

# Vegetational zonation in a swamp forest, Middle Pennsylvanian, Illinois Basin, U.S.A., indicates niche differentiation in a wetland plant community



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## ABSTRACT

A rich fossil flora occurs in the roof shale of the Middle Pennsylvanian (Moscovian) age, Springfield Coal flanking the Galatia channel, a river deposit approximately 1 km in width and 150 km long, partially contemporaneous with the Springfield peat swamp. Siltstone and sandstone, > 30 m thick, were deposited in the channel during the final estuarine phase. The river formed under seasonal subhumid climate during early deglaciation as marine waters retreated from the land surface. It existed continuously through glacial maximum, under increasingly humid climate, as a low-sediment or black-water river with peat along its flanks. During early deglaciation, under subhumid climate and sea-level rise, the river became a sediment-laden estuary, drowning the peat swamp and burying vegetation in place under extensive mudflats. This buried flora was studied in three underground mines in southern Illinois, permitting vegetation to be characterized spatially. Three transects, comprising 100 sites, a total linear distance of ~12 km, reveal distinct zonation perpendicular to the channel margin. An innermost belt, 0.5 to 2.5 km wide, consists almost exclusively of the pteridosperm *Neuropteris flexuosa*. North of a river bend, three belts succeed the *N. flexuosa* zone: mixed pteridosperms and marattialean tree ferns; mixed arborescent lycopsids and marattalians; lycopsids with rare marattalians. South and inside the same bend, *N. flexuosa* is succeeded by mixed lycopsids, particularly *Sigillaria*, and marattialean ferns. Within the transects, marattialean ferns have wider distribution than other groups, suggesting broader environmental tolerances. *Neuropteris flexuosa* channel-margin mono-dominance may reflect high sedimentation rates, elevated nutrient conditions, or floating-seed dispersal. Lycopsid dominance in interior areas conforms with tolerance of deep, standing water. The spatial scale examined affects our perception of community assembly. Overall, distinct vegetational zonation suggests niche-assembly; however, within vegetational bands, there is considerable small-scale spatial variation suggesting stochastic properties.

## 1. Introduction

Terrestrial ecosystems of the late Paleozoic wet tropics were of considerably lower species richness than those of today in similar settings. The diversity difference is manifest at all but the smallest sampling scale of a typical paleobotanical excavation (Wing and DiMichele, 1995), which largely captures the vegetation living within the surrounding 0.5 ha or less (Burnham, 1993). At larger spatial scales, the species richness of entire Pennsylvanian-age drainage basins approaches only 100–125 species of all growth forms, within the humid-to-perhumid climate species pool (Pfefferkorn, 1979; King et al., 2011; Cleal et al., 2012; Moore et al., 2014). This stands in marked contrast to the notable species numbers in many modern tropical rainforests, including seasonally flooded habitats, where the number of tree species alone can greatly exceed 100 in a single hectare (e.g., Gentry, 1988;

Valencia et al., 1994; Wills et al., 1997) and is well over 10,000 in the Amazon river basin (e.g. Hubbell et al., 2008; Wittmann et al., 2011). It is, therefore, possible that at least some, if not many, Pennsylvanian species had broader environmental tolerances than those typical of modern tropical, humid-climate plants, there being fewer species on the landscape to partition resources. Alternatively, the Pennsylvanian tropical, humid-to-perhumid climate, species pool may simply have encompassed a smaller range of resource use than today. Under such conditions, particularly in wetlands, where spatial microhabitat variability would have been suppressed compared to well drained landscapes, niche differentiation might be difficult to detect in fossil assemblages. Studies of autochthonous floras, preserved in ash falls and floods (e.g., Gastaldo, 1986; DiMichele et al., 1996; Pryor and Gastaldo, 2000; Gastaldo et al., 2004; Opluštil et al., 2007, 2009; Pfefferkorn and Wang, 2007; Libertin et al., 2009; Wang et al., 2012), or

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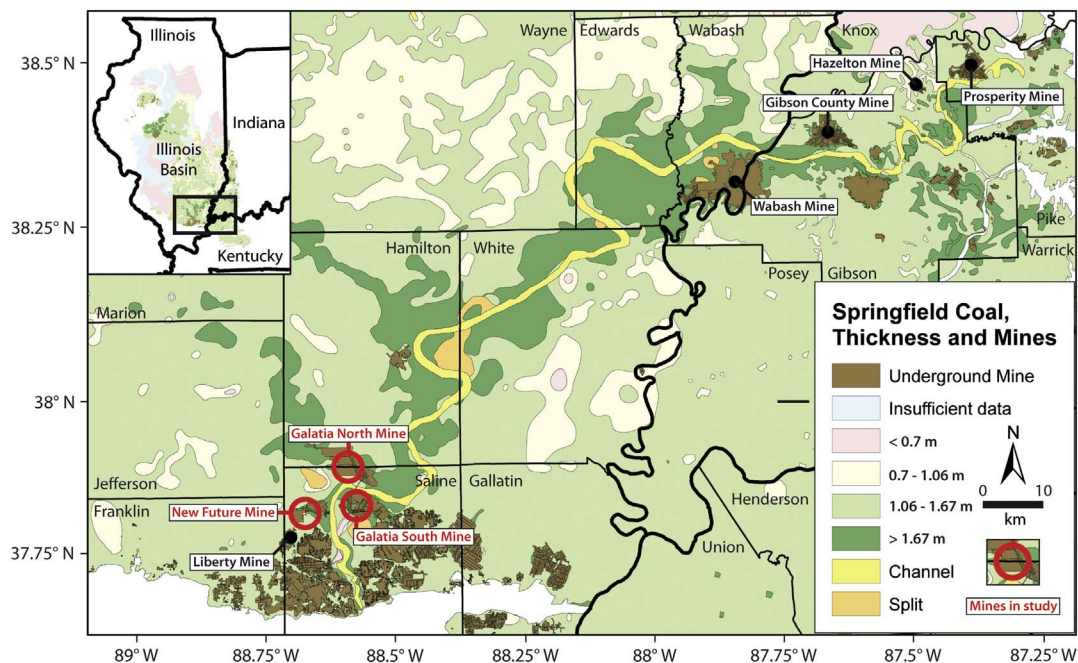


Fig. 1. Distribution of the Springfield Coal in the Illinois Basin. Location of Galatia channel, visited coal mines, and location of the Galatia North, Galatia South, and New Future coal mines in which detailed study of the roof vegetation and sedimentology was carried out. Coal mine extents and Springfield Coal data based on ISGS publication IM118 (Treworgy et al., 1999), and GIS data downloaded from the Indiana Geological Survey <https://igs.indiana.edu/IGSMap>.

parautochthonous floras preserved in permineralized peat deposits (e.g., Phillips et al., 1977; Phillips and DiMichele, 1981; Raymond, 1988; Winston, 1988; Pryor, 1996; DiMichele and Phillips, 1988; Willard et al., 2007), have yielded conflicting interpretations of assembly dynamics. However, enough of these studies now exist to reconcile the conflicts and, when considered in light of taphonomic studies of modern vegetation (e.g., Scheiing and Pfefferkorn, 1984; Gastaldo et al., 1989; Burnham et al., 1992; Burnham, 1993; Ferguson, 2005), suggest that the spatial scale of the study is an essential consideration (Patzkowsky and Holland, 1999, 2003; DiMichele et al., 2007; Bennington et al., 2009; Bennington and Aronson, 2012).

In this study, we report the results from three transects, comprising a total of 10 km, through the autochthonous to parautochthonous remains of a Middle Pennsylvanian swamp. These transects extend roughly perpendicularly from the margin of a river contemporaneous with the swamp, out into the swamp interior. The fossil assemblage was preserved during a brief window of time as the swamp was drowned and rapidly buried by sediment. This occurred as sea-level rise inundated the coastal regions, converting the river to an estuary, accompanied by development of large tidal mud flats along its flanks (Archer and Kvale, 1993; Archer, 2004; Nelson et al., 2008, in press). As such, it represents a  $T^0$  landscape (Johnson, 2007; DiMichele and Falcon-Lang, 2011; Opluštil et al., 2014) that unambiguously captures the original spatial arrangement of the plants on the land surface. The patterns suggest strong spatial differentiation among the plants in relation to channel proximity, and thus niche assembly of the plant community on a landscape scale (see Weiher et al., 2011 for discussion). Within any one of the vegetational bands that parallel the river margin, there is, in contrast to the pattern at the larger scale, a high degree of compositional variation among samples. Thus, at smaller spatial scales, and within a particular set of sub-environmental conditions, compositional variation is similar to expectations from neutral models of assembly (e.g., Hubbell, 2005).

Underground mines can reveal the spatial distribution of the final vegetation of peat swamps, presenting opportunities found nowhere else to examine a large surface area representing time scales from an instant to a few years. Even the finest natural exposures provide at best a limited three-dimensional view and generally only two-dimensions.

Consequently, mapping a continuous time horizon is rarely possible on the outcrop. Room-and-pillar underground mines, in contrast, allow mapping areas as large as 100s of  $\text{km}^2$  and also reveal at least a limited view of the vertical dimension. As an aside, underground coal mines, and coal mines in general, are becoming fewer in number and gaining access is becoming more difficult as pressure on electric utilities to find non-Carbon-based fuels increases. Thus, studies such as that described here may become difficult or even impossible. Witness the closing of the British deep coal mines, from which coal balls were first described in the mid-1800s (e.g., Binney, 1862) and on which our understanding of Pennsylvanian plant anatomy was established (e.g., Williamson, 1871) – now completely inaccessible.

The Galatia mine complex in southern Illinois, in which this study was carried out, extracted the Springfield Coal on either side of an approximately 1 km wide, ribbon-like belt of siltstone and sandstone, from which the coal bed was absent. These siliciclastics mark the path of a river channel that existed contemporaneously with the peat swamps from which the coal formed. The channel was a key control on peat accumulation and sedimentation dynamics. Moreover, a set of mine tunnels was driven entirely across the channel deposit, linking the workings on either side, which allowed study of the plant remains preserved in the immediate roof of the coal right up to the channel edge. The underground exposures also revealed and permitted interpretation of the environmental changes that were taking place as the channel was converted from a river drainage to a tide-dominated estuary (Archer et al., 2016; Nelson et al., 2008, in press; Elrick and Nelson, 2010), and the temporal succession of environments that flanked it during that transition, from peat swamp, to mixed peat-siliciclastic swamp, to mudflat (Archer and Kvale, 1993), the latter ultimately becoming free of vegetation as water levels rose and water cover became permanent (Elrick et al., 2013, in press).

## 2. Geological setting

The study was carried out in the now-closed American Coal Company Galatia and New Future mines, in Saline County, Illinois. These mines were situated in the southern part of the Illinois (Eastern Interior) basin, USA (Fig. 1). The study focused specifically on plant

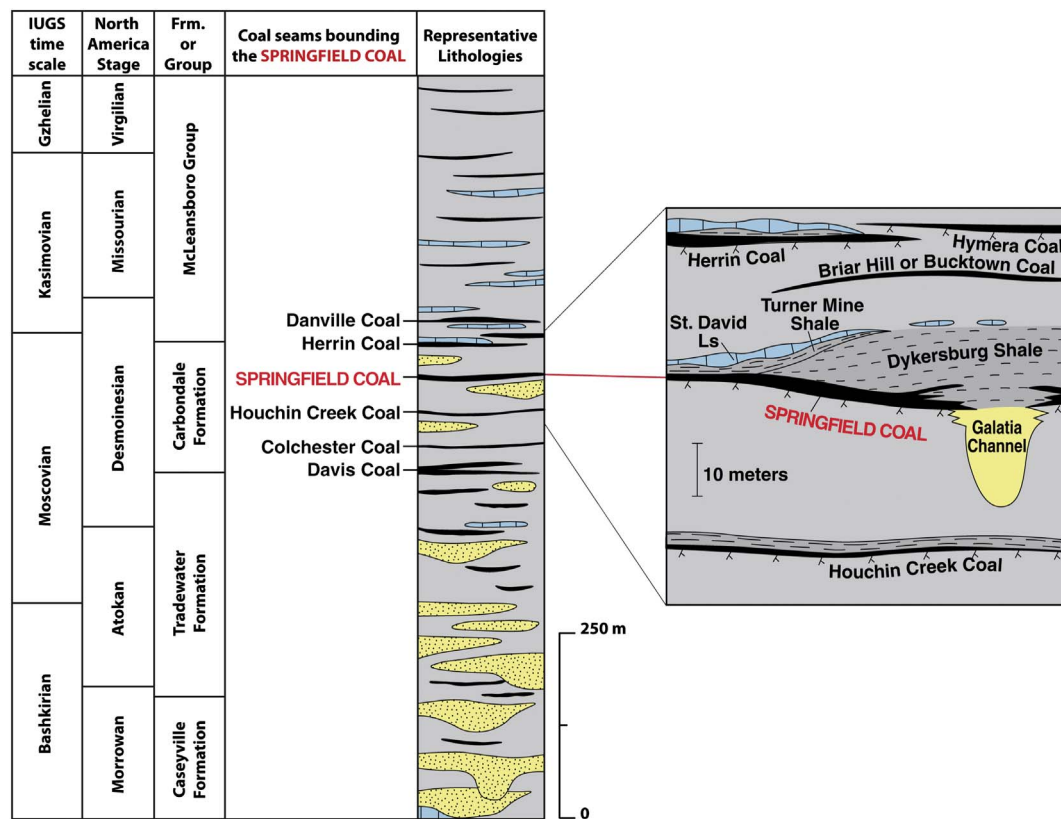


Fig. 2. Stratigraphic relationships of the Springfield Coal and major lithologic units mentioned. Based on ISGS publication Bulletin 95 (Willman et al., 1975).

fossils preserved at the interface of the Springfield coal and its immediate gray shale roof rocks, in proximity to a feature known as the Galatia channel (Hopkins et al., 1979), siliciclastic rocks deposited during the final phases of a river channel that existed prior to and contemporaneously with peat accumulation (Potter, 1962, 1963; Nelson et al., in press). The Springfield Coal is in the Carbondale Formation, in the mid-upper part of the Desmoinesian provincial series (Willman et al., 1975), which corresponds to upper Moscovian in the global standard section (Fig. 2). The Springfield Coal is believed to correlate with the Summit Coal of the Western Interior Basin and the Middle Kittanning coal bed of the central Appalachian Basin (see Falcon-Lang et al., 2011 for a recent correlation chart), and thus was part of a peat-covered landscape of enormous, contemporaneous original extent.

During the time of the Galatia channel, the Illinois Basin was close to the equator, and was located in the west central portion of the supercontinent of Pangea (e.g., Rowley et al., 1985). At this time, the Earth was in the midst of long, complex cold interval, the Late Paleozoic Ice Age, which began in the Mississippian and extended into and possibly through the early Permian (Isbell et al., 2003; Montañez et al., 2007; Fielding et al., 2008; Montañez and Poulsen, 2013). The time period was characterized by regular glacial-interglacial cycles (e.g., Heckel et al., 2007), likely driven by orbital factors, much like such cycles in our modern ice age (e.g., Van den Belt et al., 2015), and accompanied by changes in sea level and climate during each cycle, in concert with ice-volume changes (Cecil et al., 2003b; Horton et al., 2012; Cecil et al., 2014; Montañez et al., 2007). The regular glacial-interglacial cycles also were accompanied by vegetational changes in the equatorial lowlands, as the volume of tropical rainfall fluctuated (Falcon-Lang, 2004; Montañez et al., 2007; Falcon-Lang and DiMichele, 2010; Opluštil et al., 2013a, 2013b).

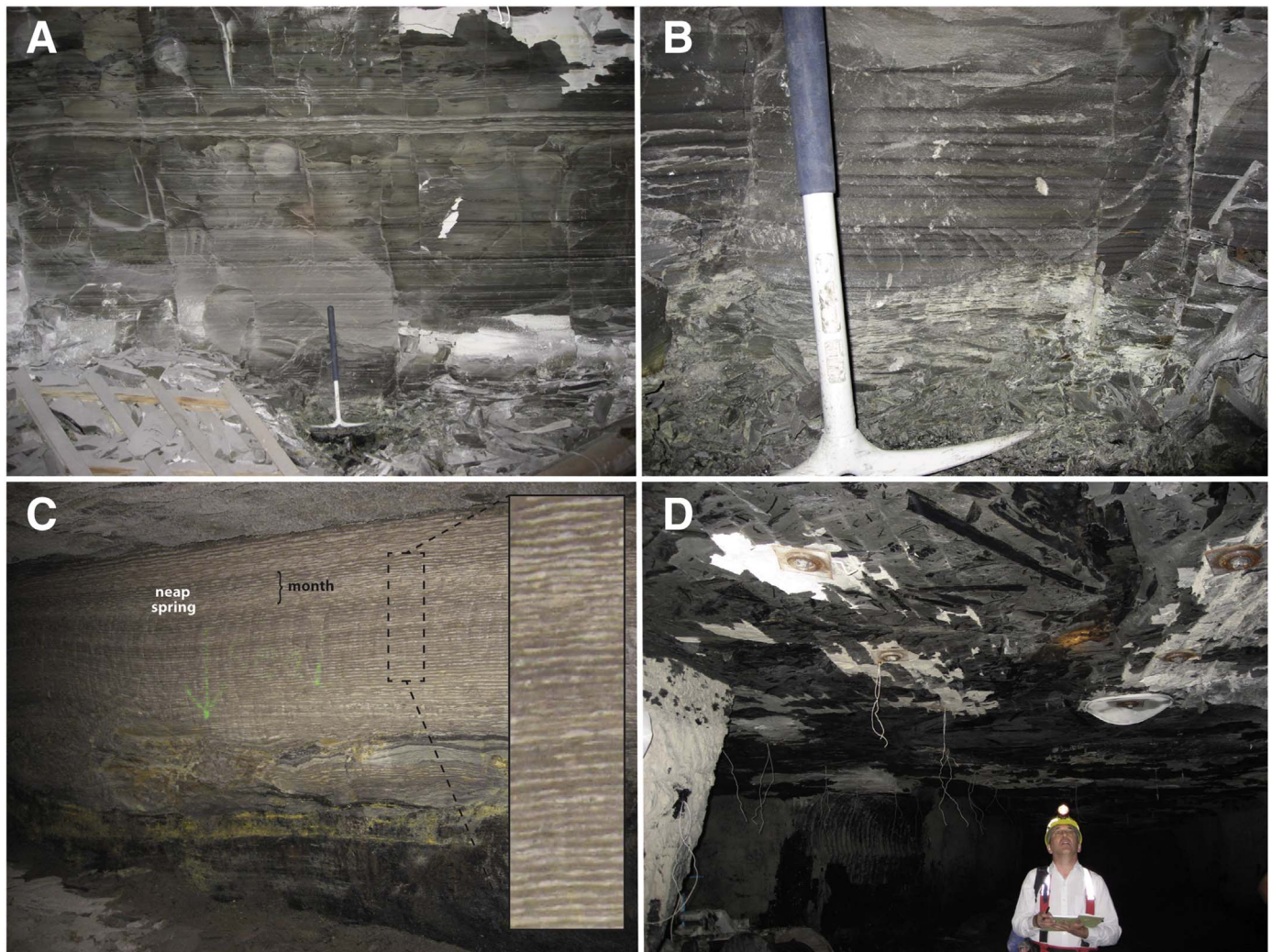
The Galatia channel, located in the southeastern portion of the Illinois Basin, extends southwestward, covering a straight-line distance from outcrop to outcrop of about 150 km in a broadly meandering

course. Channel width varies, but is about 1 km. Coal is absent from the former course of the channel, which is filled with mudstone, siltstone, and sandstone. Along the flanks of the channel, in bands 10s of kms wide, Springfield coal thickness may exceed 3.0 m. In contrast, throughout most of its extent in the Illinois Basin, the Springfield coal is 1.5 to 2.5 m thick. In a narrow belt, a few hundred meters wide, on either side of the channel, the coal is interbedded with laminae and thin beds of dark gray claystone and siltstone. These siliciclastic laminae and beds increase in number and thickness approaching the channel. Commensurately, coal laminae diminish in number and occurrence approaching the channel, reflecting a lateral facies change. The siliciclastic laminae represent clay-sized sediment that was carried from the channel into the flanking swamp while peat was actively accumulating.

The immediate roof rocks of the Springfield Coal in proximity to the Galatia channel differ considerably from those typical throughout most of the Illinois Basin. In areas distant from the channel, the immediate roof of the Springfield is the black, fissile, phosphatic Turner Mine Shale, a product of anoxic, restricted marine conditions. The thin, open-marine St. David Limestone overlies the Turner Mine Shale (Fig. 2). These marine lithologies were deposited as the sea transgressed the land surface during glacial melting and accompanying sea-level rise. Overlying the coal close to the channel, however, is non-marine gray mudstone and siltstone referred to as the Dykersburg Shale. The Dykersburg Shale mainly forms a wedge up to 30 m thick between the coal and the black, marine Turner Mine Shale (Fig. 2), indicating that it was deposited prior to marine inundation of the land surface.

The Dykersburg Shale is present primarily in those areas where the coal is thickest (Hopkins, 1968; Gluskoter and Simon, 1968; Gluskoter and Hopkins, 1970; Hopkins et al., 1979). In the transitional area between the coal and Galatia channel, Dykersburg Shale can occasionally be found penetrating laterally within the coal seam, sub-parallel to bedding and coal laminae, as a series of low profile wedge shape bodies 10s of centimeters thick, and 10s to 100s of meters wide and deep; this zone is marked as the “split” on Fig. 6. These wedge-shaped bodies of





**Fig. 3.** Sedimentary facies of Springfield Coal roof shale in study area. A. Gray siltstone with tidal features. B. Gray siltstone with tidal features. C. Sandstone channel in gray siltstone with distinct tidal lamination. Part is magnified to show lamination. An exemplary monthly neap-spring cycle is labeled. D. Room and pillar mine entry exposing plant fossils in immediate gray shale roof of the coal.

Dykersburg Shale are in erosional contact with the coal and often are highly irregular in thickness, shape and extent. They record a history of preferential clay winnowing at the channel margins, partial suspension and tearing of the newly exposed peat ‘flaps’ at the margin, resulting in the development of floating peat mats (Elrick et al., 2008) and deposition of Dykersburg sediment in the evacuated void spaces (Elrick et al., 2008; Elrick and Nelson, 2010; Nelson et al., in press). Where the Dykersburg Shale is immediate contact with the coal, forming the roof shale, the contact may be gradual or disconformable; the shale coarsens from claystone at its base to siltstone and fine sandstone upward, reflecting changes in grain-size during the time of accumulation. These deposits may display planar or wavy lamination, may be ripple cross laminated and may show evidence of scour. Lamination tends to be strongly rhythmic, and in places the shale displays neap-spring tidal cycles (Fig. 3A–C) (Archer et al., 2016).

The Dykersburg Shale accumulated initially in fresh water that became brackish as accumulation proceeded, indicated by a fauna of inarticulate brachiopods, and pectenoid and other small bivalves. Fossil land plants are common and most abundant in the lower few centimeters to, perhaps, within a meter of the coal-shale contact (Fig. 3D). These include upright tree stumps, rooted in the top of the Springfield Coal (Fig. 4A), numerous prone trunks of lycopsids, pteridosperms, marattialean ferns and calamitalean sphenopsids, along with foliage, cones, and other aerial organs of plants (Figs. 4 and 5). The high

concentration of plant remains in the basal 1 m of the Dykersburg Shale makes them readily observable in the roof rocks of underground mine excavations.

The above data indicate that deposition of the Dykersburg Shale onto the peat progressed rapidly. The burial of tree stumps in growth position, along with exquisite preservation of delicate foliage, requires rapid burial (Gastaldo and Demko, 2011). Tidal rhythmites support the conclusion that the lower few meters of the Dykersburg Shale commonly accumulated in a few years to a few decades. Room (accommodation space) for thick accumulations of Dykersburg Shale above the Springfield Coal, thus outside of the channel itself, was created by a combination of rapid sea-level rise (Archer et al., 2016) and compaction of the underlying Springfield peat once sediment loading began.

### 3. Paleoenvironmental setting

This study focuses on the contact horizon between the Springfield Coal and the Dykersburg Shale, which, throughout the study area, can be considered an effectively instantaneously preserved surface. Through a thickness of < 1 m, the Dykersburg Shale entombs the final forest of the Springfield peat swamp, a planar peat swamp throughout its history. In most places, the contact between the coal and shale is sharp, and represents the development of extensive mudflats on either side of the Galatia estuary (Archer and Kvale, 1993). In some places the



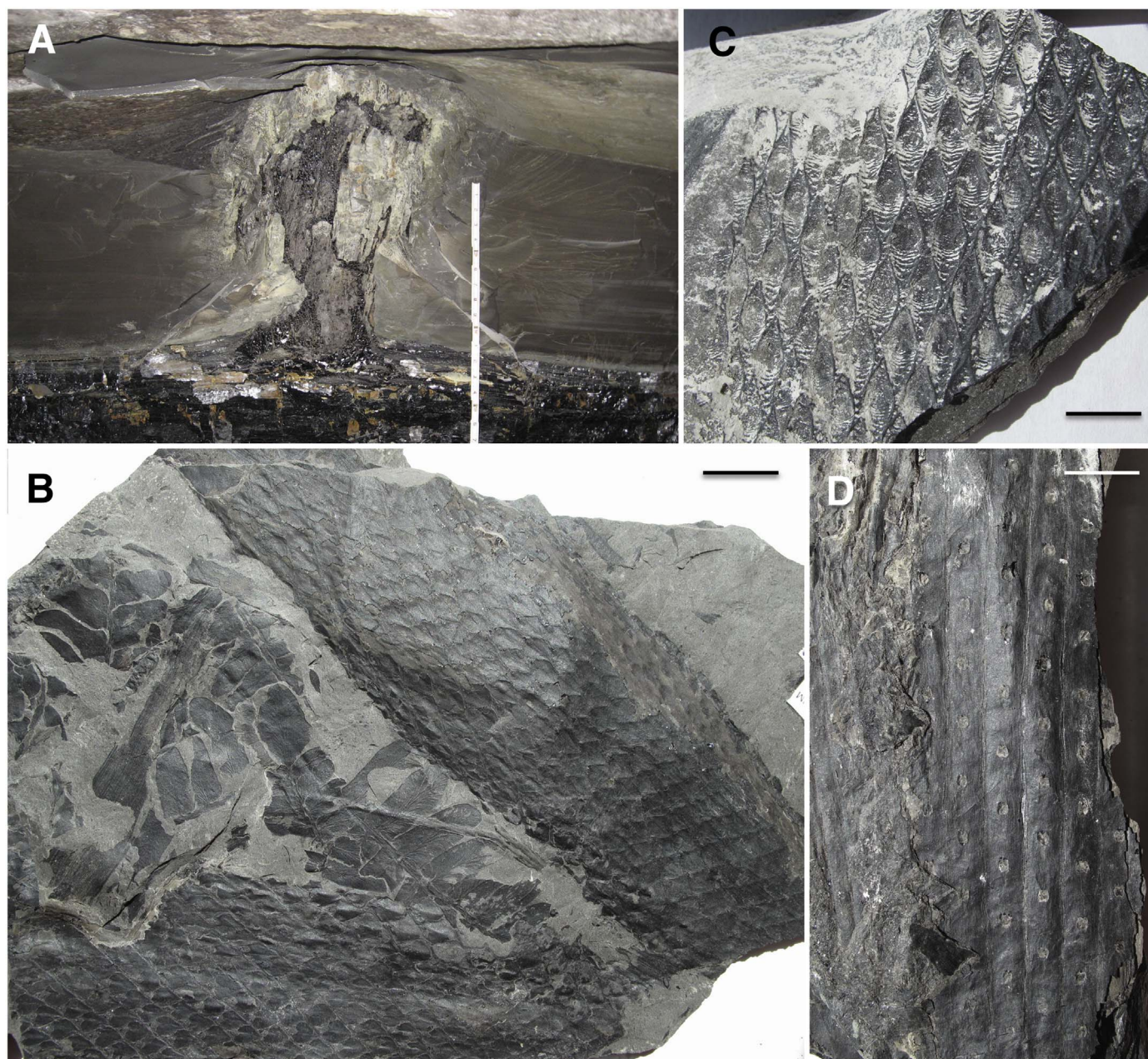


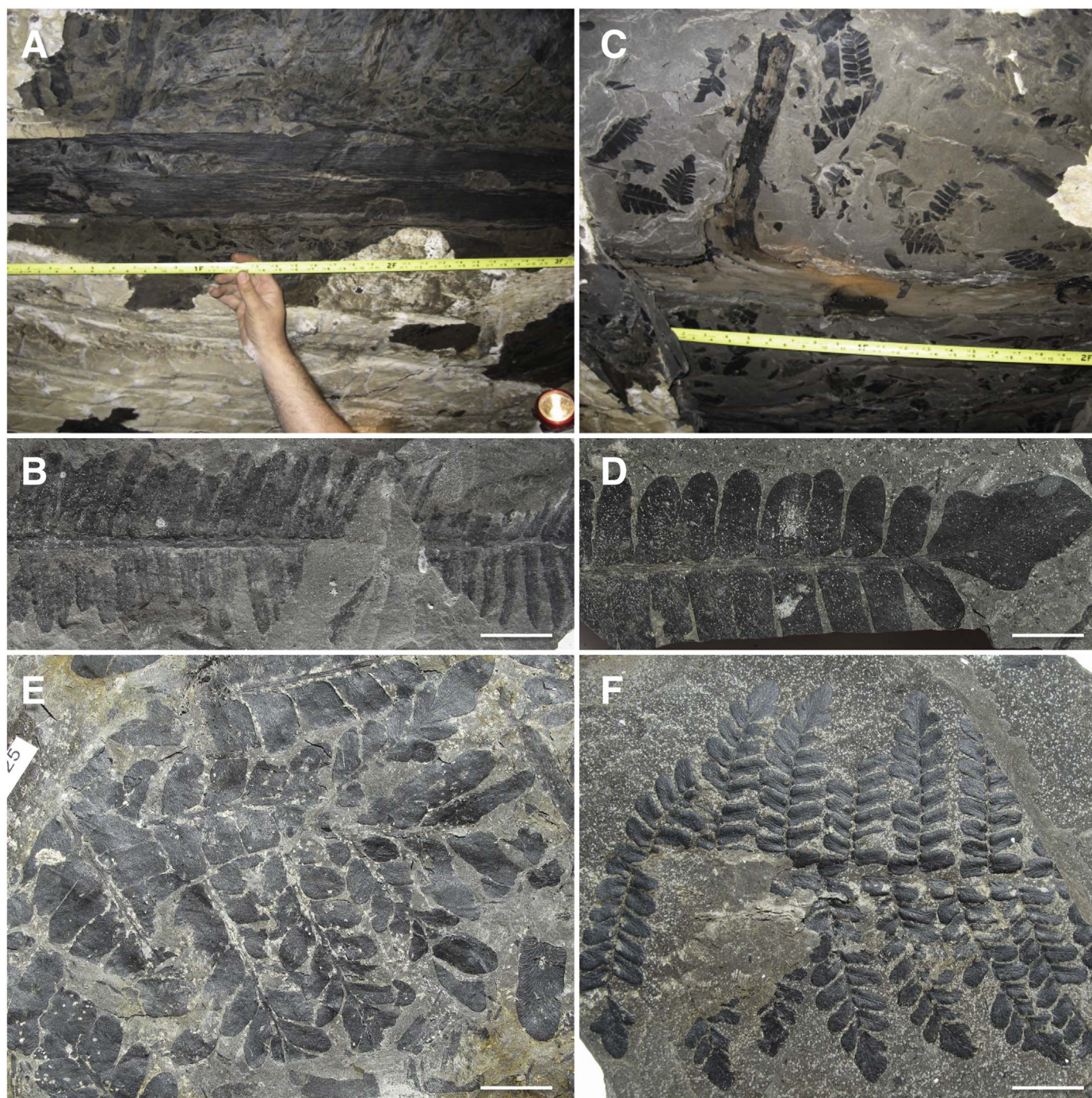
Fig. 4. Lycopoids found in the roof shales of the Springfield Coal. A. Upright tree stump with roots in coal. Scale in feet and 10s of feet; 1 ft  $\cong$  185 mm. B. *Synchysidendron* stems with *Neuropteris flexuosa*. Scale bar = 20 mm. C. *Bergeria worthenii*. Scale bar = 10 mm. D. *Sigillaria* of eusigillarian form showing parichnos prints. Scale bar = 20 mm.

contact is transitional, represented by interbedded laminae of gray shale and coal, and abundant large plant remains; these areas likely represent swales on the original peat surface and record peat-to-clastic transitional swamps within the mudflats.

The Dykersburg Shale is the physical manifestation of an intersection among several covariant events associated with the termination of the glacial phase of a glacial-interglacial cycle. This sequence of events has been summarized, in general, by Cecil et al. (2014) and for the Springfield Coal by Nelson et al. (in press). The following description summarizes, in brief, the detailed description found in Nelson et al. (in press). The events include 1) the melting of Southern Hemisphere grounded glacial ice, 2) the resultant rise in global sea level, 3) changes in climate from humid to moist-subhumid in the central Pangean tropics, 4) the latter leading to increased sediment load in rivers, and 5) conversion of the lower reaches of the Galatia channel from a river to a tidal estuary.

The surface of the Springfield peat swamp was very flat. Based on comparison with the surface of the lower Mississippi Delta, the seaward dip on a widespread peat bed in the Illinois Basin could have been as little as, or even less than, 100 mm per kilometer. This surface was flooded rapidly by rising regional base level, resulting from global sea-level rise caused by glacial melting. This melting was coincident with global climate changes that, in the tropics, were expressed as a shift from humid to moist-subhumid conditions (terminology of Cecil, 2003), reflecting the weakening of Hadley Cell circulation patterns (Peyser and Poulsen, 2008) and onset of seasonal migration of the Intertropical Convergence Zone (Cecil et al., 2003a). This seasonal ITCZ migration changed the equatorial regime from ever-wet to monsoonal, seasonally wet-dry (Cecil et al., 2003a; Eros et al., 2012; Horton et al., 2012). Seasonal drought resulted in a reduction of vegetational cover accompanied by increased soil erosion in areas surrounding the basin not covered with a blanket of peat (Cecil and Dulong, 2003; Cecil et al.,





**Fig. 5.** Ferns and pteridosperms found in the roof shales of the Springfield Coal. A. Prostrate marattialean tree fern stem; longitudinal striations are roots that mantled the stem. Scale in feet and inches. 1 ft  $\cong$  185 mm. B. *Lobatopteris vestita*, marattialean fern foliage. Scale bar = 10 mm. C. Prostrate pteridosperm stem with attached recurved leaf petiole; surrounded by *Neuropteris flexuosa* pteridosperm foliage. Scale in feet and inches 1 ft  $\cong$  185 mm. D. *Neuropteris flexuosa*. Scale bar = 10 mm. E. *Neuropteris ovata* pteridosperm foliage. Scale bar = 10 mm. F. *Laveineopteris rarinervis* pteridosperm foliage. Scale bar = 10 mm.

2003b). As a result, greater volumes of siliciclastic sediment began entering and being transported in rivers. As the transition from riverine to estuarine conditions in the Galatia estuary moved inland, and upriver with rising sea level, the locus of deposition of this increased sediment load was pushed inland and sediment was carried out, over the surface of the Springfield peat swamp.

As noted above, the physical features of this sediment are consistent with deposition under a tidal regime. Flooding and introduction of high volumes of siliciclastic sediment caused cessation of peat accumulation, development of mud flats, and death of the swamp vegetation. The peat rapidly compacted under sediment load and the weight of water,

making accommodation space for additional sediment. In this manner, a thick wedge of gray mud built up in and lateral to the Galatia estuary before continuing sea-level rise introduced permanent water cover of marine salinity across the basin (Turner Mine Shale and St. David Limestone).

As plants died, their remains were incorporated into the rapidly accumulating tidal muds. The rapidity of sediment accumulation is indicated by the volume of plant material, the large size of the plant fragments, and overall excellent state of preservation. More importantly, perhaps, is the large number of buried trunks of various kinds of plants, most commonly lycopsid trees, but also marattialean tree



ferns and pteridosperms, which are rarely encountered in both abundance and excellent states of preservation; the anatomy of these trunks, composed mainly of parenchymatous tissues and aerenchyma (Steidtmann, 1944; Morgan, 1959; Stidd and Phillips, 1968; Stidd, 1981; Rothwell and Blikle, 1982), renders them less conducive to preservation than lycopsid stem remains, which were characterized by a thick, decay resistant rind of bark. In other examples where these more delicate kinds of stem remains are preserved, sedimentological conditions indicate rapid burial and entombment (e.g., Wnuk and Pfefferkorn, 1984; Falcon-Lang, 2006, 2009). Also, important indicators of sediment accumulation rate are the many standing tree stumps with bases flush with the top of the coal. In addition, mud-cast stigmatic axes, the rooting organ of lycopsid trees, are occasionally found within the upper 100 mm of the coal bed; the sediment cores of these axes indicate that their hollow interior space was in communication with the surface via the exposed hollow tree trunks to which they were attached. Both of these features indicate that the lycopsid trees were growing on, and rooted in, the final peat surface. Very rare occurrences of *Stigmaria* and small stems, suspected to be pteridosperms or calamitaleans, with abundant fine roots in attachment, indicate that some plant recruitment continued during the early phases of flooding, and that some plants lived for a while in the mudflat setting. Such indicators, however, are all in the lowermost parts of the Dykersburg Shale. The lack of preferential orientation or size sorting of plant remains, particularly the large trunks, indicates only weak currents and strongly suggests that plant remains were buried where, and in the orientations that, they fell.

The vegetation described in this study was growing on a peat substrate. However, it also was growing during a time of environmental transition when climate was becoming more seasonal, sea level was undergoing a long-term rise, and streams were carrying more sediment, which might be interpreted as higher nutrient loads. It would seem likely, therefore, that this final vegetation may have differed somewhat to considerably from the vegetation that grew during most of peat-swamp history, which has been characterized based on coal ball or palynological analyses (see, for example, the study of Willard, 1993, comparing Springfield coal ball and palynological records). Particularly close to the Galatia channel, the effects of changes in flooding regime and nutrient loads may have had their greatest effects. Overall, the vegetation buried by the Dykersburg Shale was one in decline, with strong selection against further recruitment and gradual drowning of the plants as water cover over the swamp surface became permanent.

#### 4. Plant groups

The plants of the Pennsylvanian Subperiod may not be familiar to many readers, although most will be familiar with various dioramas of “peat swamps” in museums and books. All are extinct and either have closest modern relatives of very different morphology that, unlike the ancient forms, are not trees, or have no close modern relatives at all. Here we briefly describe the main groups encountered in this study. We also note that we have identified the plants in the Galatia assemblage as taxa that, for the most part, were first recognized and described in Europe. One may question, as did one of the reviewers of this paper, whether the identifications are accurate. Even if the “species” have very similar morphologies to the type-concepts as originally established, they may indeed be part of species complexes, in which biological species differences can be determined only by statistical means or by the study of variation in cuticular remains. We can only plead awareness of this problem and urge interested readers to consider that many Pennsylvanian “species” may encompass greater taxonomic variability than a modern plant species.

The iconic and, on average, dominant plants in Middle Pennsylvanian peat-forming wetlands were the spore-producing arborescent lycopsids. These plants varied from small trees, a few meters in height, to the giants of the forests, over 30 m in height (Thomas and Watson, 1976). Rather than being supported by wood, they were

supported by a thick rind of decay resistant bark, likely impregnated with water-repellant chemicals (Boyce et al., 2010), making this bark one of the main tissues that makes up Lower and Middle Pennsylvanian coal beds. The wood cylinder was small, centrally located, and highly efficient at water conduction, that being its only “task” (Cichan, 1986). As a consequence of this construction, particularly the decay-resistant rind, these plants were frequently preserved as standing tree stumps filled with sediment, or as sediment-filled logs. The several genera appear to have been microhabitat differentiated, although all were centered in wetlands (DiMichele and Phillips, 1985; Phillips and DiMichele, 1992; Thomas and Dimitrova, 2017-in press).

The marattialean tree ferns were a group that had lately become important in peat-forming swamps, beginning a rise to prominence in the later Middle Pennsylvanian (Pfefferkorn and Thomson, 1982; Phillips and Peppers, 1984), ultimately becoming dominant in Late Pennsylvanian peat swamps (Phillips et al., 1974). These trees varied between 5 and 10 m in maximum height (Lesnikowska, 1989) and bore an umbrella-like crown of large fronds (Morgan, 1959), perhaps as much as 3 m in length (Rößler, 2000). Reproductive organs were borne on these fronds and a single plant might produce millions of highly dispersible spores during a single period of reproduction. The trunk was supported by a thick mantle of adventitious roots. Each root contained abundant air spaces (aerenchyma) (Ehret and Phillips, 1977; Falcon-Lang, 2006), rendering these the most “cheaply” constructed trees in Pennsylvanian wetlands (Baker and DiMichele, 1997). They also were one of the most widely distributed groups of plants in Pennsylvanian and Permian landscapes, thanks in part to their high reproductive output and the capacity of their spores for air dispersal. As a consequence, they were among the most opportunistic of late Paleozoic tropical plant groups (Lesnikowska, 1989). DiMichele and Phillips (2002) provide a summary of their paleoecology.

The sphenopsids are the final pteridophytic, spore-producing group in the Springfield coal ecosystem. These were of two major kinds: the calamitaleans, a diverse group similar in architecture to the modern horsetails (e.g., Rößler and Noll, 2006), and the sphenophyllaleans, a sprawling to thicket-forming group of groundcover plants (Batenburg, 1982). The calamitaleans were generally a relatively common group of plants in swamp vegetation (Phillips et al., 1985), although they were rarely abundant in such habitats. Their highest concentrations tended to be in disturbed environments (e.g., Gastaldo, 1992), where their clonal growth habit allowed them to spread and form dense stands (Thomas, 2014; Falcon-Lang, 2015). As with the tree ferns, they occurred very widely in Pennsylvanian tropical landscapes, including moisture limited landscapes, where they were confined to margins of water bodies or riverine corridors. The sphenophylls also were relatively insignificant as biomass contributors in wetland landscapes, due to their small stature. They are, however, excellent indicators of substrate exposure, and will be referred to in that role in the following discussion.

Several groups of seed plants occurred in Pennsylvanian wetlands. By far the most important and widespread during the later Middle Pennsylvanian were the medullosan pteridosperms (Cleal, 2008). DiMichele et al. (2006) provide a summary overview of medullosan pteridosperm ecology. There are no close living relatives of the medullosans, perhaps the Cycadales being the closest, although unlike medullosans architecturally. The group was highly diverse and there is a large literature on its taxonomy (e.g., Cleal et al., 1990), which has been important in plant biostratigraphic schemes (Wagner, 1984; Cleal, 1991). Growth habits varied, but the plants were characteristically small trees with large fronds (Pfefferkorn et al., 1984; Wnuk and Pfefferkorn, 1984; Laveine, 1986), either free standing or forming entangled thickets. A wide range of different seed types were produced by medullosans, all large, some up to several centimeters in length (e.g., Taylor, 1965), many of which, given their stony interior layers and fleshy outer layers, may have both floated and been resistant to predation by tetrapods or fish. Few of these seed-types have been

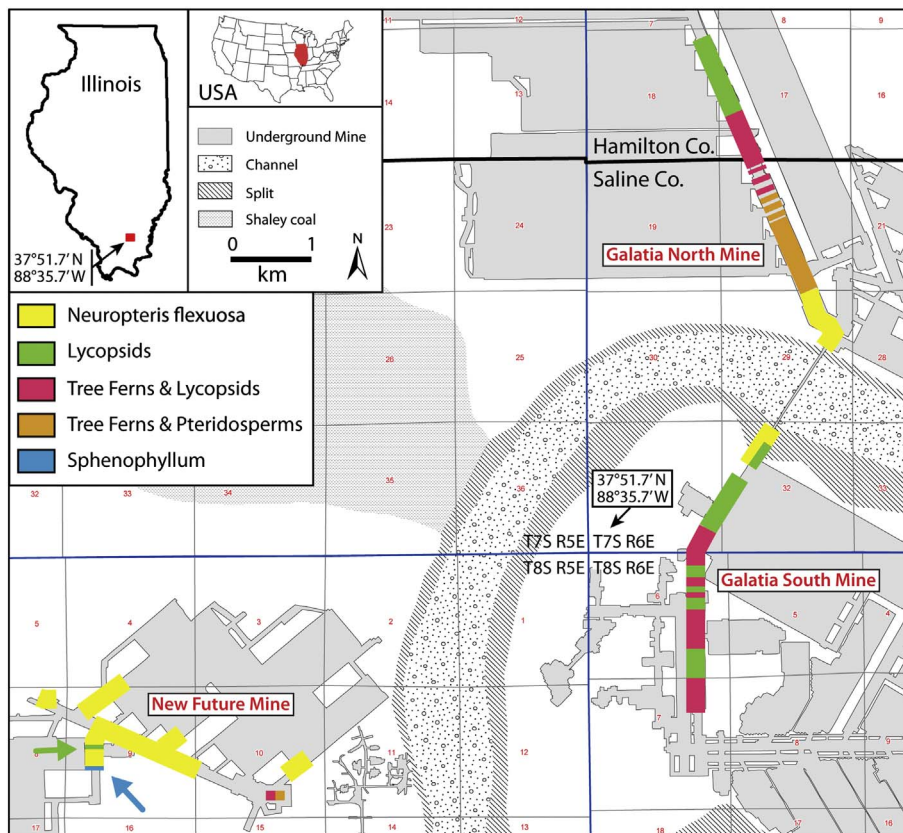


Fig. 6. Distribution of plant assemblages in the Galatia North, South and New Future transects. Siliciclastic partings of sand and silt (“splits”) in erosional contact with the coal are a few meters thick adjacent to the channel, and pinch out distally. The “split” sediment contains coal stringers, rip ups and erosive upper and lower contacts with the coal indicating post-peat emplacement. Shaley coal area northwest of the study area is indicated from company maps and drilling. This area may indicate a persistent pond or lake during the peat forming interval. The map grid is in miles (1 mile = 1.609 km).

confidently associated with vegetative foliage. However, by good fortune, the most prominent medullosan in the landscapes described here, *Neuropteris flexuosa*, has been found with a seed in attachment to a frond (Zodrow and McCandlish, 1980) – a 12 mm long, multi-ribbed form attributable to the *Pachytesta* group of seeds. This is one of the smaller medullosan seeds, but still large given the full range of sizes displayed by seeds in the plant kingdom (Sims, 2012).

## 5. Study design

Fossil vegetation in the Dykersburg Shale was identified and quantified along three transects, each about 4 km long and roughly perpendicular to the Galatia channel (Fig. 6). The Galatia North (4.2 km) and Galatia South (3.8 km) transects are connected via the mine entries that cross the no-coal belt containing the Galatia channel siliciclastic deposits. The Galatia South transect lies inside a large meander loop of the channel, whereas the Galatia North transect lies outside the same loop. The New Future transect (4 km) lies approximately 6.5 km to the south of the Galatia transects, outside the same bend and down-river; it begins approximately 1 km west of the channel (closest accessible approach) and proceeds west, away from the channel.

Vegetation was examined at a series of sampling areas along each transect. Areas were selected where fossils were not obscured by rock dust, the powdered limestone sprayed onto coal and roof surfaces in order to suppress explosive coal dust (Fig. 3D). Areas of approximately 20 m<sup>2</sup> were laid out in order to quantify plant taxonomic composition. The area size was dictated by the dimensions and spacing of entries (main haulage ways) and cross-cuts between entries, determined by the mine plan. The size of these areas varied as much as 20%, depending on the amount of exposed roof and the conditions of roof (how stable was it to walk under and how much of it had fallen out). Whenever possible, two or more adjacent areas were independently quantified as replicates. In areas where only a sparse cover of organic remains was preserved no

estimate of biomass was attempted. Where estimates were made, the relative abundance of each taxon was recorded semi-quantitatively, by visual assessment of the proportion of the total specimen-cover within the sampling area represented by each taxon. This proportion was recorded as one of three major categories: Abundant (> 50% of total cover), Common (10–50% of cover), Rare (< 10% of cover). Two minor categories also were recorded for elements of the flora represented only by small fragments: Two Observed Specimens, and One Observed Specimen. Tree stumps, almost always of lycopods, were counted within each sampling area and the distances between them recorded and mapped. Overall, this produced a form of Braun-Blanquet estimation of relative abundance (Westhoff and van der Maarel, 1978). This approach had been used in a previous study (DiMichele et al., 2007) and was tested there by having two, independent observers produce quantitative abundance estimates of a selected suite of sites.

One hundred total sample sites were semi-quantitatively characterized. Thirty-six sample sites comprise the Galatia South transect (Table 1). Galatia North includes 20 sample sites (Table 1). The New Future transect consists of 44 sample sites (Table 2). These sites were complemented by descriptive observations. For example, if the roof was sufficiently exposed, but not enough to warrant detailed abundance estimation, or if there were long stretches of continuously exposed roof, qualitative descriptions were made noting the common and abundant elements without making a detailed census at every point. Shortcuts often were necessary due to time constraints dictated by the coal company. Such qualitative data were usually bracketed by quantitative census data. Data were plotted on publicly available maps of the mines (Fig. 6).

## 6. Data analysis

Distinct distributional patterns in the composition of the roof-shale vegetation relative to distance from the Galatia channel were observed by inspection during visits to the three mines that comprise this study.



Table 1

Galatia North and South transect data. Channel position marked. For each transect, sample sites numbered from most distal to most proximal to channel. Sites subtexted a/b are side-by-side replicates. Abundant (5) and Common (4) occurrences highlighted. 3 – rare, 2 – two occurrences, 1 – one occurrence (see text for details). Pteridosperm stems were subdivided into two groups: those with smooth surfaces and those with small oval holes, probably caused by the emergence of adventitious roots. "Indet." = indeterminable to a particular genus or species.

Galatia south transect																													
Sample site	5	6	7	8	9	12	13	16	17	18	20	21	22	23	24	25	26	27	29	30	31	32	33	35	36	37	38		
Pteridosperms																													
<i>Neuropteris flexuosa</i>	1																			1									
<i>Laveineopteris rarninervis</i>																													
<i>Macroneur. scheuchzerii</i>						1																							
<i>Alethopteris</i> sp.																													
Pteridosperm stems holes																													
Pteridosperm stems smooth	1																	2											
Pteridosperm striate axes																													
Sphenopsids																													
<i>Calamites</i> sp.	3			4										3															
<i>Sphenophyllum</i> sp.																													
Cordaitaleans																													
																			1										
Lycopsids																													
<i>Lepidostrobus</i> sp.																													
<i>Lepidostrobophyllum</i> sp.					5					5																			
<i>Sigillaria</i> sp.													4																
Lycopsid leaves indet.																													
Lepidodendrid stems															3			4											
Lycopsid stumps indet.																													
<i>Lepidodendron</i> sp.																													
<i>Lepidophloios</i> sp.																													
<i>Asolanus camptotaenia</i>																													
<i>Synchysidendron</i> sp.																													
Ferns																													
Tree fern stems																													
Tree fern rachises	5	5	5	5		5	5						4	5				4	4	5	5	4	3	4			3		
Marattialean foliage indet.																													
<i>Lobatopteris</i> sp.																													
<i>Sphenopteris</i> spp.																													
Galatia north transect																													
Sample site	39	40	41	42	43	44	45	46	Channel	23	22	21	20b	20a	19b	19a	18	17b	17a	15	14	13	9b	9a	8b	8a	6	5	3
Pteridosperms																													
<i>Neuropteris flexuosa</i>																													
<i>Laveineopteris rarninervis</i>																												1	
<i>Macroneur. scheuchzerii</i>																													
<i>Alethopteris</i> sp.																													

Table 1 (continued)

Sample site	Galatia south transect										Galatia north transect																			
	39	40	41	42	43	44	45	46	Channel	23	22	21	20b	20a	19b	19a	18	17b	17a	15	14	13	9b	9a	8b	8a	6	5	3	
Pteridosperm stems holes					3								3	1	1	3	1													
Pteridosperm stems smooth												5																		
Pteridosperm striate axes				3	5	4	5	5		5	5									5										
Sphenopsids													1	1	1	1														
<i>Calamites</i> sp.												5			1	1					3		1	1						
<i>Sphenophyllum</i> sp.															1	1					3	3		1	1					
Cordaitaleans			4			3											1													
Lycopsids																														
<i>Lepidostrobus</i> sp.																					1					1				
<i>Lepidostrobohyllum</i> sp.																							1							
<i>Sigillaria</i> sp.	5	3	3	4			3	4		1																			4	
Lycopsid leaves indet.												1																		
Lepidodendrid stems															1													4		
Lycopsid stumps indet.	3		2	1																	1		1	1	1	1	3		1	
<i>Lepidodendron</i> sp.							4	1							1															
<i>Lepidophloios</i> sp.																														
<i>Asolanus camptotaenia</i>																														
<i>Synchysidendron</i> sp.																														
Ferns																														
Tree fern stems													1									1				1				
Tree fern rachises								3				3	5	5	5	5	5	5	5	5	3	3	3	5	3					
Marattialean foliage												1				1					1				1	1				
Indet.																														
<i>Lobatopteris</i> sp.													5	3	3	3	3	5	5	3		5	5	5	5					
<i>Sphenopteris</i> spp.																														



Table 2

New Future transect data. Transect was broken into three legs, with leg 1 closest to the channel. Sample sites numbered by leg and sample site within leg. Abundant (5) occurrences highlighted (there were no 'common' [4] occurrences noted). 3 – rare, 2 – two occurrences, 1 – one occurrence (see text for details). Pteridosperm stems were subdivided into two groups: those with smooth surfaces and those with small oval holes, probably caused by the emergence of adventitious roots. Pteridosperm axes were divided into two groups: those with irregularly disposed longitudinal striae visible on the surface and those with bumpy (pimply) surfaces. "Indet." = indeterminable to a particular genus or species.

Sample site	New Future transects																					
	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8a	1.8b	1.1	1.12	2.2	2.6	2.7	3.1	3.2	3.3	3.4	3.5	3.6	3.7	
Pteridosperms																						
<i>Neuropteris flexuosa</i>	3	5	5	5	5	5	5	5	5	5	1		5	5		5	5	5	5	5	5	
<i>Lavineopteris rarinervis</i>													1									
<i>Macroneur. scheuchzerii</i>	1	3	3	3	3	3	3		3				1	1	1	1			1			
Neuropterid foliage indet.						1																
<i>Mariopteris</i> sp.																						
cf. <i>Pseudomariopteris</i> sp.																						
Pteridosperm stems holes																						
Pteridosperm stems smooth																						
Pteridosperm striate axes	5	5	5	5	5	5	5	1	3	5		1	3	3	3	3	3	3	3	3	1	
Pteridosperm pimply axes																						
<i>Pachytesta</i> sp. large												1										
Sphenopsids																						
<i>Calamites</i> sp.	1								1													
<i>Annularia</i> sp.																						
<i>Asterophyllites</i> sp.																						
<i>Sphenophyllum</i> sp.					3				1													
Cordaitaleans	1	1				1	1		1				1									
Lycopsids																						
<i>Lepidostrobus</i> sp. large												1										
<i>Achlamydocarpon</i> sp.				1		1																
<i>Sigillaria</i> sp.								5			3											
Lycopsid leaves indet.						1																
Lepidodendrid stems indet.																						
Lycopsid stumps indet.																						
<i>Lepidodendron</i> sp.																						
<i>Lepidophloios</i> sp.	1											3										
<i>Diaphorodendron</i> sp.						1	3		1													
Ferns																						
Tree fern stems																						
Tree fern rachises							1															
Marattialean foliage indet.			1									5										
<i>Sphenopteris</i> spp.									1			3		1								

(continued on next page)

Table 2 (continued)

New Future transects																							
Sample site	3.8	3.9	3.1	3.11	3.12	3.13	3.14	3.15	3.16	3.17	3.18	3.19	3.2	3.21	3.22	3.23	3.24	3.25	3.26	3.27	3.28	3.29	
Pteridosperms																							
<i>Neuropteris flexuosa</i>	5	5	5	5	5	3	5	1	5	5	1	3	5	5	5	5	5	1	5	5			
<i>Laveineopteris rarinnervis</i>						1		1	1	1		3		1			1			1	3	3	
<i>Macroneur. scheuchzerii</i>	3	1	1	1	3	3		1	1	5	5	3	1	3	5	3		1	3	5	5	3	
Neuropterid foliage indet.																							
<i>Mariopteris</i> sp.																					1		
cf. <i>Pseudomariopteris</i> sp.					1																		
Pteridosperm stems holes	1								1														
Pteridosperm stems smooth			1	3			5	3		3			3			3	3		1	3	3	3	
Pteridosperm striate axes	3		3			3	5	3	3	3	1	3	3	3	3	3	3		3	3	3	3	
Pteridosperm pinnly axes																							
<i>Pachytesta</i> sp. large																				1			
Sphenopsids																							
<i>Calamites</i> sp.						1										1	1		1				
<i>Annularia</i> sp.						1										1							
<i>Asterophyllites</i> sp.													1										
<i>Sphenophyllum</i> sp.																							
Cordaitaleans		1					1	3				1					1	1	1	1	5	5	
Lycopsids																							
<i>Lepidostrobus</i> sp. large																							
<i>Achlamydocarpon</i> sp.																							
<i>Sigillaria</i> sp.						1																	
Lycopsid leaves indet.																							
Lepidodendrid stems indet.				1																			
Lycopsid stumps indet.				1			1																
<i>Lepidodendron</i> sp.													1										
<i>Lepidophloios</i> sp.																							
<i>Diaphorodendron</i> sp.								1								3		3	3				
Ferns																							
Tree fern stems																							
Tree fern rachises																							
Marattialean foliage indet.							1			1	1									1	3	1	
<i>Sphenopteris</i> spp.																						1	



In order to assess these patterns beyond the level of visual inspection two types of statistical analysis were carried out on the data, a non-metric multidimensional scaling ordination (NMDS) of all data points (quantitatively characterized sampling locations), and an analysis of similarities (ANOSIM) assessment of the in-mine identified patterns. Statistical analyses were carried out using the R statistical software (R Core Team, 2016), specifically the Vegan package (Oksanen et al., 2013).

### 6.1. NMDS

NMDS is a member of a family of data-exploration techniques known as ordination (see discussion of the method in McCune and Grace, 2002). As implemented here, the NMDS ordination compares sampling locations based on their relative-abundance-based taxonomic composition. The pair-wise distances between samples were calculated using Jaccard dissimilarity (see McCune and Grace, 2002). NMDS permits the a priori designation of the number of dimensions in which the data are to be displayed; for visual simplicity, two dimensions were used in the analysis presented here. A plot of sample sites (points) in the two-dimensional space provides a template on which the relative compositional characteristics can be overlain, permitting us to see if the same kind of clustering of sample sites as observed in the transects is recovered statistically. Sampling sites from all three transects were combined in the ordination analysis.

### 6.2. ANOSIM

ANOSIM is a confirmatory statistical technique. It first calculates a distance matrix then converts pairwise distances to rank values and separates them into within-group and between-group distances, the groups having been pre-determined. This permits a comparison of the degree of dissimilarity within the groups to the dissimilarity between those groups. The degree of dissimilarity is represented by the distance values with larger distances equating to higher dissimilarity. Dissimilarity values are displayed as a box-and-whisker diagram. For the ANOSIM analysis reported here, we used the Jaccard dissimilarity measure.

The objective of the analysis was to test the hypothesis, formulated from observational data, that several distinct plant assemblages could be recognized in accordance with their spatial distribution. The results are shown graphically in Fig. 8. ANOSIM calculates the statistic 'R' to determine if these dissimilarities are significantly different. Four groups were identified in the Galatia North and Galatia South transect; the New Future transect was excluded from this analysis due to its compositional homogeneity. (1) *Neuropteris flexuosa* dominance, located spatially closest to the Galatia channel margin (Group c in Fig. 8). (2) Mixed pteridosperms and tree ferns, located immediately north of the *N. flexuosa*-dominated area, and present only in the Galatia North transect (Group d in Fig. 8). (3) Mixed tree ferns and lycopsids (Group a in Fig. 8). (4) Lycopsid-dominated, the most spatially distant assemblage from the channel (Group b in Fig. 8).

## 7. Results

Refer to Fig. 6 for patterns of vegetational composition. These patterns are visible by inspection of the Figure.

### 7.1. Galatia North transect

The Galatia North transect shows four distinct vegetation zones. Measurements of the width of these zones, reported below, are given both as the measured width along the transect line, and as the estimated width of the zone measured at right angles from the channel margin. Because the transect path was dictated by the disposition of the mine works, layouts strictly orthogonal to the channel margin could not be

made. The estimated widths, therefore, are projections.

In the descriptions below we use the widely understood name *Lobopteris vestita* (Lesquereux) Wagner for a species of marattialean tree fern foliage, recognizing that the name *Crenulopteris acadica* (Bell) Wittry et al., has been proposed for this foliage (Wittry et al., 2015) in light of certain taxonomic considerations. Our use of *L. vestita* does not signify a rejection of *C. acadica* but rather a desire to be conservative at this point in time and to continue to use the name that is most widely recognized.

Four distinct vegetational zones can be recognized in the Galatia North transect. The first of these begins at the edge of the Galatia channel and extends approximately 0.8 km (0.6 km estimated width, measured perpendicularly from the channel edge) north. Fossils are almost exclusively laminate foliage, frond rachises, and stems of the pteridosperm *Neuropteris flexuosa*. A few stems of the arborescent lycopsid *Sigillaria* also were noted but no in situ, upright tree stumps.

The contact between the first vegetational zone and the second zone to the north is abrupt. The second assemblage is dominated by marattialean tree ferns, particularly *Lobopteris vestita*, with a few occurrences of the pteridosperms *Macroneuropteris scheuchzeri* and *Laveineopteris rarineris*. Isolated Calamitalean stems occur at several sample sites. Lycopsid remains are practically non-existent, and no upright stumps were noted. This zone is 1.3 km long in transect (1.1 km estimated width, measured perpendicularly from the channel edge).

A gradual transition marks the contact of the second and third vegetational zones. Marattialean tree-fern dominance continues, again primarily *Lobopteris vestita*, but the remains of arborescent lycopsids appear and, continuing to the north, become abundant. Lycopsids are represented primarily by upright stumps and fallen, decorticated logs, the generic identities of which could not be established. However, most of these lycopsid trunks did not have the distinct characteristics of decorticated *Sigillaria* stems, which generally preserve some degree of marked ribbing, even if leaf bases are lacking. The observed specimens were most similar to the Lepidodendraceae or Diaphorodendraceae (sensu DiMichele and Bateman, 1996), in which the more interior layers of decorticated large stems consist of a network of elongate, rugose grooves and ridges. Zone 3 is about 1 km long in transect (0.9 km estimated width, measured perpendicularly from the channel edge) and terminates about 2.5 km, measured along the transect, from the channel margin.

Zone 4, the most distal part of the transect, consists of stem and in situ tree stump remains of arborescent lycopsids. The near monodominance of these plants is possibly a taphonomic happenstance. At this distance from the channel, 4 km, it must be considered that the more delicate types of plant remains may have decayed prior to burial. Nonetheless, the preserved, lycopsid assemblage is in situ and representative of a component, if not the entirety, of the original vegetation. Zone 4 is 1.1 km long in transect (1 km estimated width, measured perpendicularly from the channel edge) and terminates about 3.5 km, measured on the transect, from the channel margin. At the end of this transect zone, plant fossils were too sparse to map effectively.

Few ground-cover plants were observed in the Galatia North transect. The most commonly occurring of these was *Sphenophyllum*, a small, thicket-forming groundcover sphenopsid (Batenburg, 1982; Bashforth and Zodrow, 2007). In a single sampling site in Zone 1, near the channel-margin, where the roof flora was otherwise dominated by *Neuropteris flexuosa*, a small patch of abundant *Sphenophyllum* was recorded.

### 7.2. Galatia South transect

The Galatia South transect shows distinct vegetational zonation different from that of the north transect. This transect lies within a bend of the Galatia channel, and thus presumably differed to some degree from the north side with regard to the amount of sediment initially delivered to the area, and the amount of energy with which flood

waters penetrated the swamp – lower on the south side in both cases. There also may have been hydrological differences between the two areas in terms of standing-water period.

Zone 1 is adjacent to the channel and extends out from it for approximately 0.5–0.6 km (at this point, the transect path was perpendicular to the channel margin). As on the north side of the channel, this vegetation immediately adjacent to the channel margin is dominated by the pteridosperm *Neuropteris flexuosa*. Also present are lycopsid stem remains, mostly *Sigillaria* but also *Lepidodendron* (sensu stricto – DiMichele, 1983), and rare tree fern foliage, *Lobatopteris vestita*. This assemblage likely occupied an area of greater width than is presently preserved; the channel margin at this location is considerably disrupted and the coal appears to have been torn up at the peat stage, probably by the effects of tidal action, removing some of the original swamp surface. As with the Galatia North transect, the pteridosperm-dominated, channel-margin assemblage is replaced spatially, with little or no transition, by a compositionally distinct assemblage.

Beyond Zone 1 to the end of the transect the vegetation of Zone 2 is a spatially heterogeneous mixture of tree ferns and lycopsids. Tree ferns are represented principally by rachial axes and stems, and by foliage attributable to *Lobatopteris vestita*. Lycopsids consist almost exclusively of *Sigillaria*, with patchy occurrences of *Lepidodendron* and rare appearances of *Asolanus* and the more typically peat-swamp forms, *Synchysidendron* and *Lepidophloios*. At the juncture between Zones 1 and 2 cordaitaleans were observed; occurrences of this plant group are generally rare in the Galatia mine complex. Total transect length measured is 3 km; a small side transect was measured also, adding an additional 0.2 km of length. Due to the layout of the mine plan, the Galatia South transect makes an angular bend in the middle; it terminates approximately 3.6–3.8 km measured orthogonally from the

channel margin at two points on the river bend, and 2.2 km from the margin to the immediate west side of the bend.

Even more extreme than in the Galatia North transect, no plants identifiable as ground cover were noted anywhere in the Galatia South transect.

### 7.3. New Future transect

The transect in the New Future Mine began approximately 1.6 km west of the edge of the Galatia channel, the closest possible approach within accessible workings (Fig. 6). It terminated 4.3 km west of the channel margin, measured perpendicularly, and included several side excursions. The New Future Mine is west of the Galatia channel, just south of the river bend separating the Galatia North and South transects, thus downriver from these. In this position, it would have been subject to a degree of river energy similar to or greater than that affecting the area of the Galatia North transect.

Vegetation was nearly uniform throughout this transect. Overwhelmingly, the most abundant plant was *Neuropteris flexuosa*, mirroring the channel margin patterns in the Galatia North and Galatia South transects. *Macroneuropteris scheuchzeri* and *Laveineopteris rarinervis* were generally uncommon although widely distributed, and the former was abundant a several sample sites. The only lycopsid observed more than once was *Diaphorodendron*, always a rare element. Marattialean tree fern foliage and stems, and calamitalean remains were rare and sporadic in occurrence.

At the west end of this transect were two sampling areas where *Sphenophyllum*, a ground-cover plant, was the most abundant taxon. These sites also included foliage of tree ferns and of the pteridosperms *M. scheuchzeri* and *L. rarinervis* – but lacked *Neuropteris flexuosa*. The

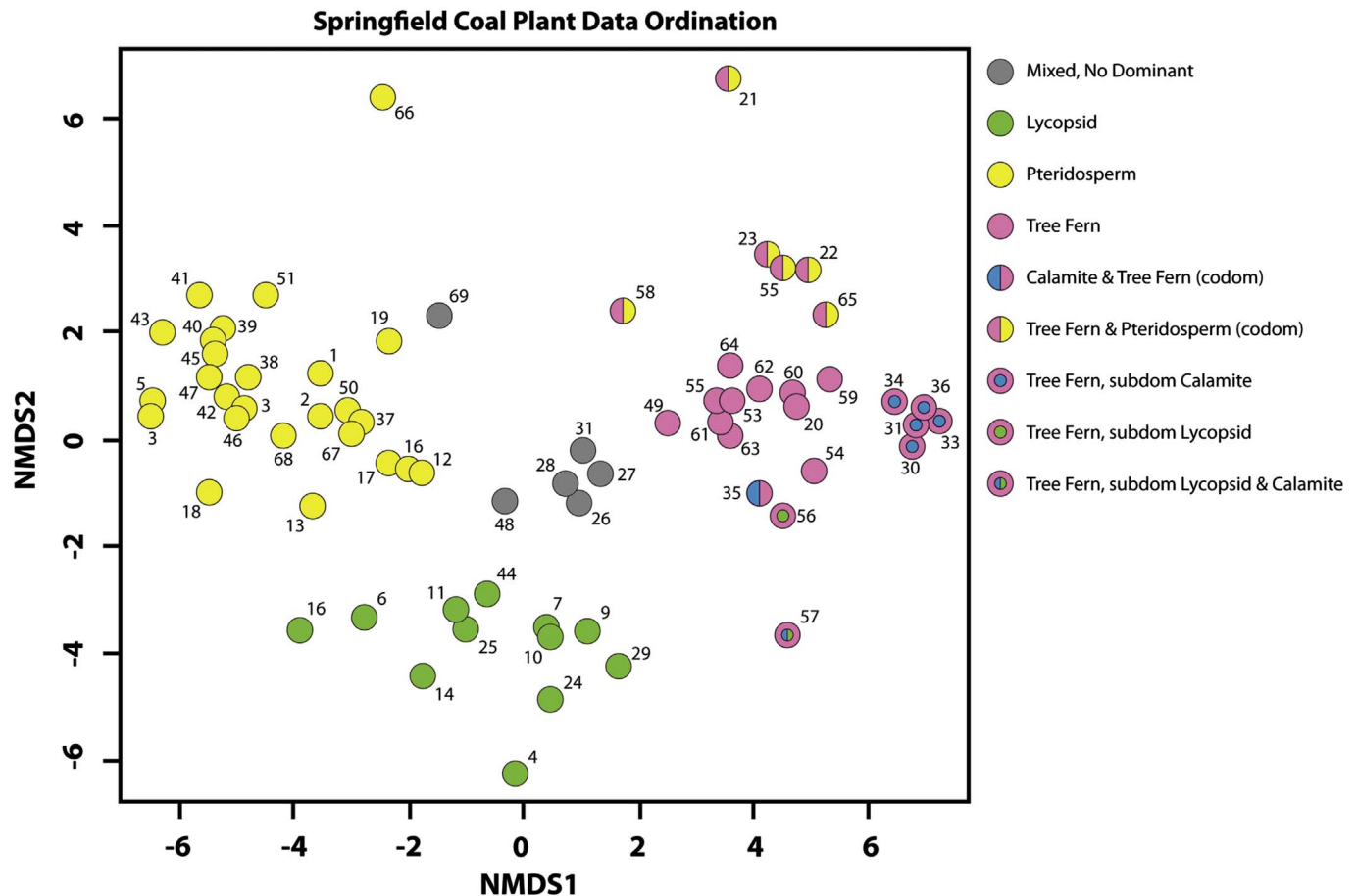


Fig. 7. Nonmetric multidimensional scaling ordination of sampling sites in the Galatia North, Galatia South and New Future transects. “Subdom” = subdominant; “Codom” = codominant.



abundance of *Sphenophyllum* at these two sites suggests that its absence elsewhere is not merely a preservational happenstance. Groundcover is nearly absent throughout the extensive area of the three transects in combination. However, delicate foliage of arborescent plants is well preserved. In addition, relatively fragile stems of pteridosperms and tree ferns are frequently common in areas where their foliage is also abundant. Thus, the preservation of ground cover, especially in the absence of *N. flexuosa* may suggest a particular set of substrate conditions, perhaps exposure due to a local rise in the peat surface. Were these plants to have been growing on fallen trunks of lycopsids or other kinds of trees, emergent from the flooded swamp floor, we would expect to see evidence of such trunks, and more such occurrences throughout the areas sampled, in many of which lycopsid trees were common to abundant.

#### 7.4. Statistical analyses

The points in the NMDS ordination (Fig. 7) are quantified sample locations that have been arrayed in two dimensions based on their quantitative taxonomic composition. When the relative-abundances of taxa are plotted on the ordination, in order to provide visual clarity, three main vegetational centroids can be seen clearly. One dominated by medullosan pteridosperms (on the left of Fig. 7, in yellow), one by arborescent lycopsids (at the bottom of Fig. 7, in green), and one by marattialean tree ferns (on the right of Fig. 7, in pink). A few mixed assemblages were identified in which there was no clear dominant taxonomic group (in the center of Fig. 7), and there was overlap between tree-fern rich assemblages and all of the other groups, broadly defined. This pattern reflects strongly two aspects of that seen and recorded in the transects “by inspection”. The first is the strong separation between medullosan pteridosperms, particularly assemblages dominated by *Neuropteris flexuosa* (along the river margin) and those dominated by arborescent lycopsids (variably distant from the river margin, but never up against it). The second is the intermixture of tree ferns with pteridosperms near the channel and with lycopsids for some distance between the river margin and the most distal, nearly purely lycopsid-dominated assemblages.

The pteridosperm-dominated assemblages are composed nearly entirely or principally of *Neuropteris flexuosa*. These assemblages are the ones that were located only close to the channel margin in the Galatia North and Galatia South transects, and that made up most of the sampling sites throughout the New Future transect. A variety of other kinds of pteridosperms, most commonly *Macroneuropteris scheuchzeri*, *Neuropteris ovata*, and *Lavineopteris rarineris*, were identified in areas dominated by tree ferns, but these never were common enough to constitute the dominant element.

Lycopsid dominated assemblages come largely from those areas of the Galatia North and Galatia South transects located the farthest from the Galatia channel. Note that there is no overlap in the ordination between pteridosperm-dominated assemblages and those dominated by lycopsid trees. Not only do these two kinds of assemblages differ in taxonomic compositional and dominance patterns but they were widely and almost completely separated spatially in the transects. This was particularly the case with *Neuropteris flexuosa*, among the several kinds of pteridosperms identified in the transect areas, and lycopsid trees. A few sightings of lycopsids were made in areas otherwise dominated by *N. flexuosa*, but these were extremely rare. Furthermore, no in situ lycopsid tree stumps were identified in any of the areas that contained abundant or common pteridosperms. Interestingly, the lycopsid assemblages cluster in the two-dimensional space, even though there are a number of different lycopsid taxa involved.

Tree-fern dominated or tree-fern rich assemblages show the broadest patterns of overlap with the other groups in Fig. 7. Not only is there a core area of tree-fern dominated assemblages, but tree ferns overlap with each of the other groups and are codominant with them in one or more of the sampling sites. These samples are drawn from the

Galatia North and Galatia South transects and indicate areas where more than one taxon was identified at frequencies of abundant or common (possible when carrying out a quadrat-based, frequency analysis). This kind of pattern is in keeping with the broader biogeographic and paleoecological distribution of marattialean ferns. Their high reproductive capacity, high dispersal capacity, and tolerance of a wide range of physical conditions allowed them to occur throughout the Pangean tropics more widely than almost any other group of plants.

Calamitaleans did not dominate any assemblages but were codominant with or subdominant to tree ferns in several. The calamitaleans were habitat specialists best adapted to disturbed or aggradational settings, mainly, as far as we know, in high-moisture substrates, but tolerant of water-table fluctuations (see Section 4.0 above on the plant groups).

Results of the ANOSIM analysis (Fig. 8) indicate that the median between-group dissimilarity is much higher than the dissimilarity within any individual compositional assemblage (identified by inspection of transect patterns and by assessment of the NMDS). The R statistic for the reported analysis is 0.2579, which has a significance of 0.009. This indicates that the dissimilarity within any given assemblage zone is significantly less than that among the zones. The ANOSIM is broadly consistent with the patterns found in the two-dimensional NMDS ordination and with in-mine observations. Of greatest note are the distinct separation of lycopsid-dominated and pteridosperm-dominated assemblages in the ANOSIM (Groups b and c), and the partial overlap of each by tree-ferns (Groups a and d).

## 8. Discussion

### 8.1. Environmental implications of Springfield vegetational zonation

The zonation of vegetation flanking the Galatia channel most likely reflects a primary influence of the river. In modern environments,

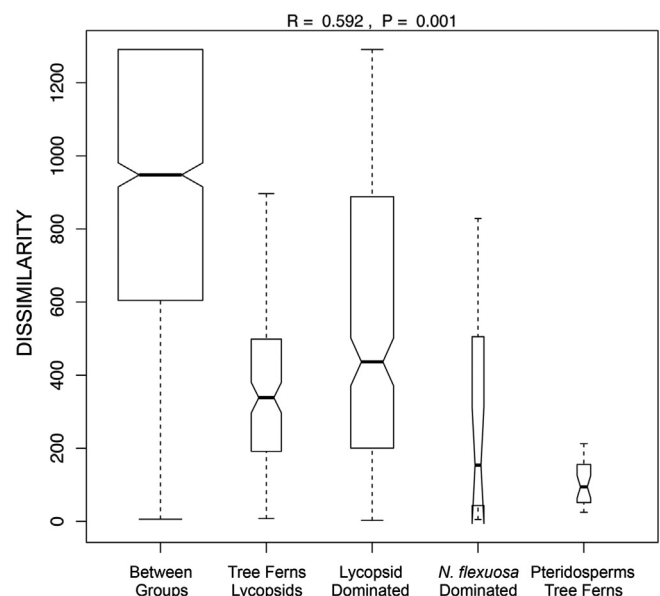


Fig. 8. Analysis of similarities (ANOSIM) plot showing dissimilarity between and within predetermined plant assemblage groups. Median - bold horizontal bar within box; Bottom of box - 25th percentile; Top of box - 75th percentile; Extreme data point marked by whiskers, which are no more than the range times the interquartile range from the box; Box width - directly proportional to sample size. Lack of overlap of notched areas is considered 'strong evidence' for differences among medians (Chambers et al., 1983, p. 62). The ANOSIM statistic R is based on the difference of mean ranks between groups ( $r_B$ ) and within groups ( $r_W$ ), such that:  $R = 1/4 (r_B - r_W) / (N(N-1)/4)$ . Key: Between - between-group dissimilarity; Tree fern-Lycopsid assemblage = GN Zone 3; Lycopsid-dominated assemblage, GN Zone 4; *Neuropteris flexuosa*-dominated assemblage, GN Zone 1; Mixed pteridosperm-tree fern assemblage, GN Zone 2.

factors such as flood frequency and intensity, landscape morphology, and vegetational history, can create complex vegetational mosaics along riverine corridors (e.g., Naiman et al., 2008). Lowland rivers, particularly in areas where river confinement is relatively low, often have high flood frequencies that vary in intensity (Lake et al., 2006). Such effects may alter or stabilize species distributions along river corridors by creating access to space and resources, while enhancing the nutrient status of soils. Consequently, plants of riverine margins generally possess many specialized morphological, physiological, and life history traits (Lytle and Poff, 2004), particularly in those environments where flooding periods are long and flood depth great (e.g., Wittmann et al., 2011).

It is difficult, with paleontological and associated sedimentological data, to make concrete inferences about various environmental factors that may have been at the root of a gradient. Possible variables to consider include disturbance, nutrients, the temporal duration of flooding, and salinity. And, of course, it is very likely that environmental variables interacted to varying degrees with dispersal factors. We frame this discussion within the context of the physical factors but also consider dispersal attributes where appropriate.

It is fairly certain that salinity was not a factor in the distribution of vegetation described here. There are no indicators of salinity, such as brackish water mollusks or brachiopods associated with the plant remains in the lower Dykersburg Shale. Such indicators indeed do appear in the Dykersburg, but only in its upper portion, which, given the thickness of the shale, likely was deposited when water cover over the peat body was meters deep and permanent.

The possibility of disturbance as a major factor is suggested most strongly by vegetational patterns along the river's edge. Both flanks of the Galatia channel were populated overwhelmingly by one species, *Neuropteris flexuosa*, which forms the most clearly delimited of the vegetational zones. *N. flexuosa* was a medium-sized medullosan pteridosperm tree, perhaps several meters in height, bearing large, highly divided, frond-like leaves and producing large seeds (Zodrow and McCandlish, 1980; Zodrow and Cleal, 1988) (*N. flexuosa* is sometimes considered a variety of *Neuropteris ovata*, see comments in Zodrow and McCandlish, 1980). The belt of *N. flexuosa* varies in width from 0.5 km to at least 3 km and is best developed on the outer (north) side of the major bend in the Galatia channel. Most likely, flooding and associated flood energy, and associated disturbance, were more frequent and intense on the outside of this meander than on the inside. It also must be considered, given the size and nature of *N. flexuosa* seeds, that the plant was distributed along the channel margins in part because of the combination of flood energy, nutrient levels, and effects on the transport of these reproductive organs from one area to another. In other words, a dispersal-limitation factor, reflecting not only a preference by or tolerance of channel margin conditions by the parent plant, but also the means to colonize such microhabitats.

*Neuropteris flexuosa* may have a modern counterpart in *Nypa*, a mangrove palm that fringes river and distributary channels in parts of Southeast Asia (Tsuji et al., 2011). Perhaps more appropriately, *N. flexuosa* might be considered a “mangrove associate”, because there is no evidence that it was growing in saline waters and it appears, from other reports of the species, not to be confined strictly to this particular habitat. “Mangrove associates” are plants that may occur with true mangroves, in saline waters, but also may line channels in more landward areas where streams or estuaries are fresh-water, even extending into vegetation fringing or exclusive of mangrove swamps (Wang et al., 2011).

The boundary between the belt of *N. flexuosa* and the vegetation behind it is sharp in both the Galatia North and Galatia South transects. Although the patterns in the two, opposite transects differ in detail, the sharpness of the boundary in each instance suggests an equally abrupt environmental change.

The possibility of a nutrient gradient is intriguing, although difficult to evaluate. The concentration of *Neuropteris flexuosa* along the Galatia

channel margin may reflect elevated nutrient levels as much as disturbance. Dykersburg Shale is thickest along the channel margin, indicating both early and sustained sediment input. Furthermore, along the Galatia Channel, the Springfield Coal is characteristically enriched in fine-grained siliciclastics, mainly clays, indicating flooding and clay flocculation during peat-swamp development. This concentration of fine siliciclastics in the coal only near the channel margin supports the idea that nutrient concentrations were higher along the channel margin throughout peat accumulation. Thus, it also would have been in this area that sediment, and associated nutrients were introduced first and in the greatest volume during the final drowning phases of the peat swamp.

In addition, it is along the Galatia North transect that a mixture of pteridosperm taxa other than *N. flexuosa* and tree ferns is most strongly expressed. Falcon-Lang (2009) described the medullosan pteridosperm *Macroneuropteris scheuchzeri* (common in Springfield coal roof-shale plant assemblages) as mangrove-like, suggesting that a skirt of dead leaves helped support its flexuous stem. Stull et al. (2012) considered the same possibility in noting that *M. scheuchzeri* appeared to favor habitats with long hydroperiods. This pteridosperm was found only in areas behind the channel margin, *N. flexuosa*-dominated, vegetation, in the Galatia North transect, where it would have been protected from the environmental conditions prevailing at the channel margin. On the immediate outside of a channel bend, flood force would be expected to be strongest and to have introduced silt-bearing waters over the largest spatial extent, diminished by the filtering and energy-dissipating effects of vegetation.

The differences in the arborescent lycopsid profiles of the Galatia North and South transects is considerable, and most likely reflects environmental differences, although what those might be is not obviously apparent. The North and South differences also may reflect the happenstance of which species were the first into the sites as conditions were changing, thus establishing a large pool of source plants from which propagules could be derived. We cannot distinguish the effects of these. The large lycopsids, based on their common modes of preservation and species associations, encompassed a range of habitat conditions, but all appear to have been tolerant of various degrees of flooding. Based on their modes of preservation, most appear to have grown on wet soils composed of peat and/or non-peat, some perhaps even tolerating periodic drought via specialized root morphologies (Pfefferkorn and Wang, 2009). In the Galatia North transect most specimens were not identifiable to genus but where this was possible, *Lepidodendron*, *Synchysidendron*, and *Diaphorodendron* were the most common and *Sigillaria* occurred only sporadically. *Diaphorodendron* and *Synchysidendron* were among the dominant lycopsids of late Middle Pennsylvanian peat-swamps (DiMichele and Phillips, 1985) but also occurred in mineral-substrate swampy settings (e.g. Wnuk, 1985). In the South transect *Sigillaria* was the dominant lycopsid tree, with smaller numbers of *Lepidodendron*. These latter genera are more common in compression-impression assemblages than in peat-swamp settings (e.g., Phillips et al., 1985; Wagner and Álvarez-Vázquez, 2010), suggesting a preference for siliciclastic/mineral substrate wetlands. Some species also occurred variably in peat-substrate assemblages during the Pennsylvanian (e.g., Phillips and DiMichele, 1998; Opluštil, 2010) but are only rarely common to abundant in fossil assemblages from those environments based on studies of permineralized peat stages of the coal (“coal balls”: Phillips et al., 1985; DiMichele et al., 2002) or inferred from coal palynology (e.g., Butterworth and Smith, 1976; Mahaffy, 1988; Willard, 1993; Peppers, 1996; Eble, 2002). *Sigillaria* was one of few arborescent lycopsids to survive in abundance into the Late Pennsylvanian in Euramerica, where one species was locally common in peat swamps (Delevoryas, 1957; Phillips et al., 1985; Peppers, 1996); along with some other tree lycopsid genera, it survived into the Permian in China (Wang et al., 2009).

In the Springfield Coal, however, *Sigillaria* and *Lepidodendron* are more commonly represented than in other late Middle Pennsylvanian

coals of the Illinois and Appalachian basins, based on coal-ball (Willard, 1993; Phillips and DiMichele, 1998) and palynological analyses (Mahaffy, 1988; Willard, 1993; Peppers, 1996). Thus, the overall common to abundant occurrence of *Sigillaria* and, to a lesser degree, *Lepidodendron*, in the Galatia roof-shale assemblages is not out of character with the general composition of the Springfield coal. What is more important, perhaps, is the extreme rarity, nearly a general absence, of *Lepidophloios* in the Galatia transects, a plant that distributional patterns suggest to have favored and been a biomass dominant in flooded peat substrate habitats (DiMichele and Phillips, 1985). Thus, the physical conditions of this final, channel-margin wetland forest may have deviated from those typical of the peat swamp throughout most of its time of accumulation or areal extent. A further indication of the distinctiveness of these late-stage peat-to-mudflat transitional settings is the rare occurrence of *Asolanus* in the South transect (as in the Springfield roof vegetation reported by DiMichele and Nelson, 1989), a plant that is presently unknown in coal-ball peat preservation, seemingly restricted to siliciclastic, swampy habitats.

A potential puzzle is indicated by the concentration of the lycopsid dominated sample sites in the ordination analysis (Fig. 7). These assemblages are compositionally diverse. And due to the mechanics of the ordination, the different lycopsid taxa are as distinct from one another as any is from a tree fern or pteridosperm species. The clustering of the lycopsids therefore requires some consideration. We believe this clustering may reflect the conterminous distribution of unidentified lycopsid stems and lycopsid tree stumps, also unidentified to taxon, intermixed as rare to common elements at most of the quantified sites where lycopsid trees of various kinds were present.

An indication of the possible effect and extent of long hydroperiod is the low concentration of ground cover in all of the transects. Long periods or repeated intervals of surface flooding during the final phases of peat accumulation and mudflat development would have been a major factor inhibiting establishment and growth of low-growing plants. *Sphenophyllum*, a common, Pennsylvanian-age, groundcover plant, was absent from most of the sites studied, yet abundant at two sampling sites near the outer end of the New Future transect. Similarly, evidence of other kinds of groundcover, particularly small ferns (e.g., *Sphenopteris*) and pteridosperms (e.g., *Dicksonites*), also was absent. Differential preservation of these low-growing plants probably is not the cause of their absence (e.g., Scheihsing, 1980); small plants vary widely in form and robustness of construction, and other types of delicate plant remains, with little disarticulation, are fairly common and widespread in the Springfield roof assemblage, indicating favorable conditions for preservation of organic matter. In addition, plants growing on the forest floor should have been preserved commonly under the conditions of burial envisioned for the Springfield roof-shale assemblage. Small ferns, *Sphenophyllum*, small lycopsids (such as *Hizemodendron*, *Paurodendron* or *Chaloneria*) are also relatively rare in coal ball quantitative biomass analyses (e.g. Phillips et al., 1985), but occur in most assemblages at a few percent biomass, which is an expectation given their small body sizes. In addition, groundcover plants may be quite common in some roof-shale assemblages; we have found abundant and widespread *Sphenophyllum*, in particular, in the roof of the Danville Coal, which also occurs in the late Desmoinesian, but somewhat higher stratigraphically than the Springfield.

Thus, the exceedingly rare occurrence of groundcover in the transects reported here is likely real and noteworthy. The most abundant occurrence of groundcover was noted in the New Future transect, but only in areas lacking *Neuropteris flexuosa*. Though a small sample ( $n = 2$ ), it suggests a local topographic high in which the forest floor was periodically exposed, more so than in the surrounding areas that comprised most of the peat surface. In addition, although groundcover is lacking from other areas, the sharp transitions from *N. flexuosa*-dominance to mixed assemblages also may reflect topographic changes that altered the flooding regime during the terminal phases of peat formation. If this is so, then *Sphenophyllum* propagules were sufficiently

widespread throughout the area to locate such patches of exposed substrate when and where they appeared. Additionally, *Neuropteris flexuosa*, with large, likely water-dispersed seeds, may have been excluded from such sites simply by dispersal limitation factors.

There are three other analyses of the Springfield Coal flora that relate directly to that reported here. Two are from deposits associated with the Leslie Cemetery channel (Eggert, 1982, 1994), a small channel that apparently formed as a late-stage splay into the Springfield peat swamp, first becoming a lake and then a swamp during the final phases of peat formation across the larger landscape (see Nelson et al., in press, for discussion). Willard et al. (1995) carried out a detailed analysis of the sediments of the Leslie Cemetery channel and of the benches of the Springfield coal that occur below and above these siliclastic deposits. They found three principal plant assemblages. (1) The flora of the main coal seam, known only from palynology, is heavily dominated by tree lycopsids typical of late Desmoinesian coal floras, but with the notable abundance of spores from *Lepidodendron* (*Lycospora pusilla*) and *Sigillaria* (*Crassisporea kosankei*). This flora, which would have grown about 25 km from, and thus outside the immediate influence of, the Galatia channel, is more enriched in lycopsids than is typical for the Springfield close to the Galatia channel, where tree-fern spores are dominant (Mahaffy, 1988; Willard, 1993). (2) Gray-shales in the mid-portion of the channel body are dominated by pteridosperms, particularly *Neuropteris ovata* and *Macroneuropteris scheuchzeri*, and by tree ferns, especially *Lobopteris vestita*, an assemblage similar to that found in parts of the Galatia North transect, immediately behind the river-margin *Neuropteris flexuosa*-dominated zone. In addition, the most abundant tree-fern spores from this facies differ from those found in the coal bed. (3) The flora of the thin upper bench of the Springfield coal, which grades laterally to an organic shale, is dominated by a mixture of lycopsids and pteridosperms, including *Linopteris* sp., attributed to the medullosan *Sutcliffia* by Stidd et al. (1975) (see also comment in Laveine and DiMichele, 2001). This flora is mirrored by anatomically preserved plants in coal-balls from this bed, which were analyzed in a second study by Phillips and DiMichele (1998). In the coal-ball analysis, multiple coal-ball occurrences were quantitatively characterized through a 1 km transect running from the edge of the upper coal bench, where it joins the main bench, to the siliclastic-rich center portion. The flora is most enriched in lycopsids at the edge of the split; medullosan pteridosperms are dominant in areas where the coal transitions to organic shale. No *Sigillaria* was identified in these coal-ball peats. The third study is that of DiMichele and Nelson (1989), who examined the roof flora of the Springfield in a 7000 m<sup>2</sup> area, 600 m from the edge of the Galatia channel, 85 km NE of the presently described study area. That location was characterized by spatial heterogeneity centered on a core area comprised almost exclusively of the trunks and upright stumps of *Sigillaria*. On one side, this core area was bordered abruptly by a change to pteridosperms and calamitaleans, whereas on the other it transitioned gradually to a stand of mixed lycopsid trees, including *Lepidodendron*, *Diaphorodendron* and a single specimen of *Asolanus*. In addition to being compositionally similar to the Galatia and New Future transects, very little evidence of groundcover was found.

## 8.2. Zonation and assembly of the Springfield vegetation

The assembly of any local assemblage of plants, a plant “community”, can be envisioned as resulting from the interaction of three basic factors, which Belyea and Lancaster (1999) characterize as dispersal constraints and environmental constraints, external to the system, and biological interactions, internal to the system. Stated more colloquially: (1) Can a plant get there - dispersal? (2) Can it survive there - physical conditions? (3) Can it compete there - biological conditions? The question arises, however, regarding the relative importance of these three factors in the assembly of any given local plant community. The result has been a dichotomy between so-called “niche assembly” and



“neutral assembly” models (for discussion see [Weiher and Keddy, 1999](#); [Wilson, 1999](#); [Weiher et al., 2011](#)). Niche-assembled communities ([Ackerly, 2003](#); [Kraft et al., 2008](#)) primarily reflect physical environmental controls on species distribution, what has been described as habitat filtering ([Kraft et al., 2015](#)). Additionally, and possibly secondarily, effects of species interactions are important in niche assembly. These two variables are the major niche dimensions (dispersal taken as a given). Neutrally assembled communities, in contrast, are composed of a stochastically changing array of species, controlled largely by dispersal to the site, in addition to demographic factors such as birth and death rates; in the extreme case ([Hubbell, 2005](#)) there is an underlying assumption that species are competitively equivalent and have similar tolerances of physical conditions, their presence on the site controlled principally by dispersal limitation.

It has become increasingly clear that both niche and neutral processes operate in modern communities, manifested at different spatial scales in response to variation in physical and biological conditions across a landscape, and that individual species may be more likely to be environmentally vs. dispersal limited (e.g., [Karst et al., 2005](#), [Moore and Elmendorf, 2006](#), and specifically in tropical, high rainfall regions: [Kraft et al., 2008](#); [Lamarre et al., 2012](#); [Fortunel et al., 2014](#); [Kenfack et al., 2014](#); [Punchi-Manage et al., 2013](#); [Barnett et al., 2015](#)). However, where the physical variation is low over large distances, as it is in many wetland environments, scale effects resulting from variation in the physical environment may be muted (e.g. [Wittmann et al., 2011, 2013](#); [Junk et al., 2014](#)). But even in modern wetlands, as the spatial scale increases, comparison of species composition across large distances may be influenced strongly by regional changes in species pool composition ([Wittmann et al., 2006](#)), reflective of subtle changes in climate or even such physical factors as the geology of soil parent materials (e.g., [Montero et al., 2014](#)).

The spatial distribution of species that formed the final forest of the Springfield peat swamp also indicates a strong response to environmental variation, one similar to that of modern tropical, wetland vegetation. These patterns include the restriction of *Neuropteris flexuosa* to areas closest to the channel, the zonation of vegetation outward from the channel, and the intra-zonal spatial variability. The patterns suggest that both niche and neutral process were at work structuring this vegetation, but at different spatial scales. The distribution of plant taxa revealed by the three transects suggests a large role for niche-based controls on plant distribution at the largest spatial scale examined. The most obvious feature influencing zonation is proximity to the Galatia channel, a powerful habitat filter, modifier of the physical characteristics of the swamp environment, and conduit for propagule dispersal. At smaller spatial scales, however, the transects capture a fair amount of compositional heterogeneity, particularly within the outer three sub-assembly zones, despite an otherwise low-diversity, local species pool, and an overall low species diversity in the Pennsylvanian-age tropics ([Knoll et al., 1979](#); [Niklas et al., 1985](#); [Cleal et al., 2012](#)). This heterogeneity is present among both the abundant and rare species. It indicates considerable patchiness in composition at small spatial scales. At the finer scales of spatial resolution, therefore, there appears to have been a degree of species neutrality once within a broader set of favorable physical conditions. The degree to which this kind of neutral interaction might be detected, however, appears to be closely related to the size of the habitat under examination; this might be exceedingly difficult to detect if the original habitat is small, a problem that would certainly be exacerbated in sampling fossil assemblages.

### 8.3. Biodiversity and spatial variability of Pennsylvanian-age vegetation

The species that comprise the Springfield roof-shale assemblage are characteristic of many other deposits of the same age, from the same basic spectrum of wetland habitats in the Euramerican part of equatorial Pangea (e.g., [Bashforth et al., 2016a](#)). Thus, they were derived from a regional wetland species pool, drawing in a mixture of typical

peat-substrate taxa and those that required or could tolerate higher nutrient conditions, partial burial by sediment, and/or greater flood energies. This wetland-flora species pool appears to have covered a vast area and, for reasons discussed below, may have been much less spatially variable in central Pangea than are modern Amazonian species pools, for example. Studies of floras of comparable age or through time have shown remarkable degrees of identity, from the level of shared species to similar genera and families, over thousands of kilometers within broadly similar habitats (e.g., [Hilton and Cleal, 2007](#); [Wagner and Álvarez-Vázquez, 2010](#); [Cleal et al., 2012](#); [Moore et al., 2014](#); [Bashforth et al., 2016a](#)).

The great similarity of wetland vegetation across large distances does not mean, however, that there were no other biomes in the equatorial region. In fact, there are sharply marked floristic differences between the wetlands and seasonally dry habitats ([Mamay and Mapes, 1992](#); [Pryor and Gastaldo, 2000](#); [Hernandez-Castillo et al., 2003](#); [Tidwell and Ash, 2003](#); [Falcon-Lang and Bashforth, 2005](#); [Barthel, 2006](#); [Falcon-Lang et al., 2009](#); [Plotnick et al., 2009](#); [DiMichele et al., 2011](#); [Dimitrova et al., 2011](#); [Opluštil et al., 2013a, 2013b](#); [Van Hoof et al., 2013](#); [Bashforth et al., 2014, 2016b](#)). The latter are characterized by plants such as conifers (e.g., *Walchia*), cycadophytes (e.g., *Taeniopteris*), neoggerathiales (e.g., *Charliea*), possible glossopterid relatives (e.g., *Lesleya*), or certain fern-like plants (e.g., *Sphenopteris germanica*). These kinds of plants are known and reported from strata of similar age in western Pangea, in the Variscan regions of central Pangea and in deposits of interglacials to early glacial phases of cyclothem within coal bearing stratigraphic successions. So, although these other kinds of plants were regionally present, they were not part of the species pool that typified wetland habitats.

A significant difference between modern and late Paleozoic tropical vegetation is the enormous disparity in their respective biodiversities. Even though the late Paleozoic was partitioned into distinct global floristic provinces ([Wnuk, 1996](#)), within which there were distinct biomes with different climatic and edaphic tolerances ([Falcon-Lang et al., 2009](#); [DiMichele, 2014](#)), it was a low diversity world compared to any time after the rise of flowering plant dominance ([Knoll et al., 1979](#); [Niklas et al., 1985](#); [Wing and DiMichele, 1995](#); [Cleal et al., 2012](#)). Because of the practice in paleobotany of giving different taxonomic names to dispersed organs of the same whole-plant species, we restrict our remarks here, as far as possible, to what [Bateman and Rothwell \(1990\)](#) called “reconstructed whole-plant species”. On this basis, the Mazon Creek flora from the Francis Creek Shale of northern Illinois is one of the most diverse Pennsylvanian tropical plant assemblages known at somewhat over 100 species ([Pfefferkorn, 1979](#); [Wittry, 2006](#); [Moore et al., 2014](#)); it is drawn from a single, large, lowland coastal region and likely represents a single, common species pool. The Mazon Creek count reflects collecting efforts of hundreds of amateurs and professionals working at dozens of sites for more than a century, and is supplemented by a detailed analysis of the > 20,000 plant-bearing specimens housed by the Field Museum of Natural History. Similar landscape-level diversity of 100–120 species has been estimated by [Cleal et al. \(2012\)](#) based on analyses of numerous collections from the British coal measures and Western Europe. Perhaps the highest diversity reported is approximately 140 species from the Lower Radnice Member in the Czech Republic, where ash falls preserved vegetation in place, capturing many smaller plants that normally do not get preserved, but also reflecting its location in a narrow basin in mountainous terrain, thus possibly resulting in an edaphically mixed species pool ([Opluštil and Cleal, 2007](#)). Nonetheless, it is likely that even under the best of preservational circumstances, the estimate of Pennsylvanian wetland diversity is still too low, but by how much is uncertain. Palynological studies carried out side-by-side with macrofossil studies from the same beds generally reveal both a higher taxonomic diversity, and often very different dominance-diversity patterns than are found in the macroflora (e.g., [Willard, 1993](#); [Dimitrova et al., 2005](#); [Willard et al., 2007](#); [Tabor et al., 2013](#)). Nonetheless, palynological diversity of

Pennsylvanian coals or siliciclastics does not reveal anything close to modern diversities, even if it suggests that more species were present than captured by macrofloral sampling.

At the level of a local sample, a typical excavation in a Pennsylvanian siliciclastic deposit, a meter-square and some tens of centimeters to a meter in depth, typically yields 5 to 10 whole-plant species of all growth habits. This may be boosted to 20 to 30 species if the flora is allochthonous, the excavation larger, or by supplemental excavations in the same bed (Wing and DiMichele, 1995; Pryor and Gastaldo, 2000; Gastaldo et al., 2004; Opluštil et al., 2009, 2014; Wang et al., 2012). A single such square-meter excavation, sampling a parutochthonous assemblage, likely represents about 0.1–0.3 ha of original standing vegetation, based on actualistic studies of modern tropical and temperate forests (Burnham et al., 1992; Burnham, 1993). This kind of diversity pales in comparison to that found in modern tropical landscapes, both terra firma and wetland, where > 200 species of trees may populate a hectare of forest (e.g. Wright, 2002), as part of species pools of still much larger size (e.g., Gentry, 1988; Valencia et al., 1994; Wills et al., 1997; Barthlott et al., 2007; Wittmann et al., 2011; Junk et al., 2014). In the plant fossil record, transects through Cenozoic deposits reveal much greater diversity than those through Paleozoic deposits (Wing and DiMichele, 1995). Of course, tropical wetland forests, due to relatively lower environmental dimensionality, might be expected to be of lower diversity than terra firma vegetation (Chase, 2010; Junk et al., 2011). However, similarly low, or even lower species numbers (above cited seasonally dry flora references), have been documented in Pennsylvanian landscapes inferred to have experienced seasonal drought, suggesting low diversity as a characteristic of the general Pennsylvanian equatorial region, wetland or seasonally dry.

The low diversity of most Paleozoic plant assemblages, including those sampled along narrowly constrained environmental gradients (e.g., Phillips and DiMichele, 1998; Gastaldo et al., 2004; Bashforth et al., 2011), is reflected in large species geographic ranges and, thus, underlies the great similarity of assemblage composition in similar habitats throughout a paleofloristic region (e.g., Pryor and Gastaldo, 2000; Bashforth and Nelson, 2015; Bashforth et al., 2016a). With few species “in the game”, the possible combinations that could live in a given habitat-type would have been much lower than that found today. It also is possible that niche breadths might have been greater (a closer fit of realized to potential niches) under limited resource competition, and/or that significant parts of the resource landscape typically occupied today may have been vacant or underutilized in the late Paleozoic.

## 9. Conclusions

1. A strong environmental gradient has been identified as a modifier of environmental conditions in a Pennsylvanian-age wetland, the final forest of the Springfield Coal peat swamp.
2. Vegetation responded to this environmental gradient by exhibiting niche-based patterns of community assembly.
3. The plants comprising the various assemblages can be considered part of the same wetland basic species pool.
4. Fundamentally low diversity of Pennsylvanian tropical vegetation did not obscure or alter the niche-based plant responses.
5. The patterns reported here are confined to wetland vegetation. Pennsylvanian-age, tropical species-pool composition also responded strongly to climatic gradients, as indicated by patterns of change in time and space.

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