Floras characteristic of Late Pennsylvanian peat swamps arose in the late Middle Pennsylvanian

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ABSTRACT: Peat-swamp vegetation of the late Middle Pennsylvanian differed markedly from that of the Late Pennsylvanian. Dominating the former was a variety of arborescent lycopsids, medullosan pteridosperms, and increasing numbers of marattialean tree ferns. In contrast, marattialean tree ferns and medullosan pteridosperms were dominant in the Late Pennsylvanian whereas lycopsids were of lesser importance, although much species turnover occurred in each of these groups. The most severe turnover was among the lycopsids; the Sigillariaceae were the only major lycopsid lineage to survive, thrive, and attain wide distribution throughout Euramerica, represented almost exclusively by *Sigillaria brardii* Brongniart (possibly a species complex). The nature of the ecological transition that brought the marattialean vegetation to dominance is not well understood, even though the pattern has been documented across Euramerica. In a study of terminal peat-swamp vegetation preserved at the coal-bed to roof-shale transition in three major late Middle Pennsylvanian age coals of the Illinois Basin, USA, we have identified two major plant assemblages. The first, preserved at the coal-to-roof transitional interface, is autochthonous to minimally parautochthonous and appears to have been buried rapidly during the introduction of sediment to the swamp habitat, burying the vegetation close to its site of growth. This vegetation is similar in taxonomic composition to that documented from the peat swamp (based on coal balls), although the quantitative abundances of the dominant species are different from most coal-ball assemblages. In contrast, the second major plant assemblage occurs in tidal channels that traversed actively developing mudflats flanking major estuaries on the lowland landscape. These channels primarily contain the arborescent lycopsid *Sigillaria* Brongniart with scattered remains of marattialean tree fern and pteridosperm foliage. This second assemblage more closely resembles the peat-swamp flora of the Late Pennsylvanian than that of the Middle Pennsylvanian and may presage this younger flora. The pattern suggests that following the ecological disruption during the Middle-Late Pennsylvanian transition, vegetation formerly dominant in Middle Pennsylvanian clastic-swamp habitats colonized the Late Pennsylvanian peat swamps and surrounding swampy lowlands. This clastic-swamp vegetation thus appears to have harbored lineages (even if not individual species) that survived the turnover and were then able to move into the disrupted landscape from which the formerly dominant forms had been removed.

INTRODUCTION

Significant floristic turnover occurred across the Desmoinesian-Missourian (approximately Middle-Late Pennsylvanian) boundary in peat-forming swamps of the equatorial latitudes in Euramerica (central and west-central Pangea; e.g., Phillips et al. 1974). Large arborescent lycopsids, with the exception of *Sigillaria*, nearly disappeared and marattialean tree ferns became the dominant elements (Phillips and Peppers 1984; Phillips, Peppers and DiMichele 1985; Kosanke and Cecil 1996; DiMichele and Phillips 1996a; Peppers 1997; Falcon-Lang et al. 2011). The rise of tree-fern quantitative dominance was neither sudden nor catastrophic. The group started its rise during the late Middle Pennsylvanian in both mineral substrate wetlands (Pfefferkorn and Thomson 1982) and peat-substrate habitats (Phillips and Peppers 1984). Following the rapid decline of most of the major lycopsid groups in wetlands, there was a period in peat-swamp history, lasting three or four glacial-interglacial cycles and known nearly exclusively from palynology (e.g., Peppers 1979, 1996; Kosanke and Cecil 1996), during which dominance was highly variable spatially and temporally. Ultimately, a peat-swamp flora dominated by marattialean tree ferns appeared, accompanied by a significant admixture of pteridosperms and sigillarian lycopsids. These groups also were present in Middle Pennsylvanian wetlands on non-peat soils, where the pteridosperms, in particular, were abundant (DiMichele, Phillips and Pfefferkorn 2006; Cleal 2008); all also were abundant in Late Pennsylvanian mineral substrate settings (Pfefferkorn and Thomson 1982; Bashforth, Falcon-Lang and Gibling 2010; Wagner and Álvarez-Vázquez 2010). Thus, the contrast that existed between peat and mineral substrate wetland floras of the Middle Pennsylvanian was reduced in the Late Pennsylvanian.

Tree-fern dominance in the Late Pennsylvanian was presaged by a rise in the abundance of tree ferns in late Middle Pennsylvanian wetlands (Desmoinesian/Asturian and early Cantabrian), both in peat-forming and mineral substrate habitats. In some instances, particularly in areas fringing the Variscan mountains in central Pangea, tree ferns even may have dominated some peat-forming environments, inferred from palynological patterns (Dimitrova, Cleal and Thomas 2005; Dimitrova and Cleal 2007; Cleal et al. 2009; Pendelton et al. 2012; Stolle 2012). Coal-ball data suggest that sigillarian lycopsids were of relatively minor importance in peat-forming habitats in the later Middle Pennsylvanian, although they were locally abundant within peat swamps and may have been important under certain kinds of conditions (Willard 1993; DiMichele, Phillips and Nelson 2002; DiMichele et al. 2009). The late Middle Pennsylvanian also was a time of climatic change (e.g., Horton et al. 2012; Cecil, DiMichele and Elrick 2014) and of generally rising global sea level (Heckel 2008; Rygel et al. 2008), which may, in part, have driven some of the terrestrial biotic changes.

In this paper we address this appearance of a Late Pennsylvanian-type assemblage during the late Middle Pennsylvanian, within the complex mosaic of Middle Pennsylvanian wetland habitats. The observations noted above indicate that the tree-fern/pteridosperm/sigillarian association was organized much earlier, perhaps as much as several million years earlier than the turnover event at the Desmoinesian-Missourian boundary. This vegetation dominated tidal-flat environments that developed during the final drowning phases of coastal wetlands, possibly contemporaneously with deglaciation and associated changes in climatic regime that occurred during individual glacial-interglacial cycles.

STUDY SITES

Since 2005, we have been engaged in a study of plant fossils in the 'roof shales', (shales immediately overlying coal beds) of Pennsylvanian coal beds in areas proximate to ancient river systems that were contemporaneous with peat accumulation. Although we have gathered useful data from open pit mines, underground operations have proven most revealing because they permit spatial patterns to be mapped (e.g., DiMichele et al. 2007; Nelson et al. in press). Moreover, several mines we visited offered exposures of the inner margins of paleochannels, with one mine tunneling completely across a major paleochannel, affording a continuous cross-sectional profile. Underground mines also have permitted us to recognize and differentiate facies of the coal-bed roof shales, representing distinct environmental conditions.

The observations reported in this study come from several underground mines in the Springfield, Herrin, and Danville coals of the eastern Illinois Basin (text-fig. 1). These coals are in the upper part of the Carbondale Formation and lower Shelburn Formation and are of late Desmoinesian, late Middle Pennsylvanian age (Peppers 1996). In international terms, they are of late Moscovian age. These three coals are among the most widely mined in the Illinois Basin, including parts of the states of Illinois, Indiana, and Kentucky, and they continue to be the main targets of mining activity in the basin, particularly the Springfield and Herrin coals.

The mines in which the study was carried out include the following (text-fig. 2). Danville Coal: Peabody Energy Company Air Quality Mine. Herrin Coal: Peabody Riola Mine, Peabody Vermillion Grove Mine. Springfield Coal: American Coal Company Galatia and New Future (Millennium) mines, AMAX Coal Company (later Foundation Coal) Wabash Mine, Black Panther Mining Oaktown No. 1 and 2 Mines, Nubay Coal Company Liberty Mine, Sunrise Coal Company Carlisle Mine. Supplementing our own observations are those made by numerous other geologists at mines in Illinois, Indiana, and Kentucky (Illinois State Geological Survey, unpublished field notes, open files in ISGS Library).

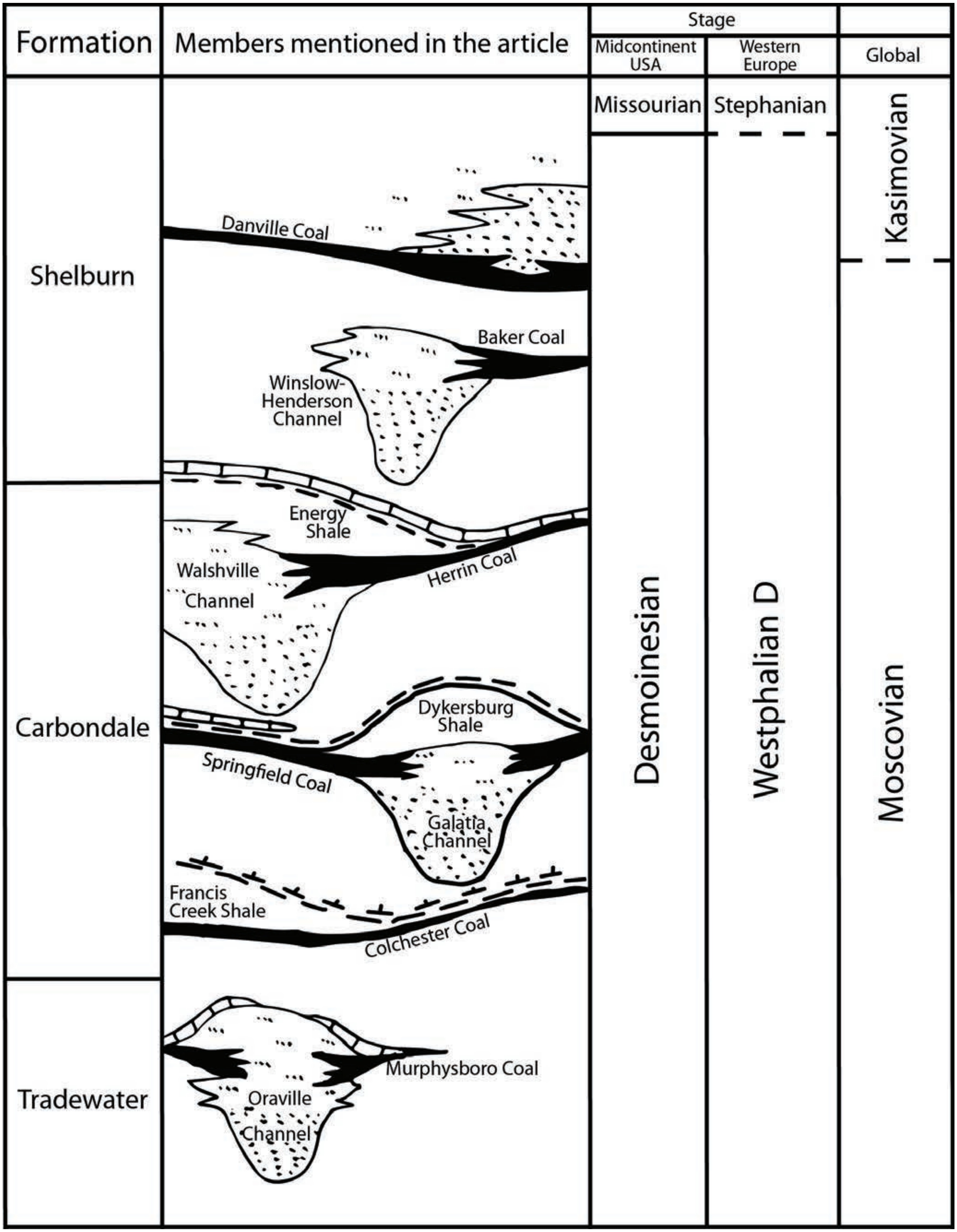
OBSERVATIONS

Geological Setting

Desmoinesian-age coal beds of the eastern United States are among the thickest and most widespread Pennsylvanian coals in the world (Greb et al. 2003). Where mined, coal thicknesses are typically 1.5 to >3.0 m, and several seams have been correlated with confidence from the Midcontinent to the Illinois and northern Appalachian basins (e.g., Cecil et al. 2003b; Heckel et al. 2007; Belt et al., 2011; Falcon-Lang et al. 2011; Eros et al. 2012). Deposits of contemporaneous river channels, active during peat accumulation, traverse many of these coals. In the Illinois Basin, these channels occur in the following coal beds (Nelson et al. in press): Murphysboro (Oraville channel, Jacobson 1983), Springfield (Galatia channel, Hopkins, Nance and Treworgy 1979), Herrin (Walshville channel, Allgaier and Hopkins 1975), Baker (Winslow-Henderson channel, Beard and Williamson 1979; Eggert 1994) and Danville (undetermined channel recognized from roof facies and associated features, observations of authors). Similar paleochannel river systems have been identified in coals of the same age from the Appalachian Basin (e.g., Bragonier, Bohan and Hawk 2007).

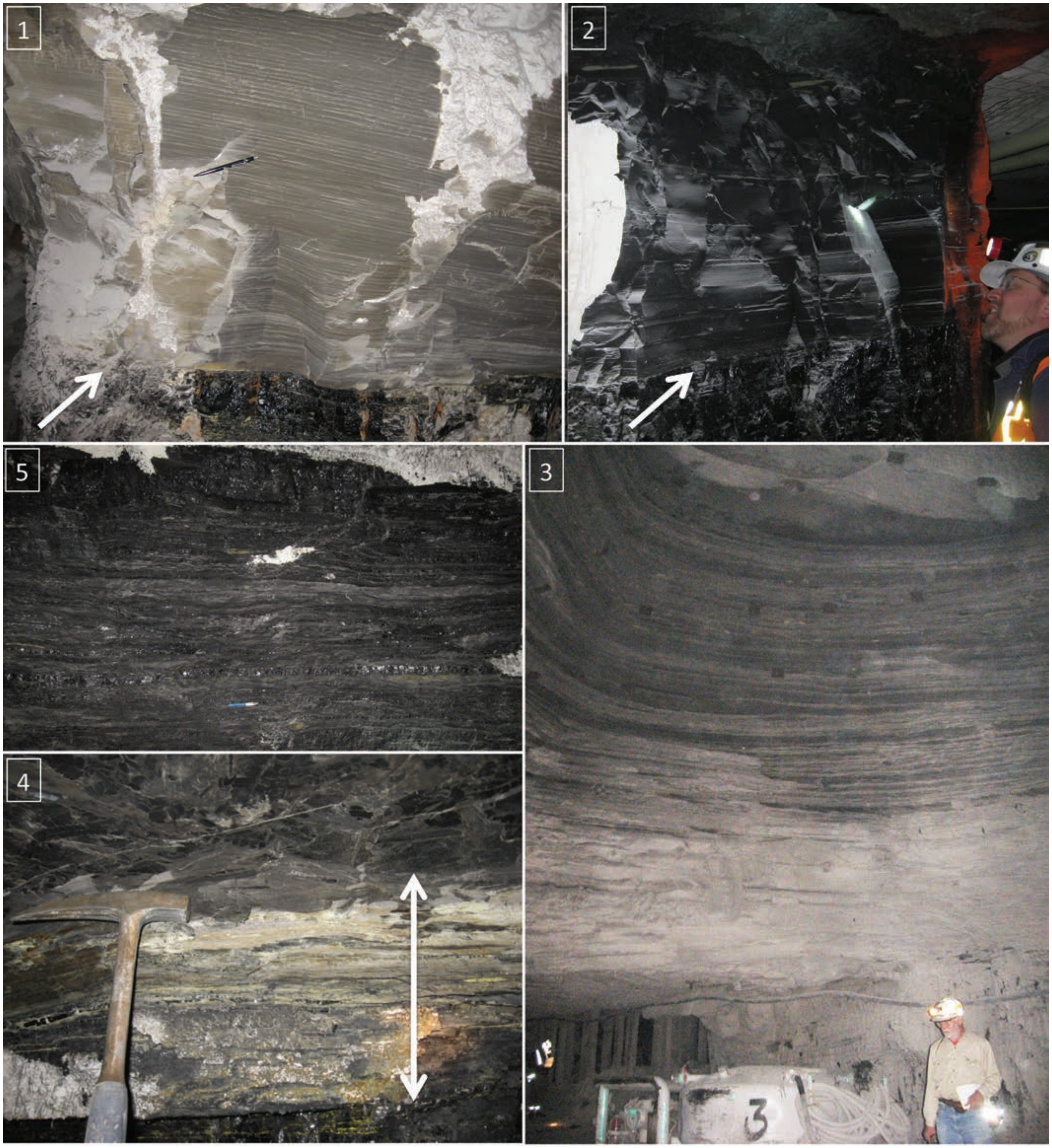
Close to the peat-contemporaneous river channels, gray mudstone or siltstone immediately overlie the coal beds. These lithologies have sedimentary signatures indicating origin in tidal mudflats (Archer and Kvale 1993; text-fig. 3.1). In contrast, the roof strata of these same coal beds elsewhere are primarily marine black fissile shales, limestones, and calcareous, fossiliferous shales (text-fig. 3.2). These marine strata onlap the tidally deposited mudrocks. The fossil content of the tidal sediments indicates origin in freshwater proceeding to brackish, but lacking any biological evidence of marine salinities. This sequence demonstrates that the tidal mudflats were deposited prior to open-marine inundation of the coastal lowlands. Tidal mudrocks are thickest close to the paleoriver channel deposits (text-fig. 3.3), where they may exceed 30 m, thinning laterally away from the main paleoriver axis, extending outward for 10s of kilometers. This pattern suggests that the paleoriver channels were the source of the tidalite sediments, likely from sea-level rise and backfilling of the existing rivers. Distinct lateral thinning has led to characterization of these deposits as gray shale or gray siltstone wedges (Archer and Kvale 1993; Cecil, DiMichele and Elrick 2014). Where the gray siltstone wedges where thick enough (> ~5 m), they appear to have protected the peat from the infiltration of sulfur-rich marine waters. As a result, bands of low-sulfur coal fringe paleochannels beneath gray shale, tidalite roof facies (Allgaier and Hopkins 1975), whereas higher-sulfur coal occurs beneath marine roof strata.

The development of coastal mudflats during the initial phases of sea-level rise terminated peat accumulation. Mudflats may have aggraded rather quickly as sea level rapidly rose, probably in a pulse-like manner in response to melting ice sheets (Archer et al. 2016). Where accommodation space was sufficient, the tops of coal beds preserve the history of this termination. In many places there is a transitional contact (text-fig. 3.4) between the coal bed and the tidalite gray siltstone in which abundant plant fossils are preserved. Coal-to-roof transitions are spatially patchy and likely reflect elevational irregularity on the original peat-swamp sur-



TEXT-FIGURE 1
Stratigraphic chart showing rock and coal units mentioned in this article. Not to scale.

TEXT-FIGURE 2
Map Showing mines included in this study. AQ = Air Quality (Knox County, Indiana), CG = Cottage Grove (Saline County, Illinois), CR = Carlisle (Sullivan County, Indiana), G = Galatia (Saline County, Illinois), L = Liberty (Saline County, Illinois), NF = New Future (Saline County, Illinois), OAK = Oaktown Nos. 1 and 2 (Knox County, Indiana), R = Riola (Vermilion County, Illinois), VG = Vermilion Grove (Vermilion County, Illinois).



TEXT-FIGURE 3
Lithologic patterns, coal-roof contact. 1, Contact (at arrow) of Springfield Coal and tidalite gray shale. Pencil for scale. 2, Contact (at arrow) of Springfield Coal and black, marine Turner Mine Shale. 3, Lower portion of gray siltstone wedge above Springfield Coal. 4, Transitional contact zone (white double-headed arrow) of Springfield Coal and gray, tidalite roof shale. 5, Siliciclastic-sediment-rich upper 1.5 m of Springfield Coal proximate (< 0.5 km) to Galatia channel. Pen for scale in bottom middle of image.

face, with these transitions occurring in low areas where the transition from peat swamp to clastic swamp (*sensu* Gastaldo 1987) was protected from subsequent erosion. In pockets many square meters in extent, the coal becomes increasingly shaley, transitioning to bone coal, then to dark, organic-rich shale, and ultimately to gray shale with large plant fossils and horizontally disposed tree trunks. Included among the fossils preserved in the lower few decimeters of the tidalite roof shales are numerous autochthonous, upright tree stumps, mainly of arborescent lycopsids, but also tree ferns and pteridosperms. These occur in both transitional roof areas and in places where gray shales are in sharp contact with the top of the coal. Such tree stumps are 'rooted' in the top of the coal bed, the former peat substrate. This rooting can be seen most clearly in two ways: (1) stumps, particularly those of arborescent lycopsids, preserved on the 'rib' (the edge of the coal body along the walls of the mine tunnels), terminate at the top of coal without evidence of root systems extending laterally into tidalite muds; (2) the presence of lycopsid stigmarian axes, filled with roof sediment, located 5–10 cm into the coal bed, indicating open conduits from the hollow tree stumps into the hollow root systems, typical of arborescent lycopsids after decay has set in. Minor evidence of rooting in the gray shales has been noted rarely and almost exclusively for calamitaleans and pteridosperms. Patches of autochthonous groundcover also may be preserved at the base of the gray roof shales (DiMichele et al. 2007; Archer et al. 2016; Nelson et al. in press). The autochthonous to parautochthonous floras at the base of the gray siltstone wedge, preserved in the finest-grained sediments of that deposit, represent the final flora of the peat-forming environment.

The contact between marine roof strata (black shale and limestone) and the underlying strata is erosional. This includes erosion of the gray shale wedge sediments, leading to an erosional contact in areas proximal to the channel, where the gray tidalites are thickest, and complete removal in areas distal to the channels, leaving patches of gray shale intact above the coal (e.g., DeMaris et al. 1983). Where marine strata lie in immediate contact with the top of the coal bed, examination of coal thicknesses above laterally continuous coal bands and in-seam clastic partings, truncation of coal laminae, irregularities in the top coal surface and, in places, a diffuse reworked contact zone with overlying marine roof reveal erosion of the former peat surface.

Elongate shoestring-like bodies of siltstone are present in the lower few meters of the tidal mudflat deposit. These are lenticular in cross section, generally from 2–10 m in width (text-figs. 4, 5.1), and can bottom-out on or erode deeply into the coal seam. In map view, these features, called 'rolls' by miners, are sinuous and occur in subparallel swarms, ranging individually from 10–100s of meters and rarely 1,000s of meters long (text-fig. 4). They are widespread in the Springfield, Herrin, and Danville coal seams under gray shale roof, and are particularly well exposed in underground mines. Rolls are erosional features, with irregular basal contacts indicating scour (text-fig. 5.2, 5.3). They frequently are scoured through surrounding tidalite siltstone (indicating active flow during tidal-mudflat deposition) as much as a meter or more into the coal bed (text-fig. 5.4, 5.5). Assuming peat compaction of at least 3:1 (Nadon 1998) or possibly less, and perhaps as much as 10:1 (Cecil et al. 1985), this modern depth of scour suggests original scour depths of <3 m to perhaps as much as 5–10 m. Rolls are infilled with tidally laminated gray shale (cross section of roll, text-fig. 5.6), the same lithology found covering the coal. Stringers of coal frequently are incorporated into the sediment filling the roll, indicating the original peat body was torn up during erosion and peat flaps or small floating peat mats were entombed as the channel infilled with sediment. Rolls are largest and most numerous where strata overlying the coal are of coarsest grain size, which is in proximity to paleoriver channels.

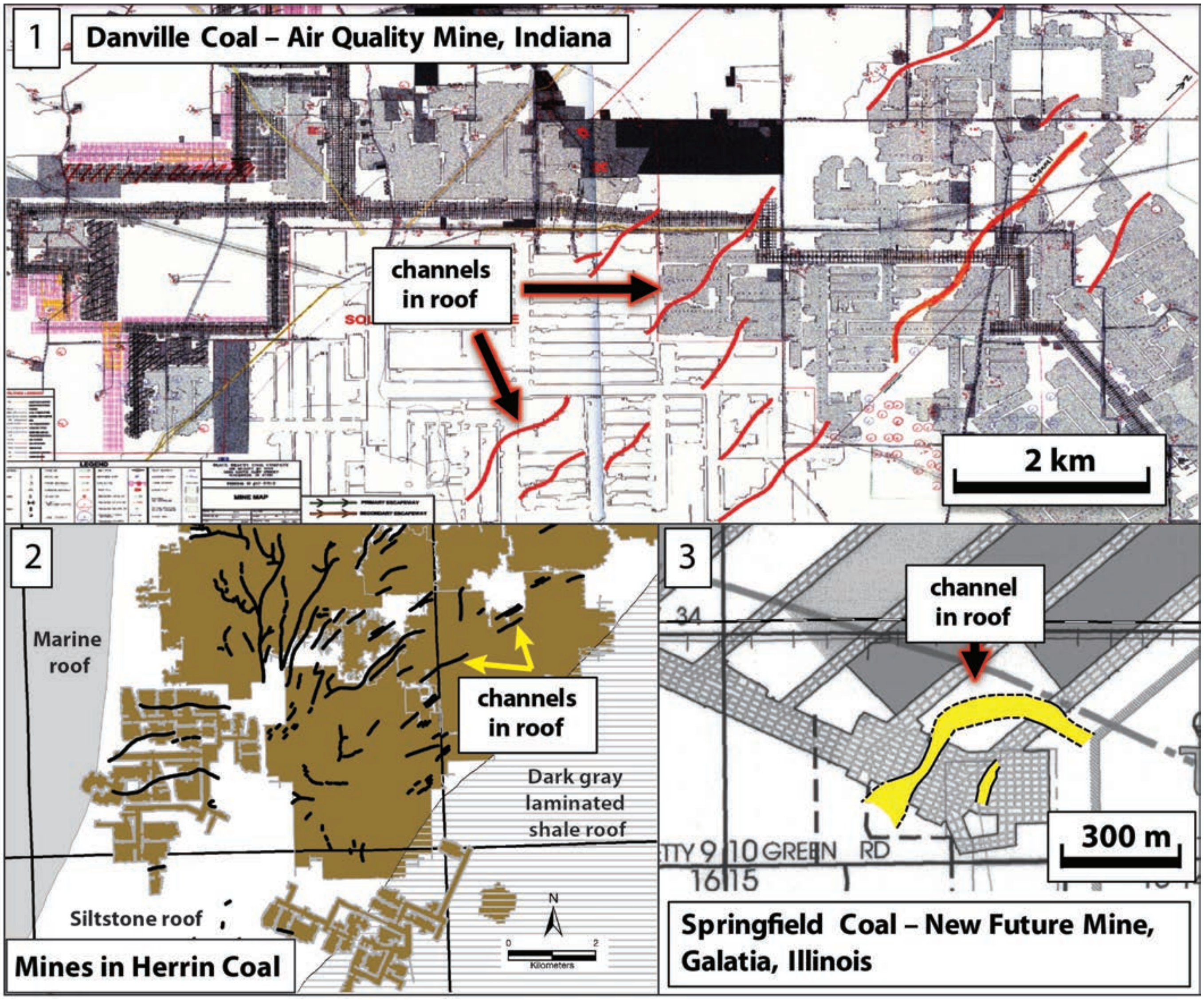
We interpret nearly all rolls to be tidal channels that formed as marine transgression encroached both up-river and into the peat swamp. Some of these channels may have originated as drainages in the peat swamp. Others may have been initiated during the latest phases of drowning of the peat swamp and continued to be active after the peat swamp had been buried by a mudflat, indicated by partial to complete entombment within the gray tidalite, siltstone wedge. In these latter cases, the tidal channels must have originated contemporaneously with or shortly after mud flats began to develop. The channels also tend to be concentrated close to the large peat-contemporaneous river systems where tidal forces would have been greatest. The sequence of events beginning with a black-water river drainage through the peat swamp and terminating with the development of an extensive mudflat and tidal channels is summarized in text-figure 6.

Of importance to our study, chaotic tangles of crisscrossing, horizontal to sub-horizontal, large lycopsid logs, perhaps numbering in the hundreds, are common within many rolls, belonging almost exclusively to the genus *Sigillaria*. We interpret these arborescent-lycopsid trunk accumulations as log jams; log jams are common in modern rivers and tidal channels. The sigillarian log jams studied here can be associated with other kinds of plant remains as well, mainly marattialean tree ferns and pteridosperms. It is this flora that we focus on next.

Paleobotanical patterns

Several kinds of wetland floras grew in Pennsylvanian lowland environments, typifying different habitats representing differing physical conditions. For the most part, the species in these various habitats are drawn from a common species pool. In the Late Paleozoic wetlands genera and higher-taxonomic groups, such as families and orders, encompassed complexes of closely related species with similar environmental preferences, thus leading to a strong overlap between evolutionary relatedness and ecological distribution (DiMichele and Phillips 1996b). Such 'niche conservatism' is a pattern now widely recognized even in much more diverse modern communities (e.g., Kraft et al. 2007; Wiens et al. 2010).

For the sake of simplicity, we divide those wetland floras under consideration in this study into two broad habitat groups: (1) Peat-swamp floras. This group encompasses macrofossil and microfossil remains of plants that grew in peat-swamp environments. The macrofossil remains are preserved primarily in coal balls, which are permineralized remains of the original peat from which the coal formed (e.g., Phillips, Avcin and Berggren 1976). In rare instances macrofossils may be preserved in siliclastics brought in by floodwaters or in volcanic ash (e.g., Opluštil et al. 2009; Wang et al. 2012). Microfossils (principally spores and pollen) are abundant in most coal beds (e.g., Peppers, 1996). Most Pennsylvanian peats formed under conditions of high, nearly aseasonal rainfall, so-called humid to perhumid (*sensu* Cecil 2003) climates. (2) Coal roof floras. This is a very broad category of environments that includes those fossiliferous strata that lie in immediate contact with the top of the coal bed



TEXT-FIGURE 4
Areal distribution map of tidal channels (rolls) in three different coal beds. 1, Danville Coal. 2, Herrin Coal, Vermilion County, Illinois. (Modified from DiMichele et. al 2007). 3. Springfield Coal, Galatia Mine, Saline County, Illinois.

and were deposited during the termination of peat-formation or shortly thereafter. In this study, we recognize two kinds of environments represented by roof strata. (2a) Transitional peat-substrate environments. These environments typify the onset or termination of peat accumulation and are represented by coaly shale and high-ash coal (‘bone coal’ or ‘rash’, among other such terms), frequently encountered immediately above coal beds (e.g., Gastaldo, Pfefferkorn and DiMichele 2005). In tropical wetlands, such environments typify subhumid to humid, mildly to strongly seasonal climates under which sediment transport is maximized (Cecil and Dulong 2003). Transitional environments also may be found below coal beds, grading into them. (2b) Environments formed during early phases of marine transgression associated with the development of muddy tidal flats (Archer and Kvale 1993). These likely formed under the transition from humid to subhumid conditions during late glacial and early interglacial phases (Nelson et al. in press). The floras of mudflat environments generally have not been differentiated from those found in transitional roof-shale facies (2a, above), given that they often are preserved immediately above coal beds. However, by appearances, mudflat environments were not transitional habitats, thus not of the kind in which the plants were growing in muddy peat substrates as the final forests of the swamps (2a, above).

Peat swamp floras

The Pennsylvanian peat-substrate flora, known primarily from coal balls and palynology, preserves the autochthonous to parautochthonous remains of the plants that occupied the swamp, those that grew on purely peat substrate. Peat substrates tend to be flooded for much of the year, particularly if of planar geometry (as the peats under study here are suspected to be), have an acidic pH, and can tie up mineral nutrients, making them unavailable or of limited availability to the plants (Schlesinger 1978). In addition, there is a growing body of geological evidence that rivers and streams flowing through Pennsylvanian peat swamps may have been black-water in character, carrying little sediment during most of the peat forming interval (Nelson, Elrick and DiMichele 2008; Davies and Gibling 2013). Along paleoriver channel margins, coal beds grade from dominantly coal with numerous thin claystone partings to dominantly claystone with numerous thin coal stringers over a lateral distance of many 10s of meters (text-figs. 3.5, 7). This coal to claystone facies change records the extent to which river sediment infiltrated the peat swamp during peat accumulation. The clays proximate to the channel margin were likely introduced from the river channel, probably as suspended fine sediment. An analogue may be tropical black-water rivers of Indonesia, some of which also drain peat-swamp habitats (Cecil et al. 2003a). The coal bed, including that part with fine-shale partings, is in erosional contact with the overlying tidalite roof and laterally adjacent channel-filling sandstone (text-fig. 7).

Middle Pennsylvanian floras. Floras from the main, late Desmoinesian (Middle Pennsylvanian) coal beds of the Illinois and Appalachian basins have been studied quantitatively (Phillips, Peppers and DiMichele 1985), and thus the parent plants and compositional proportions of peat-substrate vegetation are well known. These floras include those from the Springfield Coal (Mahaffy 1988; Willard 1993; Phillips and DiMichele 1998), the Herrin Coal (Phillips, Kunz and Mickish 1977; Phillips and DiMichele 1981; DiMichele and Phillips 1988), the Baker and the Danville coals (DiMichele, Phillips and Nelson 2002), and the Upper Freeport Coal (e.g., McCullough 1977; Feng 1989). The coal-swamp vegetation is dominated by a variety of arborescent lycopsids, averaging ~50–60% of the aerial biomass, predominantly species of *Lepidophloios* Sternberg, *Paralycopodites* Morey and Morey, *Diaphorodendron* DiMichele, and *Synchysidendron* DiMichele and Bateman. The genera *Lepidodendron* Sternberg and *Sigillaria*, although present in peat-substrate settings of this time interval, are relatively unimportant quantitatively, even though they may be locally abundant in some coals. In the single quantitative sample from the Danville coal (DiMichele, Phillips and Nelson 2002) *Sigillaria* is second in importance to marattialean tree ferns. Marattialean tree ferns and medullosan pteridosperms each account for ~10–20% of the biomass (with the exception of the one quantified Danville coal sample), with calamitaleans, filicalean vines and ground cover, and sphenopsid ground cover accounting for most of the remaining biomass.

Late Pennsylvanian floras. There also are a number of published studies on Late Pennsylvanian coal-ball assemblages from the Illinois (Phillips, Peppers and DiMichele 1985; Willard and Phillips 1993; Willard et al. 2007) and Appalachian (Rothwell 1976; Pryor 1996) basins. These assemblages differ substantially in composition from those of the Middle Pennsylvanian (Phillips et al. 1974; DiMichele and Phillips 1996a). They are dominated by tree ferns, on a whole-seam-average basis, but individual coal-ball layers may be dominated by pteridosperms or sigillarian lycopsids, likely reflecting patchy variations in habitat conditions within the swamps. Sigillarians, particularly the species *Sigillaria brardii* [= *S. approximata* Lesquereux; Delevoryas (1957) described the anatomy of this plant in detail] are the most commonly encountered arborescent lycopsids in Late Pennsylvanian fossil floras, in both peat and mineral substrate assemblages.

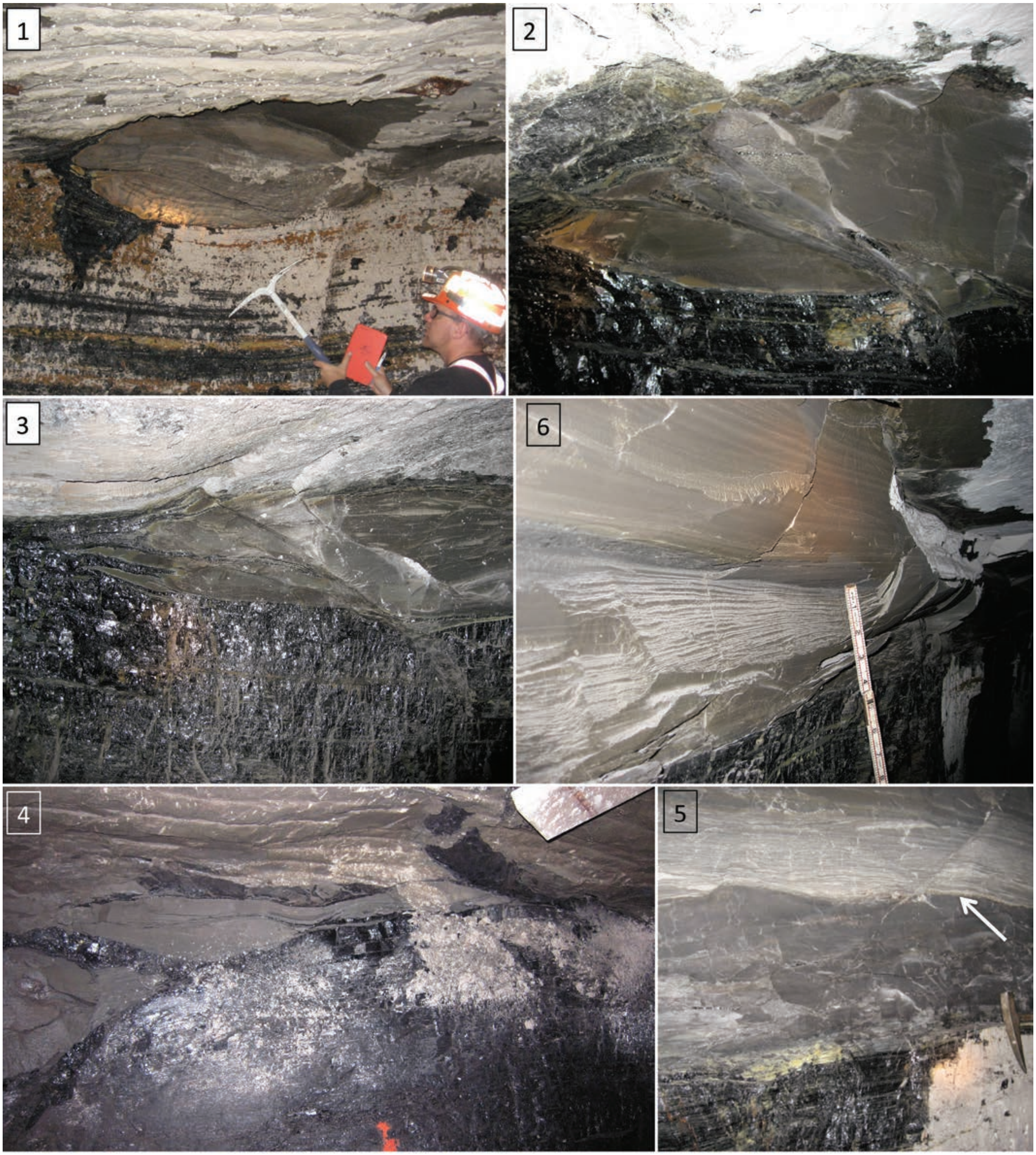
Transitional Roof-Shale Floras

The final phases of the peat-forming swamp environment are represented by both gradational coal-roof contacts (coal to shaley coal to shale) and sharp contacts (coal overlain by tidalite shales), preserving trees rooted in the top of the coal bed and parautochthonous accumulations of large, minimally transported plant remains. The transitional roof shales preserve the remains of swamp plants that were inundated early by waters carrying abundant siliciclastic sediments (Gastaldo 1987; Gastaldo, Pfefferkorn and DiMichele 1995; Bashforth et al. 2016). These floras differed quantitatively, and to a lesser extent qualitatively, from those that comprised peat substrates (DiMichele, Phillips and McBrinn 1991). The late-stage floods carried greater nutrient loads than flood waters emanating from black-water channels contemporaneous with peat accumulation. The flooding regime also may have been of longer duration, and the disturbances caused by flood energy greater than in swamps of the peat-forming phases. The switch from low-sediment, black-water conditions to increasingly sediment-rich conditions reflects climatic shifts coincident with melting polar ice, sea-level rise, and changing patterns of atmospheric circulation, resulting in increasing tropical seasonality, reduction of vegetation cover, and increased sediment runoff from the land surface (Cecil et al. 2003b; Eros et al. 2012; Horton et al. 2012; Cecil, DiMichele and Elrick 2014).

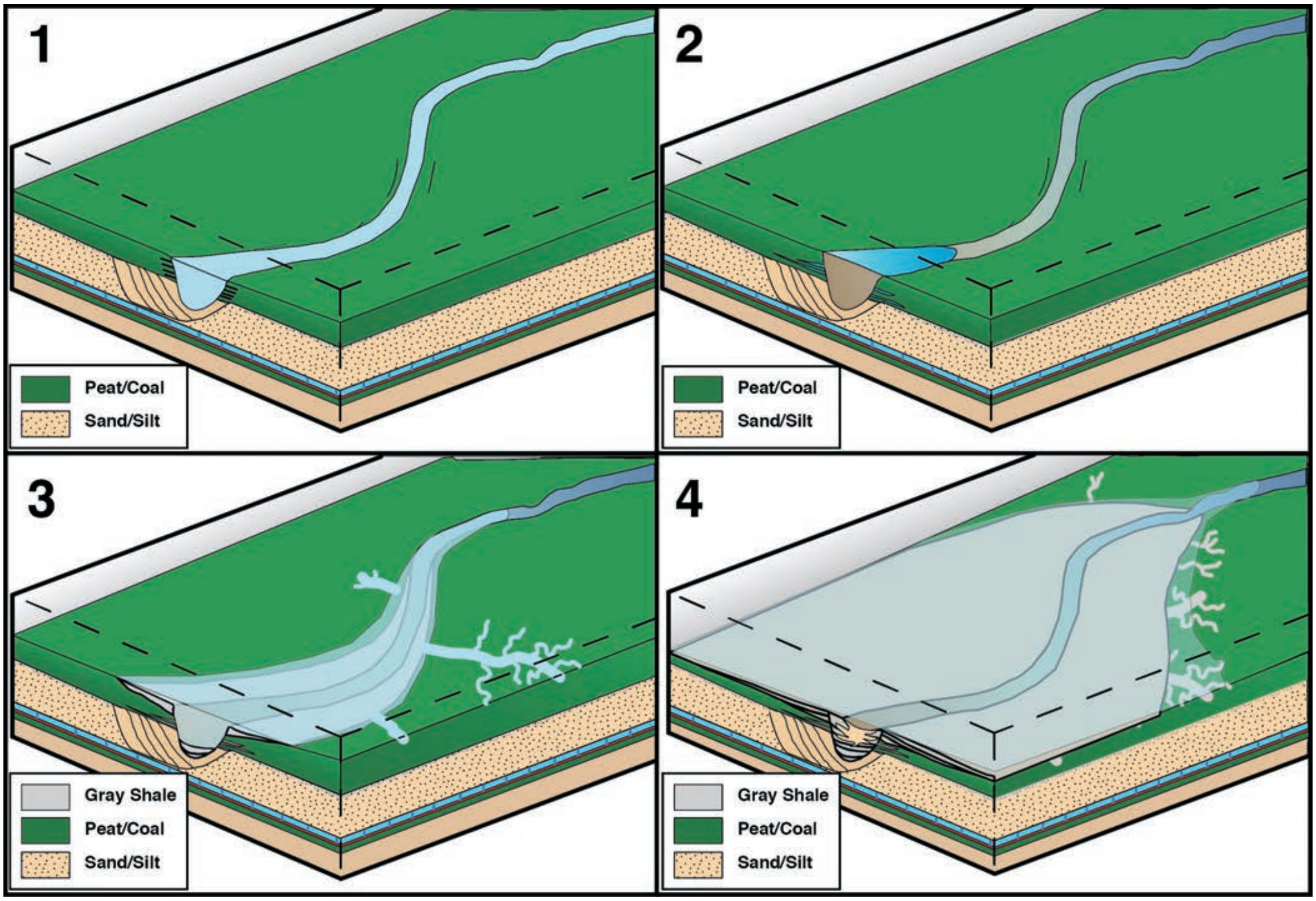
Middle Pennsylvanian floras. Quantitative floristic studies of late Desmoinesian, transitional-type roof floras from the Illinois Basin include those from the Springfield Coal (DiMichele and Nelson 1989; Willard et al. 1995), the Herrin Coal (Gastaldo 1977; DiMichele et al. 2007), and the Danville Coal (Pfeifer 1979). Similar age floras are known from the Appalachian Basin (e.g., Wagner and Lyons 1997; Blake et al. 2002) and have been studied extensively in Western Europe (e.g., see bibliographies in Cleal 1997; Cleal et al. 2009, 2012; Wagner and Álvarez-Vázquez 2010; Bashforth et al. 2011; King, Cleal and Hilton 2011; Opluštil et al. 2016). In contrast to coal-swamp assemblages, most transitional roof-shale floras that represent the final vegetation of the peat swamp are generally dominated by medullosan pteridosperms and/or marattialean tree ferns (e.g., Pfefferkorn and Thomson 1982). Lycopsids, taxonomically similar to those that dominated the peat-forming settings, also are common elements, and sometimes are dominant.

The transitional roof floras examined here are those in the lower part of the roof shales, primarily in the lower 0.5 m at the base of the gray siltstone tidalite wedge deposits. These floras are characterized by a diversity of lycopsids (text-fig. 8.1), pteridosperms (text-fig. 8.2), calamitaleans (text-fig. 8.3), and marattialean tree ferns (text-fig. 8.4). The flora is essentially that of the peat-swamp environment, usually showing no transport (autochthonous plants rooted in place, text-fig. 8.1) or minimal transport (large flattened stems and frond parts preserved without preferential orientation, text-fig. 8.2–8.4). Proximal to the channel margins the roof flora is very rich in pteridosperms, laterally giving way to mixed floras of pteridosperms, tree ferns and arborescent lycopsids of various kinds.

Late Pennsylvanian floras. Studies of transitional adpression floras associated with roof and floor strata of Late Pennsylvanian coals from the Eastern and Midwestern U.S. (Gillespie, Hennen and Balasco 1975; Wagner and Lyons 1997; Blake et al. 2002; Blake and Gillespie 2011; Stull et al. 2012; DiMichele et al. 2013; Tabor et al. 2013) are far fewer in number than those



TEXT-FIGURE 5
Lithologic patterns, tidal channels/ 'rolls' 1, Small tidal channel, Springfield Coal. 2, Tidal channel ~1 m-thick showing tapered edge with coal 'flap'and internal compactional faulting, Danville Coal. 3, Tidal channel ~50-cm thick with coal/peat flaps at margin and truncation of coal lamination, Danville Coal. 4, Complex tidal-channel margin showing peat/coal flaps and deep erosional contact with coal bed, Danville Coal. Note edge of 2 × 4-inch (~5 × 10 cm) stud in upper right. 5, Erosional contact of tidal-channel base (at arrow) with lower deposits of gray, tidalite siltstone, Springfield Coal. 6, Sedimentary fill of tidal channel illustrating tidal laminations, Danville Coal, scale in tenths of feet (0.5 ft is ~15 cm).



TEXT-FIGURE 6
Block-diagram sequence illustrating progressive flooding of coal swamp during the initial phases of sea-level rise. 1, Peat swamp drained by black-water river under humid climate. 2, Sediment load in river drainage increases as sea level rises and climate transitions to subhumid. 3, River converts to tidal estuary with continued sea-level rise. Initiation of mudflats and tidal channels in more coastal areas of the landscape, flanking the estuary. 4, Extensive mudflat development during its inland progression, including expansion in number and extent of tidal channels.

from Europe (see Kerp and Fichter 1985; Broutin 1986; Doubinger et al. 1995; Wagner and Álvarez-Vázquez 2010; Cleal et al. 2012; or Opluštil et al. 2016 for bibliographic data). As with peat-substrate assemblages, these floras are rich in tree ferns and pteridosperms, with the diversity of lycopsids greatly diminished compared to that of the Middle Pennsylvanian and with sigillarian lycopsids as the most commonly encountered arborescent forms.

In general, the congruence between the compositional and quantitative dominance-diversity patterns of Late Pennsylvanian peat-forming floras and coal-bed roof-shale floras is much greater than in the Middle Pennsylvanian, at least at the major group level. Pteridosperms and tree ferns are generally the dominant elements in both kinds of environmental settings. Sigillarian lycopsids, effectively only the single species *Sigillaria brardii*, also occur in about the same proportions in both kinds of environmental settings.

Mudflat flora preserved in tidal channels

The second type of roof flora is that confined to the tidal-channel 'rolls', which stands in sharp contrast compositionally to the early buried coal-swamp flora at the base of the gray-shale wedge. Because the base of a roll is erosional, the bottom surfaces have cut down into the mudflat deposits formed during the early phase of drowning of the peat swamp, and are of irregular elevation, leading to somewhat haphazard exposure. Thus, the flora they contain is exposed in patches throughout a mine, reflecting the combination of erosional depth of the original tidal channel, roof stability (roof falls expose strata higher above the top of the coal), the height at which the face was cut during mining, and other factors. In contrast to the taxonomic diversity of the common roof flora, the tidal-channel flora contains concentrated abundances of chaotically arranged large logs of the lycopsid *Sigillaria* (text-fig. 9.1–9.6). Intermixed with these logs are foliage of marattialean tree ferns and medullosan pteridosperms (text-fig. 9.3). In some instances, the rolls and their included flora lie in sharp contact with the surrounding roof flora into which the channels eroded as mudflat development ensued; indeed, if not recognized as a tidal-channel deposit, such occurrences could be misinterpreted to be small habitat patches within the larger, typical wetland roof-shale assemblage. They may even lead to the conclusion that the roof shale flora was allochthonous or contained a large alloch-

TEXT-FIGURE 7
Coal bed proximate to paleoriver channel, Springfield Coal, Galatia Mine, Salince County, Illinois. Two distinct sedimentary processes are illustrated. First, the coal is split into stringers separated by claystone partings deposited in floods from the nearby river, which occurred during peat accumulation. The claystone partings are progressively more abundant toward the channel axis. More distant from the channel axis, claystone partings decrease in number and thickness and disappear. Second, during mudflat development, the top of the peat became scoured by channels and currents related to the nearby estuary, formerly the river drainage. These features overlie the coal in erosional contact (at black arrows). Geologist's pick is 63-cm tall.

thonous component, particularly where contact with the autochthonous-to-parautochthonous flora was obscured by poor exposure.

Were Sigillaria *trees living in the mudflats?* If *Sigillaria* trees were living in the tidal mudflat environment and not simply rooted in the top of the coal, there should be stigmarian root systems observable in the tidalite, gray-siltstone wedge sediments above the coal bed. However, such root systems are extremely rare. We have observed a few stigmarian axes with intact rootlets in roof shale, suggesting that the parent plants were living in the mudflat settings, perhaps along the margins of tidal channels, where permanent water cover was not established during early coastal flooding. We also have observed roots emanating from small-diameter, upright axes within the roof shale deposits, which likely are medullosan pteridosperm or calamitalean stems. These observations provide some evidence to support the existence of a *Sigillaria*-dominated flora in the mudflat habitats, in association with tree ferns and pteridosperms.

There is other evidence that also might lead to the conclusion that the *Sigillaria*-dominated flora was living in the mudflat environment. For example, in the Wabash underground mine, DiMichele and Nelson (1989) mapped an area >7000 m^2 where *Sigillaria* dominated the fossil flora overlying the Springfield Coal. Surrounding this confined area, in sharp contact along one side and in gradational contact over the other, was an assemblage composed mainly of medullosan pteridosperms and calamitaleans, with only small numbers of marattialean tree-fern remains. At the time, the authors considered these various plant assemblages to reflect spatial heterogeneity of the vegetation. Recognizing that this site cannot be reexamined (because the coal mine is closed), it is worth contemplating that the *Sigillaria* accumulation, which included both upright tree stumps and horizontally disposed large trunks, was in fact growing within the tidal mudflat and not on the peat substrate of the swamp. If this were the case, it would mean that the flora was not part of the underlying peat-accumulating forest swamp but rather part of post-peat, non-peat-accumulating forested swamp/wetland.

Could the tidal channel floras be transported from external settings? Tidal environments are dynamic, and tidal channels and estuaries can migrate considerably across relatively to very flat land surfaces. In so doing, these channels may exhume the remains of standing trees or tree bases that may be hundreds of years old and capture and incorporate long-buried logs into bed load. The transport of such trees, furthermore, can lead to log jams (e.g., Davies and Gibling 2013), resulting in complex channel morphologies and dynamics. In addition, in modern tidal environments, it is not uncommon for material transported from upstream in estuaries to be transported into flanking tidal channels during flood tides.

Such cautionary observations are necessary when considering the provenance of allochthonous plant remains in channel settings. It is quite possible that the sigillarians were growing considerable distances inland and were moved into tidal channels, forming tangles and jams. They also may have been living on islands within the tidal flat landscape [an alternate interpretation of the DiMichele and Nelson (1989) study referred to above]. Either or both situations would explain the low frequency of rooting within the roof shales. Moreover, if climate were changing during sea-level rise from humid to subhumid, and if sigillarians were more tolerant of climatic seasonality as has been suggested (Pfefferkorn and Wang, 2009), their numbers may have risen in clastic-swamp wetlands fringing mudflats on the landward side. Our observations of Middle Pennsylvanian floras from non-peat-forming settings indicate that *Sigilliaria* is the most common lycopsid, found almost to the exclusion of other lycopsid-tree taxa (e.g., the small, multistory channel fill with autochthonously preserved flora reported in DiMichele, 2014, p. 143–145, fig. 17), indicating the possibility of greater tolerance than other types of arborescent lycopsids to variation in water table and perhaps to disturbance.

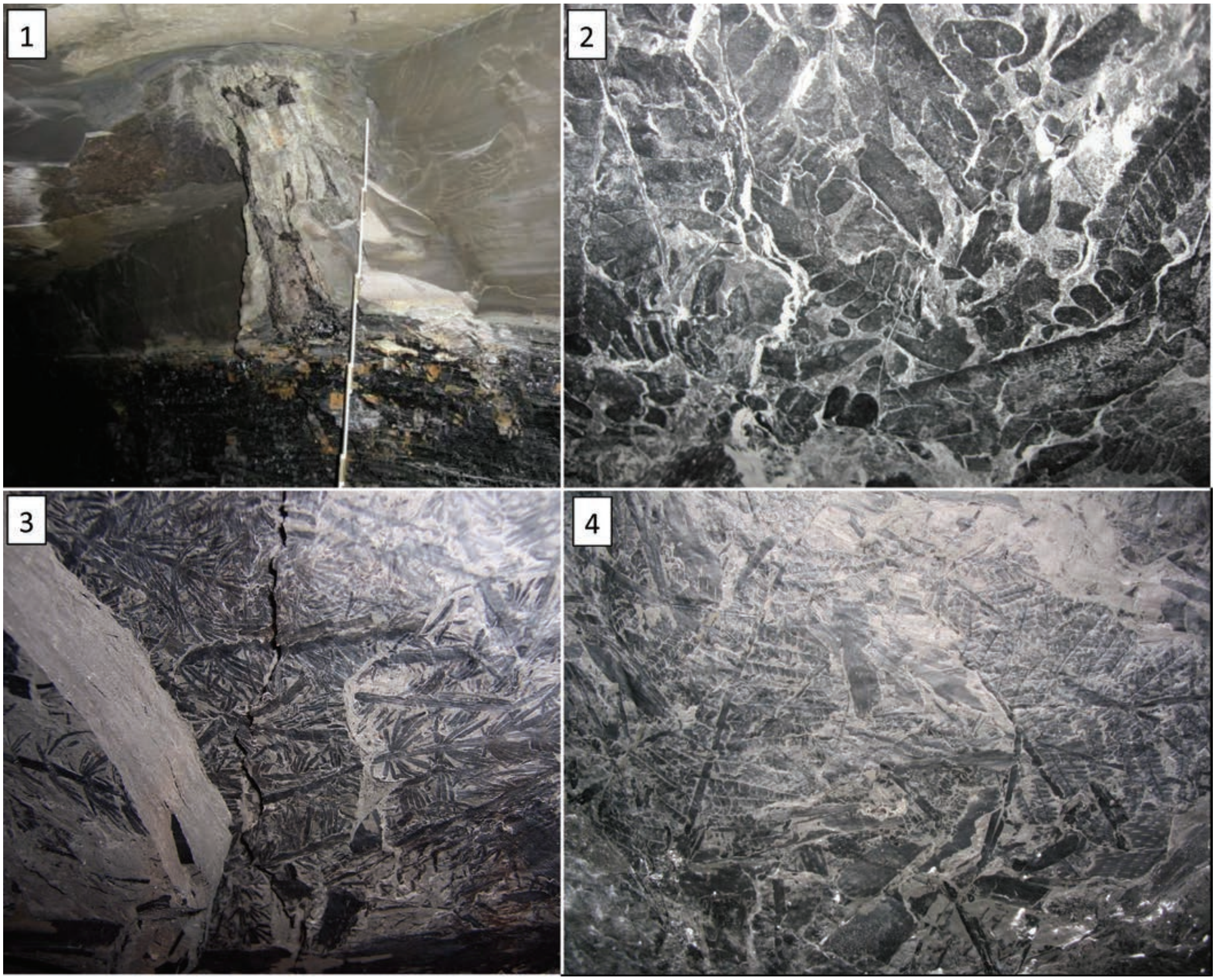
DISCUSSION

In this paper we have focused on a specific landscape feature: tidal channels formed in transgressive mudflats, developing over peat-swamps, and flanking large estuaries on the flat, lowland landscapes of the Illinois Basin. The tidal channels formed during the final drowning phases of peat-forming swamps, during which sea-level rise and associated climatic changes were altering the tropical lowlands in many ways. These tidal channels contain the remains of plants, the overwhelmingly most common of which are large trunks of the arborescent lycopsid *Sigillaria*. Intermixed with these remains are foliage fragments of marattialean tree ferns and medullosan pteridosperms. This flora is distinct from that typical of late Middle Pennsylvanian peat-forming swamps, based on quantitative analyses of coal-ball floras, and coal-shale transitional floras found immediately above coal beds; both of these latter kinds of assemblages are parautochthonous to autochthonous accumulations of plant remains from peat-swamp habitats, although the transitional floras represent unique, final-swamp environments formed during conversion of the area from peat to mineral substrate.

The significance of the Middle Pennsylvanian flora preserved in the tidal channels is its general similarity to the floras that characterize Late Pennsylvanian wetland landscapes, including peat-forming swamps. The suite of taxa in the tidal channels is, of course, much less diverse than the complex, taxonomically rich floras known from the Late Pennsylvanian throughout Euramerica. However, in its principal elements, sigillarian lycopsids, marattialean tree ferns, and medullosan pteridosperms, it bears greater similarity to a Late Pennsylvanian assemblage than to the Middle Pennsylvanian assemblages of which it is otherwise a part. There is only one species of *Sigillaria* in the Late Pennsylvanian, the unribbed *S. brardii*, attributed to the subgroup subsigillaria. However, the sigillarians found in the tidal channels, and typical in general of the late Middle Pennsylvanian roof-shale adpression floras examined in this study, are distinctly ribbed, and attributed to the subgroup eusigillaria. In addition, with the exception of some pteridosperms [e.g., *Neuropteris ovata* Hoffmann and *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute and Zodrow], the marattialean tree ferns and most of the pteridosperms of the Late Pennsylvanian comprise different species from those of the late Middle Pennsylvanian. Thus, the compositional similarity of the Middle Pennsylvanian tidal channel floras and Late Pennsylvanian peat-swamp and lowland-wetland floras is, in general, at the generic level.

The way in which the Late Pennsylvanian marattialean tree-fern, medullosan-pteridosperm, and sigillarian-lycopsid swamp flora originated is uncertain. Coal-palynological studies (Peppers 1979, 1997; Kosanke and Cecil 1996) document an interval across the Desmoinesian-Missourian (Middle-Late Pennsylvanian) boundary of high variation in dominant taxa from one coal bed to the next and distinct from the typical tree-fern dominance that characterizes most of the Late Pennsylvanian. These patterns through time and space suggest considerable disruption of the coal-swamp ecosystem. This disruption was followed by a 'sorting-out' period of compositional instability, during which vegetation ultimately dominated by marattialean tree ferns, medullosan pteridosperms, and sigillarian lycopsids spread and became dominant across the lowland landscape, including in standing-water swamp habitats. In the Illinois Basin during this transitional interval (Peppers 1979, 1996), dominance of tree-lycopsid spores declined dramatically, but the immediate replacement floras were dominated by spores of small lycopsids, such as *Polysporia* Newberry (= *Chaloneria* Pigg and Rothwell), perhaps indicative of widespread marsh-like habitats (DiMichele, Mahaffy and Phillips 1979), and calamitaleans, also possibly indicative of low-stature vegetation. Tree-fern spores do not become the dominant forms until a few coals after the decline of the lycopsid spore taxa *Lycospora* Schopf, Wilson and Benthall (several species) and *Granasporites medius* (Dybová and Jachowicz) Ravn, Butterworth, Phillips and Peppers, and of the marattialean tree fern spore *Thymospora pseudothiessenii* Kosanke emend. Wilson and Venkatachala. In the Kansas section (Peppers 1997), the transitional interval is characterized by dominance of cordaitalean, medullosan, and even coniferophyte pollen, ultimately succeeded by the rise of various types of tree-fern spores. In the Appalachian Basin (Kosanke and Cecil 1996), palynological analysis finds a similar pattern, but a thinner transitional interval (one coal bed, possibly reflecting the more inland position and lower accommodation space) than in Illinois or Kansas, with dominance by small lycopsids, prior to the onset of marattialean tree-fern dominance.

The results reported here suggest that a type of vegetation similar to that dominant in Late Pennsylvanian peat-forming swamps was already present on the landscape well back in the late Middle Pennsylvanian. Its growth environment appears to have been either nutrient-rich, siliciclastic-substrate, swampy, mudflat habitats, almost certainly freshwater, or infrequently influenced by low salinity during extreme high tides, or areas



TEXT-FIGURE 8
Roof-shale flora, base of a tidalite, gray-siltstone wedge, all from Herrin Coal. 1, *In situ* lycopsid tree base rooted in top of coal bed. Approximately 50 cm of the tree base is exposed. 2, Pteridosperm foliage, principally *Neuropteris flexuosa* Brongniart and *Macroneuropteris scheuchzeri*. 3, Calamitalean foliage, *Asterophyllites equisetiformis* Brongniart. 4, Marattialean fern foliage. Scales are lacking for these plants because of working conditions in the mine (the roof was too high and no ladders were allowed). Sizes are typical for the species shown and can be approximated from other publications in which they are illustrated.

fringing mudflats, perhaps on the landward side, ahead of rising sea level. Just how dense this vegetation was within these non-peat accumulating wetlands is uncertain. Evidence of stigmarian and other types of rooting in the mudflat deposits is not common but has been encountered, indicating the presence of at least some of these plants in the environments that succeeded the peat-forming swamps. However, as discussed above, it is possible that the bulk of the vegetation was transported from further inland and pushed into tidal channels during flood tides. Such environments would have had greater water-table fluctuations and higher levels of disturbance than the peat-substrate swamps, which may be a key to their composition, particularly the abundance of *Sigillaria*.

Mechanistically, tidal channels erode headward into the landscape from the coastline or from an estuary during relative sea-level rise (Perillo and Iribarne 2003; Hood 2006: Hughes et al. 2009; Hughes 2012), although they also may erode laterally and form as a result of high levels of sedimentation (Hood 2006). They tend to be initiated on pre-existing landscape drainages and proceed inland. As a tidal channel forces its way inland, its width expands and trees and vegetation in its path or lining its banks fall into the channel and undergo transport. Small items such as leaves and sticks freely move in the channel system and are easily transported. Large trees, however, can become lodged in the tight bends that characterize tidal channel systems, thus forming log jams. In some cases, log jams represent a concentrated sampling of a transect though the landscape, as defined by the channel course, although in tidal environments they can also represent logs that were redistributed from a larger drainage area and transported into smaller tidal creeks on marginal estuarine tidal flats during flood tides. Although redistribution by tidal mechanisms cannot be ruled out, the preponderance of *Sigillaria* in log jams means either that swamp forests in the vicinity were *Sigillaria* dominated or that *Sigillaria* trees had buoyancy properties that caused them to be preferentially transported and sorted in log jams, even if the logs came from multiple sources or compositionally mixed forests. Given the architectural similarity of arborescent lycopsid trunks (supported by a marginal rind of decay-resistant bark inside of which was softer tissue, more susceptible to decay, except for the small woody vascular cylinder), all would be expected to have had similar dynamic qualities in an aquatic environment, and all would have been more-or-less equally likely to float, and in the same way. This basic architectural similarity eliminates a physical biasing mechanism to explain the monotypic composition of the log jams. Similar log jams in tidal channels observed in the Herrin and Danville coals, and elsewhere in the Springfield Coal, show the same overwhelming dominance of large *Sigillaria*, even when the coals themselves had few *Sigillaria* and a larger diversity of other arborescent lycopsids, implying that the same mechanistic processes were operating during the swamp-termination and mudflat-development phases of all of these coals.

We have also noted that large *Sigillaria*, marattialean tree fern, medullosan pteridosperm, and calamitalean remains have been found rooted in place, in autochthonous preservation within flashy discharge, multistory channel deposits from intervals between coal beds (e.g., at the Peabody Cottage Grove Mine; DiMichele 2014), and in channels or rooted in thin, organic floodplain layers at other mines (DiMichele et al. 2009). In addition, rare *Sigillaria*, along with sparse remains of tree ferns and pteridosperms, has been identified in environments with strong seasonality, perhaps formed under dry subhumid to semi-arid climates, as far back as the Early Pennsylvanian (e.g. Falcon-Lang 2003; Bashforth et al. 2014). This indicates a long association of these taxa with wet corridors within overall drier landscapes and/or with areas of physical disturbance, either of which are atypical of most of the other arborescent lycopsids. In all of the environments the background climate was seasonally dry to some degree, although the soil in which the plants were growing was wet for most of the year, and the environments were fundamentally high in nutrients (or at least higher than would be typical of a peat swamp), based on the siliciclastic character of all the settings.

Deglaciation appears to have been the cause of the specific environmental changes that occurred during peat-swamp termination. The Pennsylvanian was a period of glacial-interglacial fluctuations (e.g., Wanless and Shepard 1936; Poulsen et al. 2007; Montañez and Poulsen 2013), most likely occurring on Milankovich temporal scales (Davydov et al. 2010; Eros et al. 2012). Changes in sea level (Heckel 2008), climate (Cecil et al. 2003b; Horton et al. 2012) and atmospheric composition (Montañez 2016; Montañez et al. 2016) occurred in concert with glacial advances and retreats. Such environmental change was strongly reflected in changing plant composition of the tropical landscape (Falcon-Lang 2004; Falcon-Lang et al. 2009; DiMichele 2014). The peat swamp to mudflat transition captures the details of the early phases of this climatic change in great detail.

The shift from a glacial to an interglacial phase during any single cycle was accompanied in the equatorial regions by a shift (potentially rapidly) from everwet (humid/perhumid) to seasonal (subhumid) climate (Cecil et al. 2003b; Horton et al. 2012). One result of this abrupt climate change was a large influx of clastics into the river systems due to a decrease in the density of vegetation throughout the tropics, including on mineral soils. Additionally, a change to seasonal climate during glacial termination meant that the overall swamp ecosystem experienced a shift to more seasonal wetness, perhaps not unlike the swamp conditions of the early Late Pennsylvanian (Phillips and Peppers 1984).

At the larger spatio-temporal scale the climate changes that appear to have occurred across the Middle-Late Pennsylvanian boundary may have been of the same kind that occurred during any of the many late Middle Pennsylvanian deglaciation events, but of greater severity. One or two consecutive, extremely dry, glacial-interglacial transitions could have had devastating effects on species that were dependent on the persistence of patchy wetlands during the dry phases of a cycle. As suggested by Heckel (1991), such extreme conditions would have filtered out the most water-dependent, wetland taxa, thus favoring those species able to tolerate seasonally drier habitats. The enhancement of seasonal drought even during the wetter phases of early Late Pennsylvanian cycles may have allowed plant assemblages previously peripheral to peat-substrate ecosystems to establish in swamplands. Such assemblages, rich in sigillarians, tree ferns, and pteridosperms, then moved into landscapes from which the formerly dominant arborescent lycopsids and associated taxa had been largely eliminated.

ACKNOWLEDGMENTS

We thank the operators of the coal mines in which this study was carried out for permission to examine exposures in their respective mines. In particular, we thank Brad Rigsby, Greg Smith, and Marv Thompson for providing resources, time, and expertise. We extend our gratitude to Tom L. Phillips for sharing his ideas about sigillarian ecology. Author W. DiMichele's participation in this study was facilitated by grant funding from the US National Museum of Natural History. Comments of reviewers Arden Bashforth and Stephen Greb helped improve the manuscript substantially.

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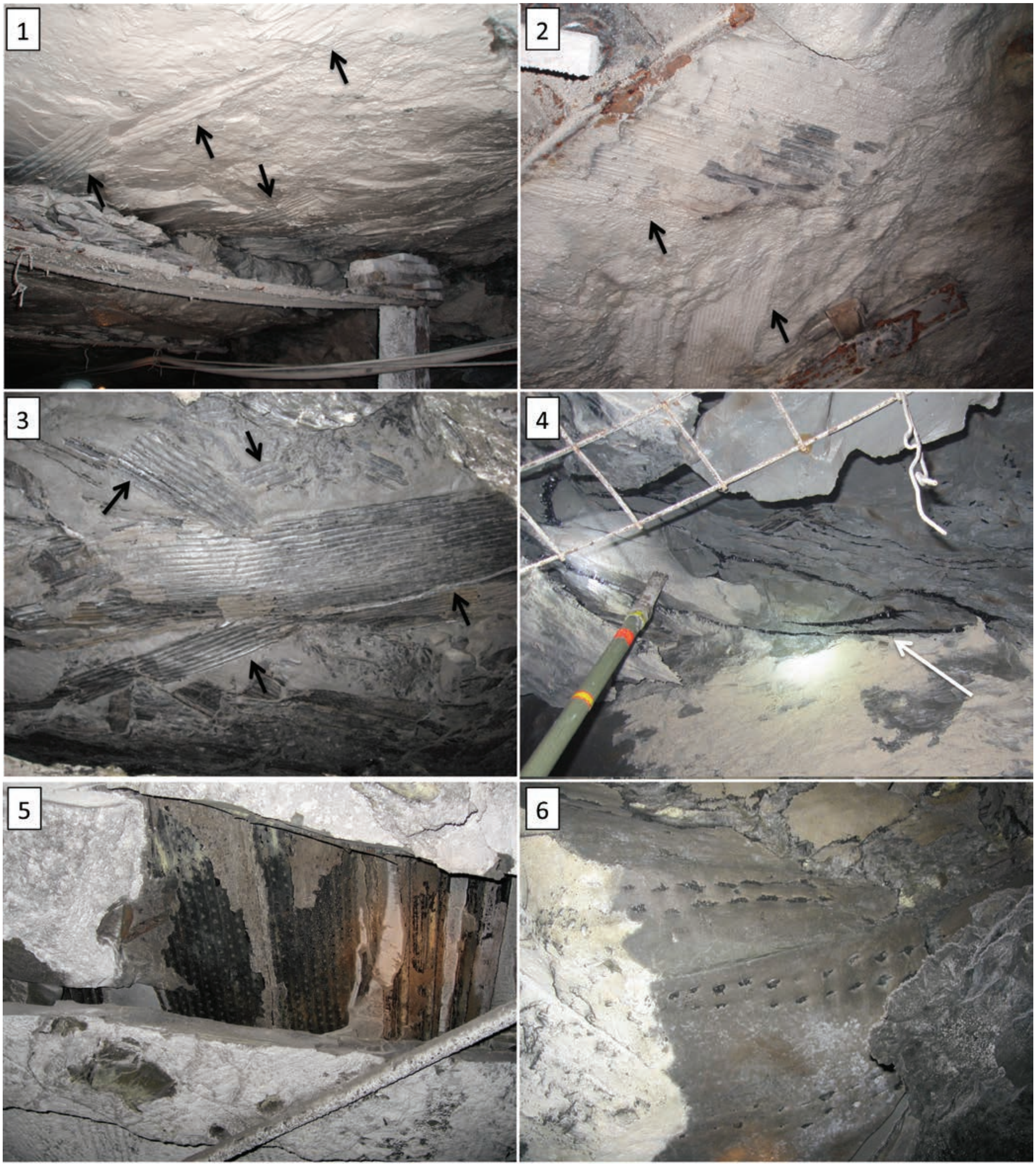

TEXT-FIGURE 9
Sigillaria tree trunks in tidal channels (note: white = finely crushed limestone applied to coal and roof surfaces to suppress coal dust). 1, Base of channel with several vertically ribbed trunks (arrows), post = 6 inches (~15 cm) per side, Danville Coal. 2, Jumble of trunks (arrows), roof bolt = 6 inches (~15 cm) per side, Danville Coal. 3, Jumble of trunks (arrows) and plant debris at channel base, Springfield Coal. 4, Sediment-filled, compacted hollow trunk (arrow) in cross section. wire mesh = 4 inches (~10 cm), Danville Coal. 5, 6, Examples of *Sigillaria* showing characteristic vertically disposed leaf scars (5) and paired 'parichnos' aerating strands (6) exposed when outermost bark has been removed, Danville Coal, pipe in 9.5 = 1-inch (~2.5 cm) diameter. Due to in-mine conditions, scales could not be provided for 9.3 and 9.6.

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