

Ecological gradients within a Pennsylvanian mire forest

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ABSTRACT

Pennsylvanian coals represent remains of the earliest peat-forming rain forests, but there is no current consensus on forest ecology. Localized studies of fossil forests suggest intermixture of taxa (heterogeneity), while, in contrast, coal ball and palynological analyses imply the existence of pronounced ecological gradients. Here, we report the discovery of a spectacular fossil forest preserved over ~1000 ha on top of the Pennsylvanian (Desmoinesian) Herrin (No. 6) Coal of Illinois, United States. The forest was abruptly drowned when fault movement dropped a segment of coastal mire below sea level. In the largest study of its kind to date, forest composition is statistically analyzed within a well-constrained paleogeographic context. Findings resolve apparent conflicts in models of Pennsylvanian mire ecology by confirming the existence of forest heterogeneity at the local scale, while additionally demonstrating the emergence of ecological gradients at landscape scale.

Keywords: Pennsylvanian, coal geology, peat mire, coal balls, spatial heterogeneity, ecological gradients.

INTRODUCTION

Pennsylvanian coal-bearing strata are widespread across Europe, North America, and China, and they preserve remains of the earliest tropical rain forests (DiMichele et al., 2001). Coal seams, the product of extensive forested mires, represent the most intensively studied element of this biome. Mire ecology has been unraveled through quantitative studies of coal balls, palynology, and petrography over many decades (DiMichele and Phillips, 1994). Results imply the existence of intergrading communities, composed of species with subtly distinct ecological preferences (DiMichele and Phillips, 1996a).

A criticism of these findings is that they are based on assemblages that are both time-averaged and taphonomically filtered (Behrensmeier et al., 2000). Only where forests are buried in growth position in a geological instant (T_0), e.g., following coseismicity or volcanic ash falls, can assemblages give unequivocal insight into spatial structure (Gastaldo et al., 2004a). In the largest published study of a T_0 assemblage, Gastaldo et al. (2004b) mapped the structure of an early Pennsylvanian mire over ~25 ha. They demonstrated interspersal of taxa that earlier coal ball studies indicated had ecologically distinct centroids (DiMichele and Phillips, 1994).

This paper analyzes the spatial structure of a newly discovered T_0 mire assemblage preserved on top of the Pennsylvanian (Desmoinesian) Herrin (No. 6) Coal in Vermilion County, Illinois (Jacobson and Bengal, 1981). This extraordinary fossil forest, exposed over ~1000 ha in the roof of underground mines, permits ecological analysis at a scale more than an order of magnitude larger than previously reported. Our work resolves the apparent conflict between competing models of mire structure.

GEOLOGIC CONTEXT

The regional paleogeographic context of this fossil forest was established through isopach and facies analysis of 185 borehole cores as well as observations in active and abandoned underground mines

over an area totaling ~560 km² (Fig. 1A; Illinois State Geological Survey, open files). The fossil forest is preserved at the contact of the Desmoinesian Herrin Coal and the overlying Energy Shale, and it lies within an ~10-km-wide, NE-SW-trending zone of maximum Herrin Coal thickness (Fig. 1B). Paleoeological work was undertaken within Riola and Vermilion Grove underground mines within the zone of thickest coal (Fig. 1C; 39°57'N, 87°43'W).

Energy Shale Facies

The basal Energy Shale is composed of three facies belts trending NE-SW, parallel to underlying Herrin Coal thickness (Figs. 1A and 1B). The first facies belt occurs in the northwest area. There, the Herrin Coal is thin (≤ 0.7 m), and the Energy Shale occurs as ≤ 3 -m-thick outliers of dark-gray shale with localized mottles and polygonal cracks. The second facies belt occurs in the central area. In the vicinity of the Riola mine, where the Herrin Coal thickens to ≤ 1.7 m, the Energy Shale thickens to ≤ 18 m, and is composed of gray shales that show rhythmic laminae bundles (~1 cm thick), wavy lamination, siderite nodules, rare sandstone channel bodies (1–2 m thick) with rhythmic lamination, and sparse brackish/marine fauna (*Dunbarella*, mytiloid pelecypods, eurypterid cuticle). Further southeast, at a location between Riola and Vermilion Grove that coincides with the greatest thickness of Herrin Coal (2.1 m), the Energy Shale abruptly thickens to ≤ 28 m, and comprises similar facies but with much greater dominance by rhythmically laminated channel bodies. Mapped throughout the central area, channel bodies comprise a SW-convergent network several kilometers long (Fig. 1A). The third facies belt occurs in the southeast area. There, the Herrin Coal thins to ≤ 1.1 m, the Energy Shale attains a maximum thickness of ~34 m, and unlike elsewhere in the study area, it shows a gradational basal contact. The transition comprises ≤ 15 cm of coal with a high clastic content (bone coal) overlain by dark gray to black carbonaceous shale with brackish branchiopods.

Basin Evolution and Paleoenvironment

Isopach data (Figs. 1A and 1B) indicate a strong tectonic influence during the deposition of the study interval. The southeastward increase in thickness of Energy Shale from 0 to 3 m to ~34 m cannot be explained by differential compaction of underlying peat, as the Energy Shale is thickest where the Herrin Coal is thin. Instead stratal patterns imply the progressive development of a southeast-facing monocline, with thin Herrin Coal and Energy Shale forming on the northwest upper limb and the much thicker succession forming on the southeast lower limb. In this model, the NE-SW-trending zone of thick Herrin Coal coincides with the inferred point of flexure where, presumably, accommodation rates were optimal for peat formation. Underlying strata (Springfield and Colchester coal intervals) show uniform thicknesses across the study area, proving that differential subsidence commenced during Herrin Coal deposition, and peak subsidence occurred near the boundary of the Herrin Coal and the Energy Shale. The monocline was likely the expression of an undocumented subsurface fault that trended NE-SW and was located between Riola and Vermilion Grove. This is supported by our observation of an identically trending linear clastic dike that cuts the Herrin Coal in this region but is sharply truncated by overlying Energy Shale. The Royal Center fault of Indiana (Keller 1998), the

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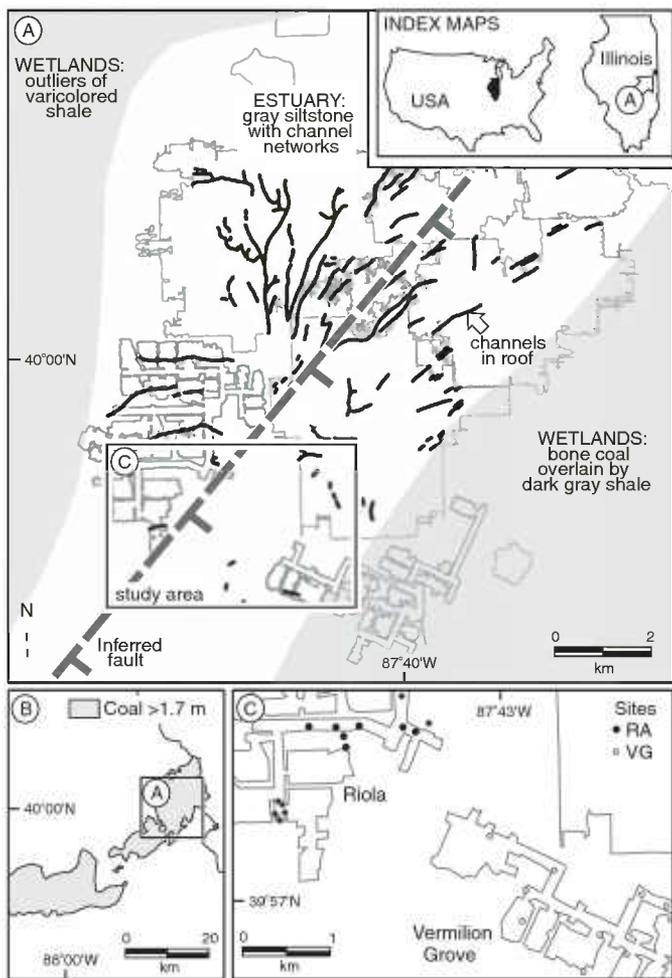


Figure 1. Paleoenvironmental context: (A) Roof facies in basal Energy Shale showing SW convergent drainage system within broad, shallow estuary. (B) Curvilinear zone where Herrin Coal attains maximum thickness. Zone is parallel to axis of estuary developed in overlying Energy Shale. (C) Detailed location of paleoecological sampling.

SW extent of which is uncertain, lies directly in line with the inferred fault, and the two structural lineaments may be related.

The tectonic model elaborated here helps to constrain the paleoenvironmental context of the Energy Shale. Sediments in the central area of study represent a shallow, NE-SW-trending estuary, some 5–7 km wide. Siltstone beds with laminae bundles were formed by spring-neap tidal cycles in quiet waters, while rhythmically laminated channel bodies represent tidally influenced drainage networks. The dendritic channel pattern implies that the estuary opened to the southwest (consistent with regional paleogeography) and was bordered by land on either side. Mottled shales on the northwest margin formed on pedogenically altered wetlands, while bone coal on the southwest margin formed in a partially drowned peat mire. While the central estuary subsided abruptly, producing the estuarine trough and preserving a fossil forest (see following), more gradual subsidence occurred on the southeast margins. This movement eventually dropped the southeast region on the lower limb of the monocline and formed the gradation from bone coal to black shale, greatly widening the estuary.

Taphonomy of the Fossil Forest

The fossil forest is limited to the central area. Siltstone-dominated facies at Riola include numerous stumps (heights ≥ 1.7 m where observable) rooted in the top of the Herrin Coal, and abundant prone trunks and

foliage compressions, concentrated in a basal 1–4 cm layer of the Energy Shale. Trunks show no preferred orientation and are extremely large; incomplete fragments are typically 1–5 m long, and the largest is 33 m long. These plant remains are autochthonous, i.e., buried in place without further transport. At Vermilion Grove, where small channel bodies are more common, stumps in growth position are rare, and the largest number are rooted in a coal stringer overlapping a channel. The stringer represents peat partially undercut along a channel margin. As in the siltstone-dominated facies, the assemblage is composed of large, randomly orientated trunks and foliage compressions. The large size of trunks relative to channel dimensions implies local transportation, i.e., parautochthony (Gastaldo et al., 1995).

The contact between the Herrin Coal and the Energy Shale is everywhere sharp in the central area, suggesting that this segment of mire forest was abruptly drowned when one or more earthquakes resulted in several meters of subsidence and the formation of the estuary. A recent analogue may be the New Madrid earthquakes of 1811–1812 that drowned a lowland forest and formed Reelfoot Lake, Missouri (Penick, 1981). Catastrophic drowning is supported by widespread and abundant *Lepidophloios* and *Cordaites* crown branches, which show full leaf arrays; both groups commonly shed leaves during natural senescence. Spring-neap cycles suggest a typical sedimentation rate of 2 cm/mo away from tidal channels, similar to those calculated for adjacent sites (Feldman et al., 1993). Although such features are not seen in the thin, plant-rich siltstone beds, the entire fossil forest assemblage was likely buried within less than two months. Because the Herrin Coal is thicker and Energy Shale channel bodies more common at Vermilion Grove, the fossil forest sites in this area are inferred to have experienced greater rates of subsidence and to have been more seaward than those at Riola.

SPATIAL STRUCTURE OF THE FOREST

The spatial aspects of forest heterogeneity were reconstructed within this paleogeographic context. Two sample areas were selected, one in Riola (RA) on the landward side of the mire, and one in Vermilion Grove (VG) on the seaward side. The total region sampled covers ~1000 ha. In each area, our standard sample site was 12 × 20 ft (3.7 × 6.1 m), the size of the “mine entries” between unmined pillars of coal. Seventeen RA sample sites were analyzed. Each site was subdivided into four 6 × 10 ft (1.8 × 3.1 m) replicates, with two exceptions where fewer replicates were obtained (hence, RA = 65 replicates). For VG, 15 sample sites were analyzed; however, time restrictions precluded subdivision into replicates for 13 of these. Consequently, 13 of the VG sample sites were treated as a single sample composed of 13 replicates; the other two sample sites were subdivided into two and four replicates (hence, VG = 19 replicates) and analyzed in the same manner as RA sample sites. A list of morphotaxa was recorded for each of the 83 replicates, and abundance data were collected using the following categories: abundant = >50% of area cover; common = 10%–50%; rare = <10% (Abundance Score). Fossil plant collections were made to confirm field identification.

Data Analysis

Morphotaxon records were resolved to the species or genera level, where possible, and stored in two matrices for analysis; one matrix contained presence (1) and absence (0) data, and the other contained abundance data scored as abundant (3), common (2), and rare (1). The 0–1 data were analyzed with the statistical package “R” (<http://cran.r-project.org>). Morphotaxon presence/absence data were analyzed using nonmetric multidimensional scaling (NMDS) in two dimensions with all once-occurring morphotaxa excluded (NMDS is an ordination technique used to explore structure within the data). Differences between sample areas were assessed using analysis of similarities. (ANOSIM uses the same underlying mathematical methods as NMDS but looks at similarity among pre-

TABLE 1. MEAN ABUNDANCE SCORE AND PERCENTAGE ABSENCE FOR EACH CLASS OF PLANT

Plant Class	Riola (n = 65)		Vermilion Grove (n = 18)		Overall (n = 83)	
	Abundance	Absences (%)	Abundance	Absences (%)	Abundance	Absences (%)
Tree ferns	2.02	8	2.00	0	2.01	7
Lycopsids	1.60	14	2.83	6	1.88	11
Cordaitaleans	1.31	31	0.56	78	1.08	41
Pteridosperms	1.26	26	0.55	61	1.06	37
Sphenopsids	1.06	32	0.33	78	0.95	39

Note: Abundance data were subdivided into three categories: 3—abundant, 2—common, 1—rare and subdivided by study area. Percentage of replicates where a plant group is absent is also given.

determined groups. According to the “R” user guide (<http://cran.r-project.org>), “If two groups of sampling units are really different in their species composition, then compositional dissimilarities between the groups ought to be greater than those within the groups.” In both analyses, the Jaccard coefficient, which varies from 0 (no similarity) to 1 (identity), was used as the distance metric (the distance metric is a measure of the dissimilarity between each pair of sample points in the analysis, based on similarity of taxonomic composition). Average similarities of replicates ($n = 83$) between and within sample sites ($n = 32$) were assessed by direct examination of Jaccard scores. Finally, a third matrix was constructed in which data were grouped into higher taxonomic groups (lycopsid, ferns, sphenopsids, pteridosperms, cordaitaleans). Dominance and patchiness at this higher taxonomic level were evaluated according to the number of replicates from which each major group was absent. Abundance data were assessed by comparison of the mean and standard deviation of the Abundance Score for each major group.

Fossil Plant Distribution

A total of 50 morphotaxa occur in the study area, representing ~28 whole plant taxa and five major groups. Abundance and patchiness data show that tree ferns and lycopsids are the most abundant and widespread groups (Table 1). Tree ferns, present in 77 of 83 replicates, are represented by abundant *Caulopteris* trunks (4-m-long maximum observed, incomplete length), rare *Artisophyton* trunks, and pectopterid foliage. Lycopsids, represented by huge trunks (≤ 33 -m-long maximum observed, incomplete length, 0.2–1.9 m diameter), are dominated by *Lepidophloios* (52 of 83 replicates) with subordinate *Sigillaria* (21 replicates), *Lepidodendron* (18 replicates), *Asolanus* (9 replicates), *Synchysidendron* (8 replicates), and *Diaphorodendron* (4 replicates). In contrast, pteridosperms, cordaitaleans, and sphenopsids show the greatest degree of patchiness and lowest abundance (Table 1). These latter groups mainly are composed of small trees, but ground cover forms may include the pteridosperms *Eusphenopteris* and *Sphenopteris*, and the sphenopsid *Sphenophyllum*.

Statistical exploration of the data sets permits spatial analysis of the forest (Fig. 2). NMDS analysis shows that the two sample areas plot as intergrading clouds (18% of RA data overlap with VG) but have distinct centroids (relative to RA, VG data are of restricted diversity). Compositional differences among these sample areas, at the largest scale of analysis, are confirmed by ANOSIM; simultaneous comparison of sample area pairs, and all sample areas together, reveals that between-area differences are significantly greater than within-area differences ($p < 0.009$). Direct examination of Jaccard scores for each of the 32 sample sites further indicates that the average within-site similarity (0.43), based on 156 comparisons, is considerably greater than that between replicates from different sample sites (0.27), based on 3374 comparisons. In other words, replicates are compositionally more alike if they are from the same sample site than if they are from different sites.

The patchy, heterogeneous nature of the mire vegetation is further illuminated by qualitative examination of the morphotaxon records. In RA, localized clusters of sample sites contain diverse pteridosperm veg-

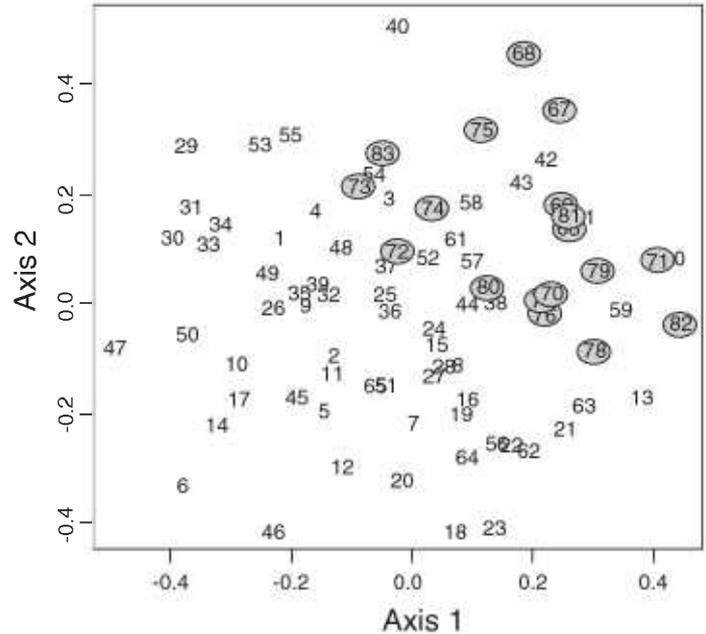


Figure 2. Exploration of presence/absence data at morphotaxon level for all 83 replicates using nonmetric multidimensional scaling (NMDS) in two dimensions with all once-occurring morphotaxa excluded. VG replicates are shaded circles ($n = 18$), and RA replicates are unshaded ($n = 65$). Riola (RA) and Vermilion Grove (VG) taxa show intergrading composition (11 RA replicates overlap with VG), but VG taxa are much more restricted in diversity.

etation, interspersed with *Sigillaria*. However, when viewed at the large landscape scale, this kind of localized heterogeneity resolves into distinct compositional gradients. *Lepidophloios* and tree ferns are the dominant canopy-forming plants throughout the entire region. In the channel-dominated facies on the seaward side of the mire (VG), however, cordaitaleans, pteridosperms, and sphenopsids drop in both diversity and abundance, while *Sigillaria* becomes more abundant. Mire sites on the topographically low seaward side would have been more prone to submergence than landward sites, which perhaps explains why ground cover, shrubs, and small trees were mostly restricted to RA.

PALEOECOLOGICAL IMPLICATIONS

Pennsylvanian rain forests are among the best-understood Phanerozoic terrestrial ecosystems (DiMichele et al., 2001). This study reconstructs a Pennsylvanian mire forest at the largest spatial scale ever attempted (Fig. 3). The picture is of a multicohort forest (indicated by trunks of variable diameter) composed of abundant lycopsid emergents (probably >40 m high) towering over a subcanopy of tree ferns, intermixed with cordaitalean, pteridosperm, and sphenopsid shrubs and small trees. Heterogeneous at the local

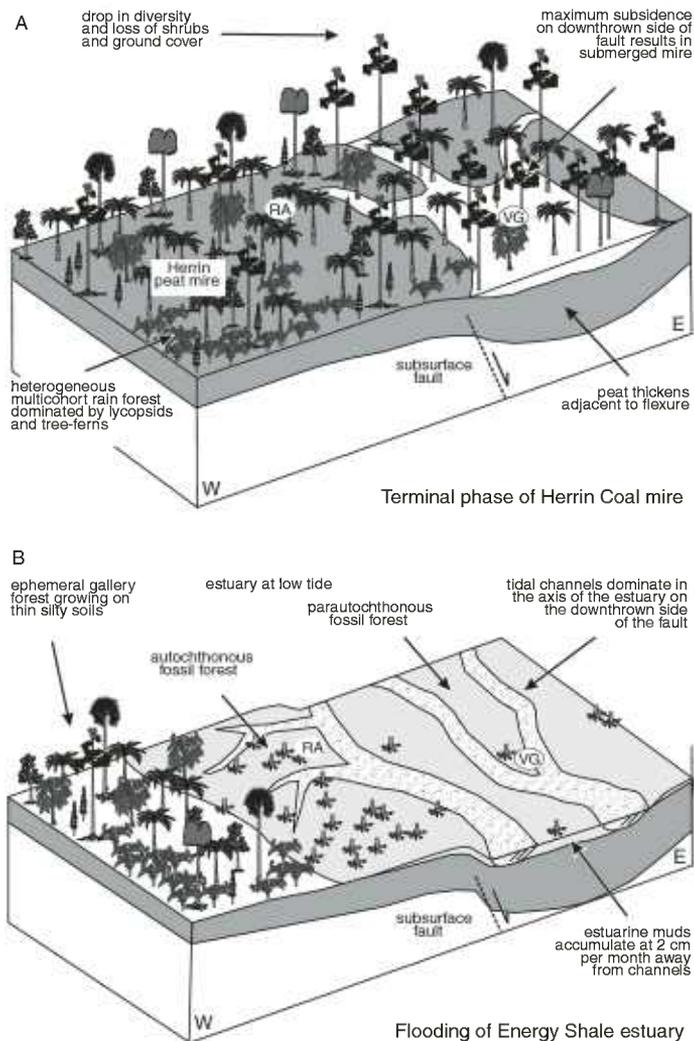


Figure 3. Model for origin of fossil forest. (A) Onset of differential subsidence and its effects on mire community structure. (B) Preservation of mire forest following abrupt subsidence of estuarine trough. RA—Riola, VG—Vermilion Grove.

scale (<10 ha), mire forests exhibited ecological gradients at the landscape scale (<1000 ha), and this information helps to resolve apparent conflicts in ecological models (Gastaldo et al., 2004a).

Although our findings are generally applicable to most Pennsylvanian mire forests, two observations imply that heterogeneity may have been accentuated in the Herrin Coal mire. First, a major reorganization of mire community structure took place in the latest Desmoinesian, when lycopsid-dominated forests were replaced by tree fern forests in both mineral-soil and peat-forming habitats (Pfefferkorn and Thomson, 1982; DiMichele and Phillips, 1996b). This turnover is recognized above the level of the Danville Coal, which overlies the Herrin Coal in Illinois (DiMichele and Phillips, 2002). Our fossil forest contains a high abundance of tree ferns and may coincide with the start of the turnover. Second, although abruptly drowned by earthquake-induced subsidence, the Herrin Coal forest likely “felt” the encroaching coastline over the final several decades of its lifetime. Such a response has been demonstrated for other Pennsylvanian mires in retrograding settings, where palynological assemblages show a distinct change at the top of coal beds (DiMichele and Phillips, 1994; Eble, 1996). Late-stage forests may not have been typical

of mire history in general. The Herrin Coal T_0 assemblage may preserve a mire forest in a state of compositional flux, both at ecological and evolutionary spatial-temporal scales.

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REFERENCES CITED

- Behrensmeier, A.K., Kidwell, S.M., and Gastaldo, R.A., 2000, Taphonomy and paleobiology, in Erwin, D.H., and Wing, S.L., eds., *Deep Time: Paleobiology's Perspective: Paleobiology*, v. 26, p. 103–147.
- DiMichele, W.A., and Phillips, T.L., 1994, Palaeobotanical and palaeoecological constraints on models of peat formation in the late Carboniferous of Euramerica: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 106, p. 39–90, doi: 10.1016/0031-0182(94)90004-3.
- DiMichele, W.A., and Phillips, T.L., 1996a, Clades, ecological amplitudes, and ecomorphs: Phylogenetic effects and persistence of primitive plant communities in the Pennsylvanian-age tropical wetlands: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 127, p. 83–105, doi: 10.1016/S0031-0182(96)00089-2.
- DiMichele, W.A., and Phillips, T.L., 1996b, Climate change, plant extinctions and vegetational recovery during the middle-late Pennsylvanian transition: The case of tropical peat-forming environments in North America, in Hart, M.B., ed., *Biotic Recovery from Mass Extinction Events: Geological Society [London] Special Publication 102*, p. 201–221.
- DiMichele, W.A., and Phillips, T.L., 2002, The ecology of Paleozoic ferns: *Review of Palaeobotany and Palynology*, v. 119, p. 143–159, doi: 10.1016/S0034-6667(01)00134-8.
- DiMichele, W.A., Pfefferkorn, H.W., and Gastaldo, R.A., 2001, Response of late Carboniferous and Early Permian plant communities to climate change: *Annual Review of Earth and Planetary Sciences*, v. 29, p. 461–487, doi: 10.1146/annurev.earth.29.1.461.
- Eble, C.F., 1996, Paleogeology of Pennsylvanian coal beds in the Appalachian Basin, in Jansonius, J., and McGregor, D.C., eds., *Palynology: Principles and Applications: American Association of Stratigraphic Palynologists Foundation*, v. 3, p. 1143–1156.
- Feldman, H.R., Archer, A.W., Kvale, E.P., Cunningham, C.R., Maples, C.G., and West, R.R., 1993, A tidal model of Carboniferous Konservat-Lagerstätten Formation: *Palaos*, v. 8, p. 485–498.
- Gastaldo, R.A., Pfefferkorn, H.W., and DiMichele, W.A., 1995, Taphonomic and sedimentologic characterization of roof-shale floras, in Lyons, P.C., Morey, E.D., and Wagner, R.H., eds., *Historical Perspectives of Early Twentieth Century Carboniferous Palaeobotany in North America: Geological Society of America Memoir 185*, p. 341–352.
- Gastaldo, R.A., Stevanovic-Walls, I.M., Ware, W.N., and Greb, S.F., 2004a, Community heterogeneity of early Pennsylvanian peat mires: *Geology*, v. 32, p. 693–696, doi: 10.1130/G20515.1.
- Gastaldo, R.A., Stevanovic-Walls, I.M., and Ware, W.N., 2004b, Erect forests are evidence for coseismic base-level changes in Pennsylvanian cyclothem of the Black Warrior Basin, USA, in Pashin, J.C., and Gastaldo, R.A., eds., *Sequence Stratigraphy, Paleoclimate, and Tectonics of Coal-Bearing Strata: American Association of Petroleum Geologists (AAPG) Studies in Geology*, v. 51, p. 219–238.
- Jacobson, R.J., and Bengal, L.E., 1981, Strippable coal resources of Illinois: Part 7. Vermilion and Edgar Counties: *Illinois State Geological Survey Circular 521*, 24 p. and 1 plate.
- Keller, J.S., 1998, Underground storage of natural gas in Indiana: *Indiana Geological Survey Special Report 59*, 77 p.
- Penick, J.L., Jr., 1981, *The New Madrid earthquakes (revised edition)*: Columbia and London, University of Missouri Press, 176 p.
- Pfefferkorn, H.W., and Thomson, M.C., 1982, Changes in dominance patterns in upper Carboniferous plant fossil assemblages: *Geology*, v. 10, p. 641–644, doi: 10.1130/0091-7613(1982)10<641:CIDPIU>2.0.CO;2.

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