	4.7	1.3	0.0	2.0	2.3	1.3	0.3	0.0	3.7	1.7	0.0	0.7	0.0	1.0	0.3
CalChanC	0.0	1.7	0.0	0.0	6.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.3	0.7
CalUC	0.3	2.0	0.3	3.7	2.0	1.3	0.7	1.0	2.3	0.0	0.0	0.0	0.0	2.7	0.0
CalA1	0.7	0.0	1.7	1.3	6.7	0.0	0.0	2.0	0.0	2.0	1.3	0.3	0.0	1.0	0.7
CalA2	0.3	0.0	1.7	0.7	9.7	5.4	0.0	2.0	0.0	10.0	16.1	0.0	0.0	0.7	0.0
CalA3	0.3	0.0	0.7	1.3	10.3	2.7	0.7	4.0	0.0	5.3	0.0	2.0	1.0	3.7	1.0
CalA4	0.0	0.0	0.0	0.7	17.1	0.0	0.0	9.0	0.0	1.3	0.0	4.3	0.0	0.7	2.0
CalChanA	0.0	0.0	3.7	1.0	16.9	1.4	0.7	4.1	0.0	7.4	0.0	0.3	0.0	2.0	2.0
Cal41	0.0	0.7	0.0	0.0	4.3	0.0	0.0	0.7	0.7	0.0	0.0	0.0	0.0	0.0	0.7
Cal42	0.0	2.7	0.0	0.0	3.3	0.3	0.3	0.0	2.7	0.0	0.0	0.0	0.0	0.0	1.3
Cal44	0.0	4.0	0.3	0.3	10.3	0.0	0.0	1.0	4.0	0.0	0.0	0.0	0.7	0.3	0.0
BH-	0.0	0.3	0.3	1.0	9.3	0.0	0.3	0.0	2.0	0.0	0.0	0.0	0.0	1.3	2.3
FlatRock															
BHMac75	3.0	0.3	0.3	0.3	7.3	0.0	1.3	0.0	0.3	0.7	0.0	0.0	0.0	1.0	1.3
BHMac76	4.3	0.7	0.7	0.3	8.7	0.0	1.3	0.0	1.3	3.0	0.0	0.0	0.0	3.3	2.3
BHMac77	1.0	1.0	0.0	0.3	8.3	0.0	0.0	1.0	1.3	0.3	0.0	0.0	0.0	4.7	0.0
BHMac3B	11.0	0.5	0.0	1.0	22.0	0.0	0.0	0.5	1.5	0.0	0.0	0.0	0.0	2.0	0.0
BHMac82	0.0	0.0	2.7	0.3	7.3	0.0	0.7	0.0	0.3	0.0	0.0	0.0	0.0	1.0	0.0
BH2771A	3.3	2.0	0.3	1.6	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	1.0
BH2771B	13.1	5.9	0.0	0.3	5.9	0.0	0.0	0.3	0.0	1.4	0.0	0.0	0.0	3.1	1.7
BH2771C	8.0	1.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.7
BH2771D	1.0	0.7	0.0	0.0	4.6	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	3.6	1.3
BH2771E	3.0	0.7	0.0	0.3	3.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	2.7	0.7
BH2790A	5.3	0.7	2.3	1.3	5.0	0.0	1.3	0.3	1.7	0.7	0.0	0.0	0.0	0.7	0.7
BH2790B	3.0	1.3	1.7	0.0	4.7	0.0	0.7	0.7	1.3	1.0	0.0	0.0	0.0	2.7	1.3
BH2790C	0.7	5.5	0.4	3.3	1.5	1.1	0.4	0.4	5.9	0.0	0.0	0.0	0.0	2.9	2.6
Mac73	1.3	11.7	2.0	10.7	7.7	0.3	0.3	0.0	21.3	0.0	0.0	0.0	1.7	0.7	2.3
FR1652AR	25.0	0.7	0.0	1.0	12.3	0.3	0.7	0.3	1.3	0.3	0.0	0.0	0.0	2.3	0.0
FR1652B	0.0	0.3	0.0	1.0	0.3	0.7	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
FR1652C	0.0	0.0	0.0	1.0	1.7	0.0	0.7	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.3
FR72	4.0	2.7	3.3	1.0	4.0	0.0	0.3	0.0	2.7	1.0	0.0	0.0	0.3	3.7	3.3
FR72Re	2.7	0.7	3.7	1.3	7.3	0.3	0.0	0.0	0.7	0.0	0.0	0.0	0.0	1.7	2.3
FR490DRR	0.0	1.3	0.3	0.0	2.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.3	0.0
FRMac1	1.7	3.4	0.3	0.0	5.8	1.4	0.7	1.4	3.8	0.3	0.0	0.0	0.0	1.0	0.0
FRHil1486B	0.7	2.0	0.0	2.0	3.7	0.0	0.0	0.7	2.0	0.0	0.0	0.0	0.0	0.7	0.7
FR2Chan	0.0	0.7	0.0	0.3	4.3	0.0	0.0	1.0	0.7	0.3	0.0	0.0	0.0	0.0	0.7
FR2437A	2.3	0.3	0.3	1.0	4.0	0.0	0.7	0.7	0.3	0.0	0.0	0.0	0.0	0.7	0.3
FR2437B	1.3	0.7	0.0	2.3	5.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.7	0.0
FR2437C	1.0	0.0	0.3	1.0	2.0	0.0	0.7	0.7	0.3	0.0	0.0	0.0	0.3	0.3	0.0
FR2437D	2.0	0.3	0.3	0.3	4.7	0.0	0.7	0.7	0.0	0.3	0.0	0.0	0.3	1.0	1.0
FR2437E	0.0	0.7	1.0	1.0	4.7	0.0	0.0	0.7	0.7	0.0	0.0	0.0	0.3	0.0	2.0

Table 4

Percent abundance of miospores of major plant groups in palynological samples from New Calhoun and Berryville sites, Calhoun coal bed, southeastern Illinois

Profile	Tree ferns	Other ferns	Sphenopsids	Lycopsids	Pteridosperms	Cordaites	Unknown affinity
BV11	61.33	28.67	3.00	1.00	0.00	1.00	5.00
BV12	70.90	20.40	0.00	0.00	0.00	3.68	0.67
BV13	45.51	45.51	0.00	0.66	0.00	0.66	5.65
CalVS2	76.33	17.33	0.00	1.33	0.00	1.00	0.00
CalVS2Yel	81.03	17.93	0.00	0.00	0.00	1.03	0.00
CalProfB	96.33	2.00	0.67	0.00	0.00	1.00	0.00
CalRoofB	45.00	13.33	4.33	22.00	0.00	3.67	1.67
CalChanC	89.00	6.67	2.33	0.00	0.00	1.67	0.33
CalUC	68.90	11.04	12.37	1.00	0.00	2.34	2.68
CalA1	62.54	20.07	9.36	4.01	0.00	0.00	1.34
CalA2	14.38	62.21	2.34	6.02	0.00	0.00	0.67
CalA3	29.67	46.67	6.00	5.33	1.00	0.00	5.67
CalA4	33.78	37.12	9.03	13.38	0.00	0.00	5.02
CalChanA	34.80	47.64	3.72	3.72	0.00	0.00	2.36
Cal41	89.30	6.02	4.01	0.00	0.00	0.67	0.00
Cal42	90.64	5.35	1.00	0.33	0.00	2.68	0.00
Cal44	77.67	12.33	4.67	0.00	0.67	4.00	0.33

during peat accumulation. Instead, the major pattern in the Calhoun peat swamp is one of consistent differences in dominance-diversity patterns at the two sites sampled (Berryville and New Calhoun), and these differences persisted through the entire time of peat accumulation. These patterns in the Calhoun coal bed suggest the persistence of populations through time. On the basis of the data in hand, it cannot be determined whether such differences signal environmental distinctions between the two sites, or simple stochastic differences related to the likelihood of local dominance once certain ratios of various taxa became established early in the history of the peat swamp-mire.

5.3. Vegetational persistence through time: ecological implications

The possibility of vegetational persistence through long periods of time, thousands to tens of thousands of years, is a matter that continues to fuel debates in ecology. Certain models of ecological organization, those that focus on the “individualistic” responses of species to environmental conditions, have focused on vegetational change through time (e.g., Overpeck et al., 1992). Others, more focused on emergent properties of multispecies assemblages have focused on rules of assembly and the potential for long-term persistence of species associations (e.g., Prinzing et al., 2001). These matters, in part, may reflect differences in scale of analysis; both individualistic responses and persistent, geographically restricted species pools may coexist, each manifested on different scales of observation and analysis (DiMichele et al., 2004).

Missourian (early Late Pennsylvanian) coal floras bear directly upon this problem and demonstrate the relationship between scale of analysis and apparent pattern. The coals analyzed in this study appear to demonstrate temporal persistence in vegetational dominance-diversity patterns. These are the same kinds of patterns of vegetational recurrence from coal bed to coal bed that occur in both the late Desmoinesian (DiMichele et al., 1996, 2002). This similarity occurs despite very different patterns of vegetational dominance and diversity between these two time periods. Desmoinesian coal beds are dominated by lycopsids, primarily by genera that did not survive the Middle-Late Pennsylvanian transition in western Euramerica (*Lepidophloios*, *Diaphorodendron*, and *Synchysidendron*), whereas Late Pennsylvanian coal beds are dominated by tree ferns (Kosanke and Cecil, 1996). Tree-fern abundance generally began to increase in wetlands during latest Desmoinesian (Pfefferkom and Thomson, 1982; Phillips and Peppers, 1984), but most of the species were different from those that dominated Late Pennsylvanian peat swamps (Lesnikowska, 1989), and few Middle Pennsylvanian coals had more than 20% tree-fern compositional abundance (Phillips et al., 1985). In addition, the species composition of the pteridosperms, ground cover ferns, and vines is markedly different, even though the basic lineages to which these plants belong were persistent (DiMichele and Phillips, 1996).

The interbedded sequence of coals and clastic rocks in the Pennsylvanian has long been taken to reflect glacial-interglacial oscillations (Cecil et al., 2003). To investigate the compositional consistency of coal-swamp landscapes among these presumptive glacial-interglacial oscillations,

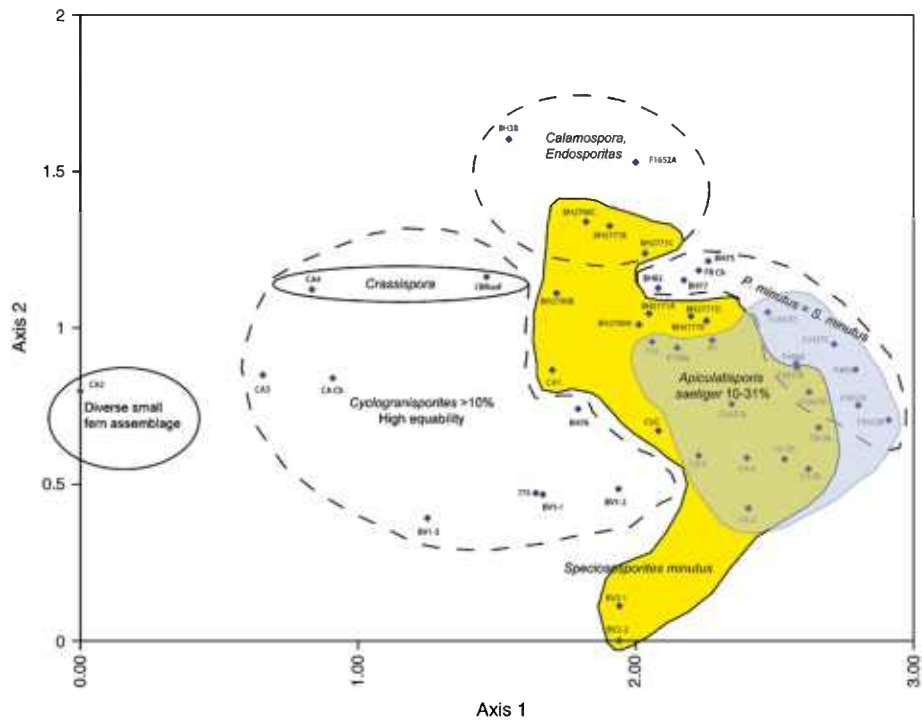


Fig. 21. Detrended correspondence analysis (DCA) of palynological samples from the Calhoun, Bristol Hill, and Friendsville coal beds. Samples used and labels are identical to those in Table 3. Clusters of samples are labeled to reflect patterns of taxonomic dominance. Most samples are dominated by the tree-fern spore species *Speciosporites minutus*, with subdominant or codominant *Punctatisporites minutus* and/or *Apiculatisporites saetiger*. The tree-fern spore *Cyclogranisporites* is abundant in an array of samples with high equability. *Crassispora*, the spore of *Sigillaria*, is dominant in few samples. Medullosan pollen is not represented in these analyses and may have been most abundant in the high-equability samples. See text for details.



Fig. 22. Reconstruction of the Calhoun peat-swamp forest.

Table 5

Taxa identified in the flora of the Calhoun coal bed (all known localities) (from Phillips, 1980)

Lycopsida
<i>Paurodendron fraipontii</i> (Leclercq) Schlanker and Leisman
<i>Sigillaria elegans</i> (Sternberg) Brongniart
<i>Mazocarpon oedipternum</i> Schopf
<i>Stigmaria</i> sp.
Sphenopsida
<i>Sphenophyllum plurifoliatum</i> Williamson and Scott
<i>Bowmanites bifurcatus</i> Andrews and Mamay
<i>Arthropitys communis</i> Binney var. <i>septata</i> Andrews
<i>Arthropitys illinoensis</i> Anderson
<i>Calamodendron americanum</i> Andrews
<i>Calamocarpon insignis</i> Baxter
<i>Calamostachys americana</i> Arnold
<i>Pendulostachys cingulariformis</i> Good
<i>Astromyelon cauloides</i> Anderson
<i>Astromyelon pluriradiatum</i> Anderson
Pteropsida
<i>Anachoropteris clavata</i> Graham
<i>Anachoropteris involuta</i> Hoskins sensu lato with lateral shoots
<i>Anachoropteris pautetii</i> Corsin
<i>Tubicaulis scandens</i> Mamay
<i>Tubicaulis stewartii</i> Eggert
<i>Apotropteris minuta</i> Morgan and Delevoryas
<i>Sermaya biseriata</i> Eggert and Delevoryas
<i>Botryopteris forensis</i> Renault
<i>Botryopteris</i> sp. “pseudoantiqua”
<i>Botryopteris illinoensis</i> Mamay
<i>Catenopteris simplex</i> Phillips and Andrews
<i>Eopteridangium dictyosporum</i> Andrews and Agashe
<i>Rhabdoxylon americanum</i> Dennis
<i>Ankyropteris</i> sp.
<i>Zygopteris berryvillensis</i> Dennis
<i>Biscaliptera musata</i> Mamay
<i>Corynepteris robusta</i> (Graham) Mickle
<i>Psaronius blicklei</i> Morgan
<i>Psaronius chasei</i> Morgan
<i>Psaronius magnificus</i> (Morgan) Rothwell and Blickle
<i>Stewartiopteris singularis</i> Morgan and Delevoryas
<i>Stiptopteris americana</i> Lenz
<i>Araiangium pygmaeum</i> (Graham) Millay
<i>Cyathotrachus altissimus</i> Mamay
<i>Scolecopteris bulbacea</i> (Graham) Stubblefield
<i>Scolecopteris illinoensis</i> Ewart
<i>Scolecopteris latifolia</i> Graham
<i>Scolecopteris monothrix</i> Ewart
Cordaitales
<i>Pennsylvanioxylon nauertianum</i> (Andrews) Costanza
<i>Cordaites validus</i> Cohen and Delevoryas
<i>Cardiocarpus oviformis</i> Leisman
<i>Cordaianthus</i> cf. <i>duquesnensis</i> Rothwell
<i>Lasioctrobus polysacci</i> Taylor
<i>Amyelon</i> sp.
Pteridosperms
<i>Callistophyton poroxyloides</i> Delevoryas and Morgan
<i>Callospermion pusillum</i> Eggert and Delevoryas
<i>Heterangium americanum</i> Andrews
<i>Conostoma platyspermum</i> Graham

Table 5 (continued)

Pteridosperms
<i>Conostoma quadratum</i> Graham
<i>Conostoma villosum</i> Rothwell and Eggert
<i>Coronostoma quadriwasatum</i> Neely
<i>Medullosa endocentrica</i> Baxter
<i>Medullosa noei</i> Steidtmann
<i>Pachytista berryvillensis</i> Taylor and Eggert
<i>Pachytista hexangulata</i> Stewart
<i>Pachytista illinoense</i> (Arnold and Steidtmann) Stewart
<i>Stephanospermum elongatum</i> Hall
<i>Callandrium callistophytoides</i> Stidd and Hall
<i>Dolerotherca formosa</i> Schopf
<i>Dolerotherca villosa</i> Schopf
<i>Halletheca reticulatus</i> Taylor

we compared the rank-order abundances of ferns in palynological whole-seam channel samples from the Calhoun, Bristol Hill and Friendsville coal beds. Channel samples were used because they are representative of the average coal seam composition and therefore can be treated as a landscape average, as if the various communities coexisted in space instead of succeeding each other in time. Palynological samples are preferred for this type of analysis because they permit clear differentiation among the dominant tree ferns, which are often difficult to distinguish from anatomical sections of vegetative organs (Willard, 1993; Lesnikowska, 1989). In addition, although this kind of analysis can be done with coal-ball samples, palynological samples draw from a broader sample and thus capture a greater proportion of the biodiversity of the landscape.

Eight samples were analyzed (Table 6), four from the Calhoun coal bed (three from the New Calhoun site and one from the Berryville site), and two each from the Friendsville and Bristol Hill coal beds. Species included in the analyses, in order of average importance in the samples, are *Speciososporites minutus* (tree ferns), *Punctatisporites minutus* (tree ferns), *Apiculatisporis saetiger* (tree ferns), *Laevigatosporites* spp. (small ferns), *Cyclogranisporites* sp. (tree ferns), and *Spinospores exiguus* (tree ferns). Samples were examined by inspection and by comparing rank-order importance of species in each sample using the non-parametric statistic Kendall's tau.

Three species predominate in these samples, based on average rank-order score. *Speciososporites minutus* is among the top three abundance classes in all samples and dominates six of the eight samples, ranging from 22–47% abundance in those samples where it dominates. *Punctatisporites minutus* is among the top three abundance classes in six of eight samples, but is dominant in none. *Apiculatisporis saetiger*, although it has the same average rank-order score as *P. minutus*, is among the top three abundance classes in only four samples, but it dominates

Table 6

Percent abundance and rank-order abundance of tree-fern spores in palynological whole-seam channel samples from the Calhoun (NC = New Calhoun locality; BV = Berryville locality), Bristol Hill (BH), and Friendsville (FR) coal beds

Percent abundance sample	Spec. min.	Pi. Min.	Apic. saet.	Laev. spp.	Cyclogr.	Spino. exig.
1—FR2437Ave	33	29	15	4	2	4
2—FR 1652	16	17	24	5	3	12
3—BH 2790	37	9	5	4	24	0
4—BH2771 Ave	37	19	3	4	10	0
5—NCCChannel C	39	14	28	6	0	8
6—NCCChannel A	14	1	7	17	12	1
7—BV 1	22	6	7	13	11	9
8—NCCal 4	47	9	18	6	4	7

Rank-order sample	Spec. min.	Pi. min.	Apic. saet.	Laev. spp.	Cyclogr.	Spino. exig.
1—FR2437Ave	1	2	3	5	6	4
2—FR 1652	3	2	1	5	6	4
3—BH 2790	1	3	4	5	2	6
4—BH2771 Ave	1	2	5	4	3	6
5—NCCChannel C	1	3	2	5	6	4
6—NCCChannel A	2	5	4	1	3	6
7—BV 1	1	6	5	2	3	4
8—NCCal 4	1	3	2	5	6	4

one sample. The other three species have variable distribution patterns. *Laevigatosporites* spp. are produced by small, mostly ground-cover ferns. A single sample is dominated by these ferns; small ferns are second in abundance in another sample. Such samples may represent areas of persistent open canopy, assuming uniform sampling of the coal bed. In other samples, small ferns range from 4–6% and occupy the fourth or fifth rank-order class. The other two species of tree ferns, *Cyclogranisporites* sp. and *Spinosporites exiguus*, are highly variable in abundance, including absences from some profiles, and they are least abundant in seven of eight samples, suggesting patchy distributions.

Comparing rank-order abundances among the eight samples was done with Kendall's tau, which provides the likelihood that the two samples are drawn from different distributions. The objective of this analysis was to determine the degree to which rank-order dominance changes among and within coals. Rank-order abundance was used instead of absolute quantitative abundance because of the limited nature of sample size, the lack of replicate analyses, and the vagaries of fossil preservation. Three of the samples (numbers 1, 5 and 8) differ by

an exchange of position of two species, and there is a less than 0.01 chance they are drawn from different distributions. One of these samples is from the Friendsville coal bed, and the other two are from the Calhoun coal bed. One additional sample (number 2) from the Friendsville coal bed differs from samples 5 and 8 (Calhoun coal bed) by three position changes all among the top three species. In addition, the two samples from the Bristol Hill coal bed differ from one another by three position changes among the dominant species. There is less than a 0.03 chance that these samples are drawn from different distributions. Extending this analysis, and recognizing that we have not corrected for a multiple samples, samples 1 and 2 (both from the Friendsville coal bed) have a complete reversal of the top three rank-order classes, and there is less than a 0.09 chance that these samples are drawn from different distributions. Samples 6 and 7, from the New Calhoun and Berryville sites in the Calhoun coal bed, are enriched in small ferns, which either dominate or are second in abundance. These samples (6 and 7) also have less than a 0.09 chance of being from different distributions.

Thus, with the exception of samples 6 and 7, which are enriched in small ferns, all samples are interlinked in the similarity matrix. On the basis of rank-order abundance, the similarity matrix indicates that these coals have the same basic pattern of fern abundance. By this analysis, it appears that same basic species pool is represented in each coal-swamp landscape and that the relative patterns of dominance and diversity are persistent from site to site within a coal and among coals.

These analyses suggest that the relative patterns of proportional dominance stay roughly the same over time as long as the climatic effects of glacially-driven climatic oscillations are moderate, which we infer from lack of background floristic extinction rates between successive coals. Under moderate climate oscillations, wetland assembly-disassembly or biogeographic range changes are accompanied by a relatively low rate of background extinction (less than 10% as measured in our samples) (DiMichele and Phillips, 1996). The marine-terrestrial cyclicity of both the Middle or the Late Pennsylvanian appear to fall within these limits. However, the transition between the Middle and Late Pennsylvanian, a possible time of brief, intense global warming (Frakes et al., 1992), caused a much larger extinction with consequent large-scale reorganization of the tropical wetlands (DiMichele and Phillips, 1996; Kosanke and Cecil, 1996). Intermittently recurrent patterns of dominance and diversity (coal to coal) presuppose survival of this vegetation outside of the preservation window during non-peat-accumulating time periods. This survival would reflect the persistence

of the basic architecture of the species pool, much as postulated by Hubbell (2001). Therefore, long-term persistence of organization may be due mainly to the difficulty of altering the numerical proportions of taxa, given a stochastically constant background of relatively uniform resources and disturbance. In other words, once conditions favorable to peat accumulation reappear, the original proportions and landscape organization are retained during reassembly for passive reasons of likelihood, even if the total number of individuals shrinks during those times between peat accumulation (times during which we have little or no knowledge of the flora). Large populations tend to have a better chance at garnering greater proportions of resources as the resources appear, if the dynamics of resource capture is lottery-like. These detailed studies of Late Pennsylvanian coal beds provide a unique opportunity to examine the impacts of glacially-driven climatic oscillations on the structure of terrestrial plant communities and their tolerance limits for climatic fluctuations of various scales.

6. Conclusions

The flora of the Calhoun coal is among the best known and most significant tropical floras known from the Pennsylvanian. It is probably the best known, most botanically influential flora known from the Late Pennsylvanian and thus is an exemplar of the plants that lived at this time in peat-forming landscapes. This study has added to our understanding of that flora by placing it within a paleoecological context. We have found regional variation in the sub-dominant components of the vegetation, within a framework of persistent tree-fern dominance. Patterns of variability in vegetational composition at local scales are more subdued, and suggest long-persistent spatio-temporal populational structure. When compared to coals of similar age, representing presumably distinct glacial-interglacial cycles, the basic tree-fern dominance patterns are found to persist on a temporal scale of hundreds of thousands of years within peat-forming landscapes. These patterns demonstrate the need to consider and accommodate patterns of vegetational dynamics from the distant past, which can contribute to our understanding of scales of variability and the generality of ecological principles, founded largely on the biology of extant organisms and systems.

Acknowledgements

We wish to thank Dan S. Chaney for his help with preparation of the plates and Christopher E. Bernhardt for his assistance in preparation of the figures. Mary Parrish prepared the reconstruction of the Calhoun coal

swamp. C. Blaine Cecil and Christopher Swezey made constructive comments on an earlier version of the manuscript. We thank numerous undergraduates for all their assistance with field and laboratory work. We thank John Nelson and Pius Weibel for assistance with geological interpretation.

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