



CATASTROPHICALLY BURIED MIDDLE PENNSYLVANIAN *SIGILLARIA* AND CALAMITEAN SPHENOPSIDS FROM INDIANA, USA: WHAT KIND OF VEGETATION WAS THIS?

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ABSTRACT

A catastrophically buried stand of calamitean sphenopsids and sigillarian lycopsids is reported from the Middle Pennsylvanian of southwestern Indiana, in the Illinois Basin. The plants were exposed in the highwall of a small surface mine and were rooted in a thin bed of coal (peat), thus representing a flooded and buried swamp surface. Coarse, floodborne silts and sands buried the forest to a depth of <3 m or more, before further incursions of water and sediment truncated the deposit. The rocks are part of the Staunton Formation. Taking up >250 linear meters of exposed highwall surface, the vegetation appears to have been a patchwork of calamitean thickets, with stems perhaps as tall as 3–5 m, within which scattered, but much larger, emergent *Sigillaria* trees grew, possibly reaching heights of 10–15 m. No ground cover was observed, nor were foliage or reproductive organs attributable to the dominant plants found. The growth of this vegetation in a peat-forming swamp indicates conditions of high water availability, likely in a humid, high-rainfall climate. This kind of plant assemblage, however, cannot be characterized as a rain forest, given that it consisted of medium-height thickets of horsetails with scattered, emergent, and polelike, giant lycopsids, thus lacking a closed upper canopy and possibly only partially shading the ground.

INTRODUCTION

The deep fossil record preserves numerous examples of vegetation that was buried catastrophically by floods, ash falls, or mudflows, created by storm surges, earthquakes, or volcanic activity. Few such examples have been documented, considering how many are routinely encountered during the course of field work. Most examples from the Pennsylvanian have been uncovered in the course of mining, particularly for coal, and may represent three-dimensional bedding surfaces of varying extent (e.g., Taylor, 1845; Gastaldo, 1985; DiMichele and DeMaris, 1987; Wnuk and Pfefferkorn, 1987; DiMichele and Nelson, 1989; DiMichele et al., 1996, 2007; Gastaldo et al., 2004; Opluštil et al., 2007) or two-dimensional exposures in highwalls (e.g., Gastaldo, 1992). Occasionally natural exposures, such as sea cliffs in Nova Scotia, may also reveal *in situ* forests in two dimensions (e.g., Falcon-Lang, 2006a; see Falcon-Lang and Calder, 2005, for discussion of the work of Sir William Dawson at Joggins).

These sorts of fossil deposits represent what can be described as t_0 assemblages, by which we mean a 10° level of temporal resolution, as close as we can come to a preserved instant from the geological past. Such assemblages tend to be of rather low species richness because they completely lack time averaging (Behrensmeier and Hook, 1992) and include no transported elements; they generally lack even parautochthonous elements that have been slightly transported within or very near the environment of growth, which typically characterize most fossil-plant deposits (Behrensmeier et al., 2000). Consequently, they provide the closest

view in the terrestrial record of the composition and spacing of living vegetation in the deep past. The accumulation of such records is critical to a richer understanding of the ecology of the past and to putting that ecology to use in service of ecological models and theory testing.

The small area reported here is representative of a peculiar kind of vegetation, a low-diversity swamp forest buried by a rapid influx of >2–3 m of waterborne sediment. We use the term forest with caution here. The vegetation was composed of calamitean sphenopsids and giant lycopsid trees of the genus *Sigillaria*. Although the sheer density of the calamiteans may have shaded some parts of the floor of the swamp, they do not represent a subcanopy or understory but formed what might be described as an interstory between more widely scattered sigillarian trees, which, based on reconstructions from various sites, lacked a dense, light-intercepting canopy and were likely emergent through the patchy thickets of calamiteans.

GEOLOGICAL SETTING

The autochthonous fossil deposit described here was found in the now-closed Black Beauty Coal Company's Jenlin Pit of the Miller Creek Mine, Clay County, Indiana, in Section 6, Township 9 North, Range 6 West, on the Clay City U.S. Geological Survey 7.5' Topographic Quadrangle map (Fig. 1).

Three coal beds were exposed in the Jenlin Pit (Figs. 2, 3A); two were >1.5 m thick and targets of a surface mining operation. Between these major beds is a thin, normally bright banded coal, ~20 cm thick, overlying 60 cm of olive-gray, distinctly bedded claystone with bands and nodules of siderite and abundant stigmarian rooting systems of lycopsid trees. The thin coal bed can be seen at the base of the upright *Sigillaria* trunk in Figures 3A and 4A. Above the thin coal bed and in sharp contact with it is ~20 cm of coarsening-upward mudstone with sandstone laminae grading upward into thick, fine-grained, light-gray sandstone, with argillaceous laminae and streaks, irregular bedding, and no sedimentary structures. The sandstone consists of several units, each compositionally similar and each as much as 3 m thick; all except the lower unit exhibit erosional bases (Figs. 2, 3A–B).

The fossil forest remains are entombed in the shale and sandstone overlying the thin coal bed up to a height of ~2–3 m (Fig. 4A, arrows), at which point they are truncated by an erosional scour within the sandstone body (Figs. 2, 3B; the scour surface is marked by arrows in Fig. 3A). Surface mining operations exposed the fossil forest along an L-shaped face ~250 m long (Fig. 1).

These strata are in the lower part of the Indiana Staunton Formation (= upper Tradewater Formation in Illinois; Hutchison, 1956). The Upper Block Coal, which is in the middle of the Indiana Brazil Formation (= lower Tradewater in Illinois), lies about 15 m below this interval (Pepers, 1996). The physical stratigraphic position of these unnamed Staunton Formation coal beds was established by comparison with a Staunton Formation regional marker bed that has a positive gamma ray-density log signature, identifiable in a nearby core drill hole 7.5 m above the upper coal mined in the Jenlin Pit. This unit is a black shale tentatively

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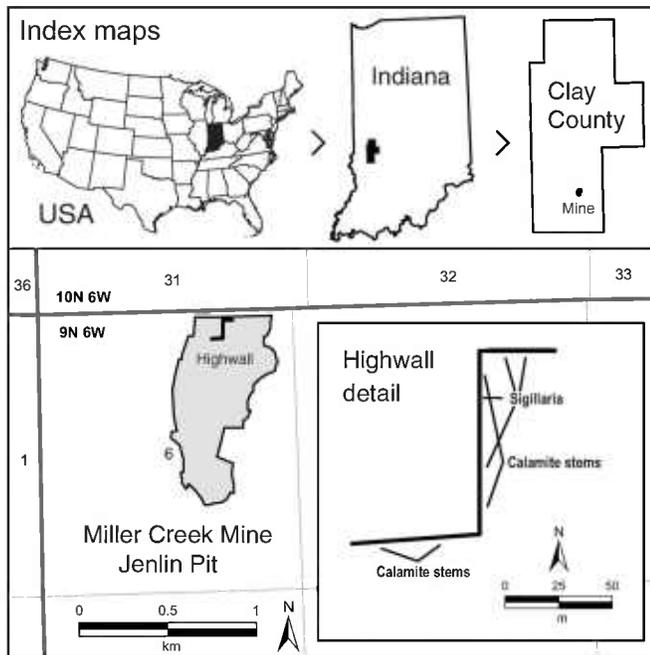


FIGURE 1—Location of study area in southern Clay County, Indiana, United States. Extent of highwall at time of study with positions of various plants indicated.

identified as the Logan Quarry Shale Member of Zangerl and Richardson (1963). The rocks are of Atokan age in North American midcontinent terminology, which is approximately equivalent to the middle Moscovian (early Asturian) in international terminology.

FOSSIL DEPOSIT

The fossil forest is exposed on the highwall above the thin, middle coal bed. *In situ* plant fossils consist exclusively of rare specimens of large trees (five or six) attributable to *Sigillaria* sp. and more abundant specimens with vertically disposed axes (>20) attributable to the calamitean sphenopsids. The location of these plants on the highwall is outlined in Figure 1. The *Sigillaria* trees and some of the calamites could be seen to be rooted in the top of the middle coal bed (Figs. 3A–B). Because of the angles at which the calamites were preserved, however, many could not be followed with certainty to their bases. Consequently, it is possible that some of the calamites were either rooted in the overlying sediments or had regenerated after burial in a manner similar to that described by Gastaldo (1992). Based on the disposition and sizes of those stems that were clearly rooted in the thin coal bed, however, we believe that all the calamites were rooted there.

No dispersed foliage was found in the beds associated with these fossils. This means that no reproductive organs or leaves of either of these genera were found. If, as is likely, the area was flooded shortly before the influx of the clastics in which the stems were buried, it is possible that all such nonstem material either was carried away by water currents or decayed in oxygenated waters.

Sigillaria

Sigillarians belong to an extinct group of plants, the arborescent lycopsids, whose nearest living relative is the diminutive aquatic-to-semiaquatic quillwort, *Isöetes*. This group reached its zenith of diversity and ecological dominance in wetland ecosystems of the late Paleozoic. The plants were large, with many species >30 m in height and stem diameters >1 m at the base, but determinate in growth (Eggert, 1961) and exhibiting several different tree habits (Bateman et al., 1992). *Sigillaria* trees were identified by characteristic external morphology, which is visible on

the trunks all the way to the base. The diagnostic features consist of vertical ribs with paired impressions of parichnos tissue (thought to be aerating strands) disposed on the ribs (Fig. 4B; see Boureau et al., 1967, or Taylor and Taylor, 1993, for references). These features are exposed in some species of *Sigillaria* after minor exfoliation of the external layers of the epidermis. The trunks are preserved such that the basal lobes of their stems, indicating the positions of stigmarian rooting organs, are exposed (Fig. 4A). Trunks taper gradually from a flared base to a straight trunk over a distance of ~1.5 m.

The barely disrupted presence of the features on the outer bark, which are much like the surface features of stems with limited secondary tissue (i.e., periderm) development, suggest that secondary tissues in *Sigillaria* may have formed in synchrony with primary body formation, including primary vascular tissue, very early in stem development and elongation, perhaps in the manner seen in secondary thickening meristems in extant palm trees. Such early ontogenetic development of the wood and bark would have allowed surface features to persist in basal parts of mature plants (Phillips and DiMichele, 1992).

Only one *Sigillaria* trunk is fully exposed (Fig. 4A); three other trunks are partially buried in the box-cut portion of the highwall exposure. These trees are widely spaced, from several to >10 m apart, and all appear to be of the same diameter, ~40 cm. Based on reports in the literature (see discussion below), we estimate that these sigillarians may have been as tall as 10–15 m.

Calamitean Sphenopsids

Calamiteans are identified by the characteristic jointed appearance of their stems, formed by the alternation of distinct internodes with nodes that bear leaves or lateral branches in whorls; this external morphology is typical of the Equisetales in general. At this site they are found in abundance, particularly on one limb of the exposure, unquestionably in association with the sigillarian trunks (Figs. 3B, 5A–B). Many of these stems were tilted during sediment influx and so are rarely exposed in full (Fig. 3B, arrows). They are 7–15 cm in diameter, with variable internodal lengths; some are as closely spaced as 25 mm (Fig. 5B), and others, >100 mm (Fig. 5A). Stem heights of ~1–2 m are seen, and these are truncated by erosion within the deposit in which the stems were buried. Branch scars were not noted. In one instance, it appears that several of the upright stems are converging toward a common base (Fig. 5A), although the actual attachment to a root mass, or to a common prostrate rhizome (stem), is not apparent. The calamitean stems appear to be relatively widely spaced, even if abundantly disposed across the exposure area. In two or three instances it appears as if the base of a calamitean stem was located on a dipping scour surface within the sandstone overlying the thin, middle coal bed; however, this was most likely an artifact of the nature of the exposure and the skewed angle of the calamitean trunks.

Estimating the maximum height of the calamitean stems in the Jenlin deposit is problematic. Spatz et al. (1998) estimated that woody calamite stems could be <3.5 m tall, with a basal stem diameter of ~0.5 m, and Daviero and Lecoustre (2000) estimated heights to be <2.1 m in *Calamites multiramis* stems that were 15 cm in diameter, results that also showed the plant as bearing a small crown of leafy branches. Heights of <10 m have been asserted (e.g., Boureau, 1964; Rößler and Noll, 2006, p. 146), with maximum diameters reported for Permian specimens (Rößler and Noll, 2006; Wang et al., 2006) of <60 cm. Because calamitean foliage was not identified in the litter or trapped in the sediments that buried the deposit, further meaningful identification of these stems is not possible.

DISCUSSION

The Jenlin fossil forest, to the extent that it was preserved and exposed, was a thicket of calamitean aerial stems, possibly a series of clones, given the clumping of some of the stems. The calamites do not appear to have

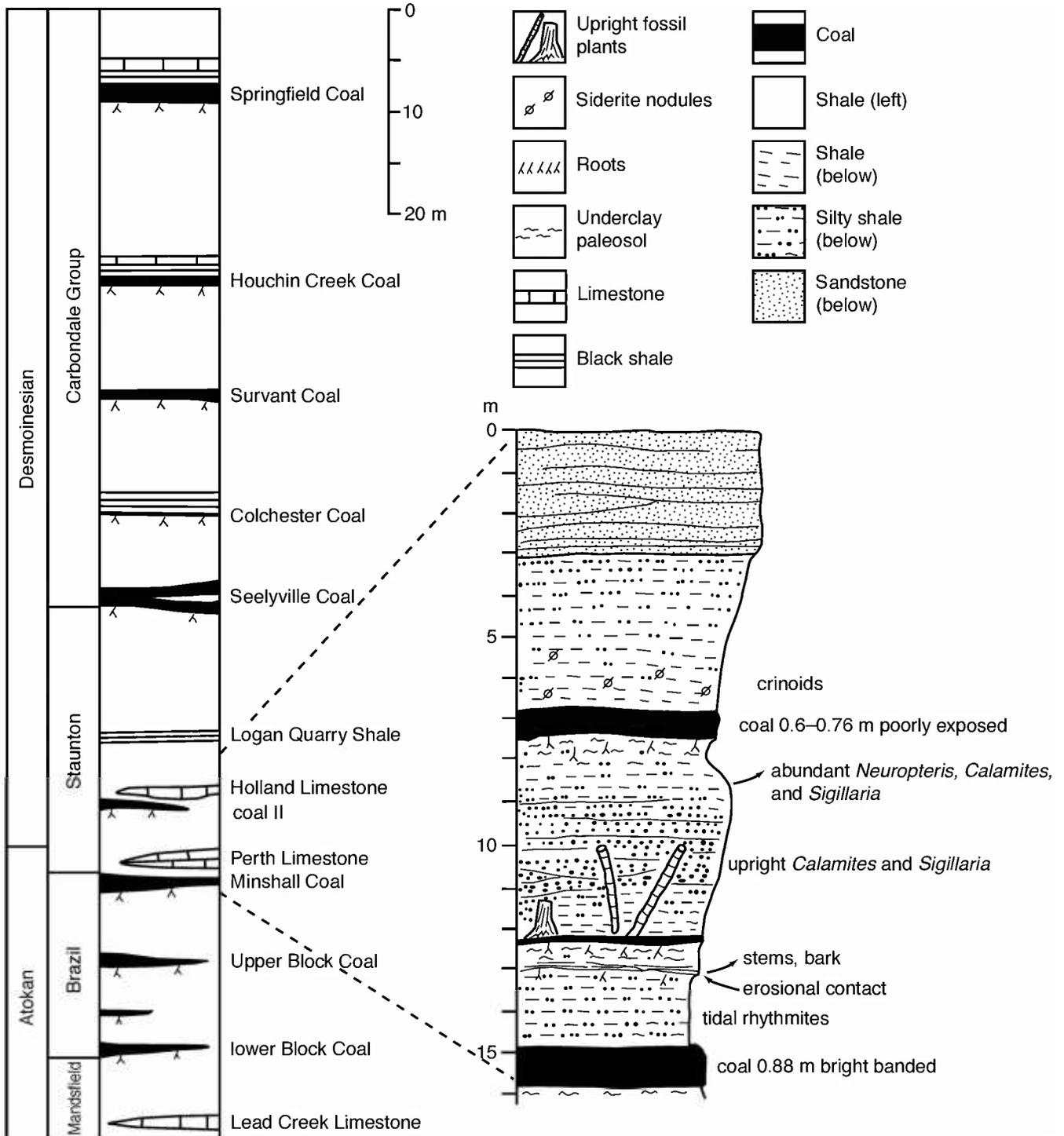


FIGURE 2—Pennsylvanian stratigraphic section in the region of the study site. The general Atokan and Desmoinesian rock column is shown on the left (see text for correlation with international stages). The exposure in the Jenlin Mine is shown on the right, with the position of the fossil forest illustrated by schematic *Sigillaria* and calamite stems.

been uniformly dense over the exposed area, although locally dense areas seem to have been present. Within these patches of calamitean thickets, *Sigillaria* trees of much larger diameters and presumed heights were scattered. Although all sigillarian remains are incompletely preserved, they are interpreted as mature trees based on stem diameters comparable to those found prostrate in mine exposures elsewhere, where trunks often exceed 10 m in length (e.g., Taylor, 1845). This area can be envisioned as a swamp populated by open vegetation consisting of clumps of tall,

but thin (bamboolike) calamitean stems forming variably dense thickets, among which emerged polelike sigillarians with coverings of grasslike leaves, casting little shade. The vegetation is reconstructed in Figure 6. Sigillarians and calamites have been reported to co-occur in other environments, in some circumstances under what appear to be streamside settings in otherwise moisture-limited areas (e.g., Falcon-Lang et al., 2004; Falcon-Lang, 2006b). Such vegetation may indicate conditions of disturbance or physiological stress that restrict access by other species.

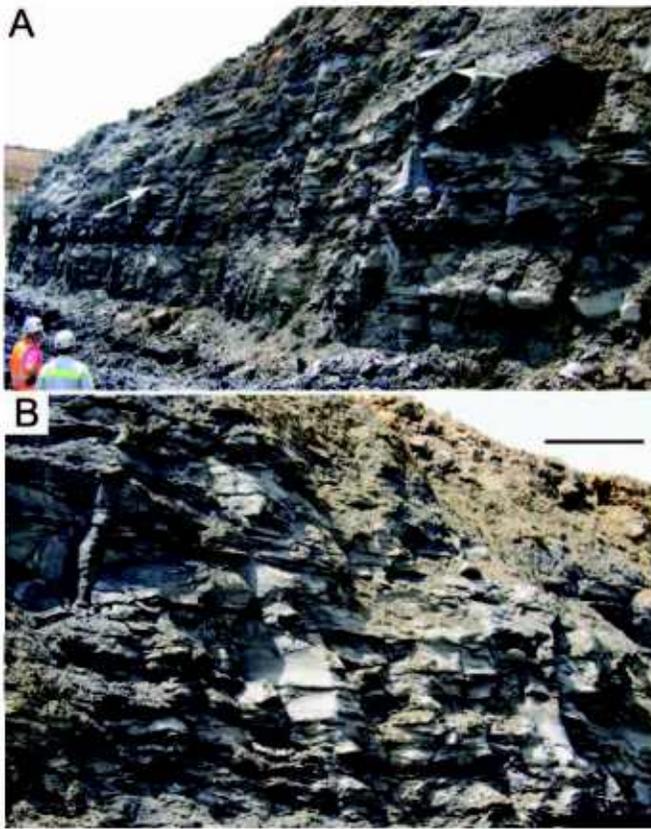


FIGURE 3—Two views from opposite ends of the east-facing highwall exposure in the Jenlin Mine. A) Face viewed from west with stumps of *Sigillaria* (right) and calamitean stems rooted in thin coal bed in center of exposure. Arrows mark bases of scours; left arrow marks the truncated top of the fossiliferous unit. B) Part of face viewed from east with same *Sigillaria* stump as in A (lower right-hand corner) and large calamitean stem at left. Scale = ~1 m, allowing for parallax.

Sigillaria has been reconstructed as a plant with a limited crown consisting of only a few branches (e.g., Grand'Eury, 1877; Hirmer, 1927; Lemoigne, 1961), with those present only at the end of the life of any individual plant. Trees spent nearly all of their lives as unbranched poles, producing cones on small, lateral, peduncle-like branches. *Sigillaria* trunks of very large size have been reported in North American rocks of Pennsylvanian age, including stumps >1.6 m in diameter at the base (e.g., Walters, 1891) and prostrate stems >1.5 m wide and 15 m long, the latter without discernable tapering at either end (Taylor, 1845). *In situ* sigillarian stumps of much smaller size also have been reported, <26 cm in diameter tapering to 18.5 cm over the length of slightly less than a meter (Dawson, 1861). Large stems have been reported from Europe as well (e.g., Hirmer, 1927, and references therein). A peculiar aspect of all these specimens (see Hirmer, 1927, figs. 286–287, for comparison with the photos here) is that the primary features of the outer surface of the stem, including leaf traces, extend all the way to the base of the tree and that the trunks may undergo very little tapering prior to late-stage branching. Both of these observations call into question the timing of the development of the periderm. Such tissue must have developed essentially simultaneously with the primary tissues in order for the external morphology of the stem not to be disturbed. The mechanisms by which these giant lycopsids developed have yet to be elucidated empirically.

Stands of calamitean stems are commonly encountered in the Pennsylvanian fossil record, often in aggradational environments and in dense thickets (e.g., Falcon-Lang, 2006b, who reports such stands in many horizons of alluvial fan deposits); these thickets may occur along bodies of standing water in any kind of background climatic setting, as long as adequate water is available locally. Many species of these plants were

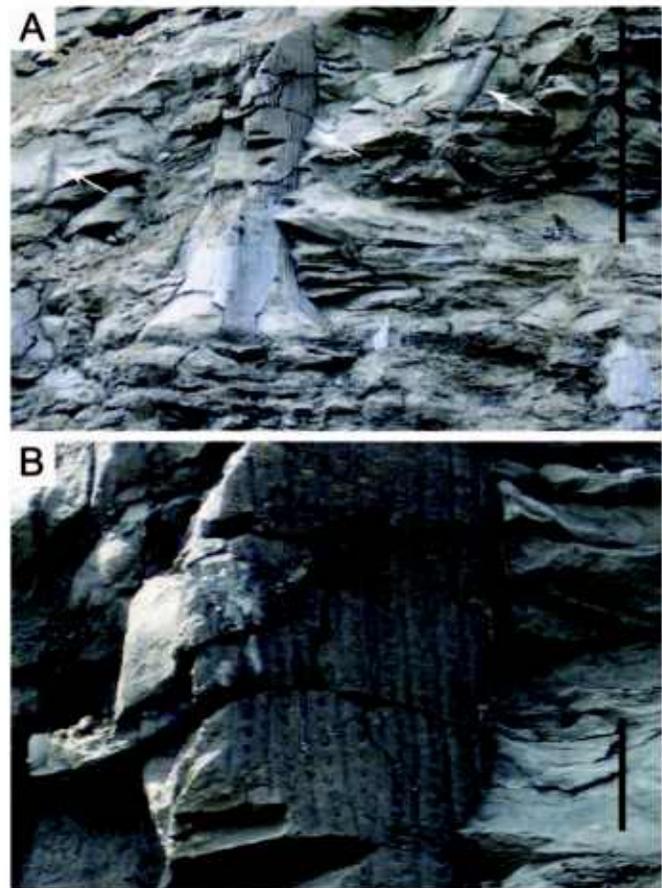


FIGURE 4—*Sigillaria* stump and calamitean stems *in situ*. A) Stump (center) flanked by calamite stems, which are marked by arrows. Note flared stigmarian base of sigillarian. Scale = ~1 m. B) Detail of trunk in Fig. 5A showing vertical rows of parichnos scars. Scale = ~10 cm.

rhizomatous, as those in the Jenlin exposure appear to have been, which permitted them to recover from repeated burial by sediments (Gastaldo, 1992; Falcon-Lang, 2006b).

The habit of calamiteans is open to question. Hirmer (1927) suggested several possible growth habits, of which the one he attributes to *Stylocalamites* (Hirmer, 1927, fig. 496) may be most like that found here—that is, largely unbranched in the lower parts and <5 m tall. Our specimens show no evidence of lateral branching in the lower few meters of the narrow stems (all that is preserved) and in some instances appear to have been clumped, as if the aerial stems arose from a common rhizome. Daviero and Lecoustre (2000) suggest a somewhat smaller plant, ~2 m in height, with a crown of branches when mature, somewhat like a tree fern, and with the branches contributing to mutual support among plants in a dense stand. The various reconstructions, offered both from empirical observations and biomechanical analyses, indicated that the calamites clearly were a diverse group, both in architecture and ecology, and, as others have suggested (e.g., Rößler and Noll, 2006), in need of considerable additional study.

The stems of the Jenlin calamiteans appear to have been of relatively small diameter with, at most, modest amounts of wood to aid in their support. Their small diameters, clear nodal-internodal patterns, and vertical ribbing are typical of what are generally described as pith casts, which are assumed to have formed when the hollow pith area was filled with sediments upon death and burial of the plant, thereby preserving the form of the pith as the external tissues rotted away. We assert here, however, that the Jenlin stems closely approximate the actual diameters of living plants. They were preserved as casts after the buried stems rotted

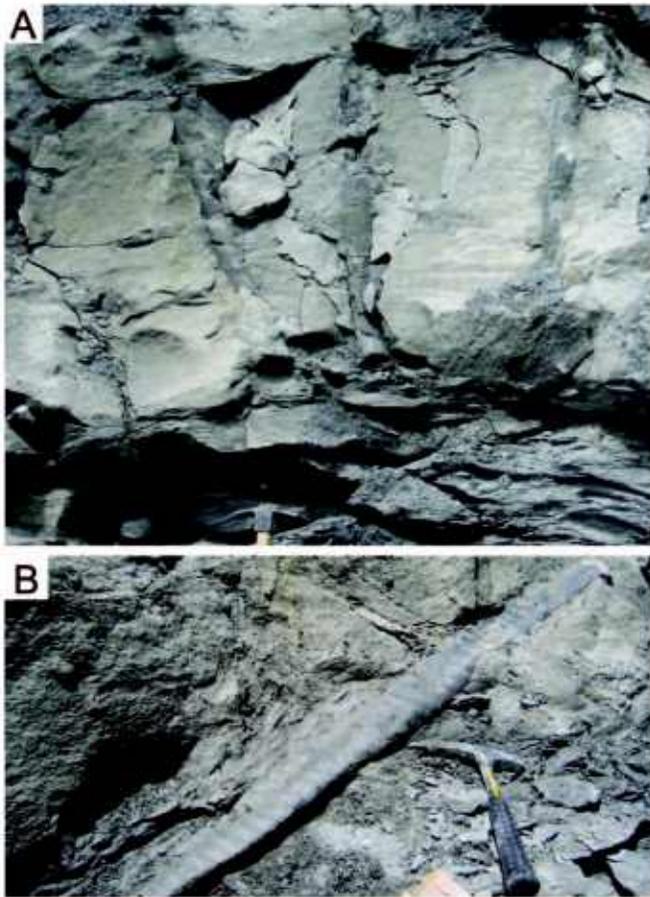


FIGURE 5—Calamitean stems *in situ*. A) Several stems apparently converging toward a common, prostrate stem or rhizome. Head of digging tool is 25 cm. B) Leaning stem with closely spaced nodes. Head of hammer = 19 cm.

from the inside out, preserving the external morphology (as also happened for the buried *Sigillaria* stems). There are several reasons for this conclusion. The axes have a rind of coalified organic matter, indicating that external tissues were preserved. The stems were catastrophically buried, in which case the original entombing sediments would have surrounded the live plants and preserved their original girths. Had the pith been filled with sediment prior to the decay of a large amount of external tissue, a large empty space would have been created in the deposits that would had to have been filled secondarily; the Jenlin specimens show no discontinuities between the edge of the stems and the surrounding sediment, and the original bedding laps up against the stems. Furthermore, in many instances, the Jenlin calamitean stems are very close together spatially, leaving no space for large, woody exterior tissues. Thus, they were more likely to be preserved whole stems instead of pith casts. If secondary xylem were present, it must have been thin, partially or nearly completely rotted, and compressed to coaly material given the external appearance of the specimens on outcrop. It is generally assumed that calamiteans were woody, based on petrifications that can show quite thick stem and root wood (e.g., Andrews and Agashe, 1965; Rößler and Noll, 2006). Compression-impression axes that show node-internode preservation are, thus, assumed to be casts of the pith area of large woody axes. The rapid burial of these Jenlin stems; the preservation of external organic matter; the clear visibility of nodes, internodes, and internodal ribs; and the close physical proximity of axes, however, suggest that structurally they were more like large versions of the modern horsetail, *Equisetum arvense*. They point to the possibility of considerable structural diversity in the calamitean clade.

No ground-cover plants were noted at the bottom of the mudstone in



FIGURE 6—Reconstruction of vegetation during early stages of flooding and burial showing *Sigillaria* emergent through patchy calamitean thickets. Reconstruction by Mary Parrish, Smithsonian Institution.

which the Jenlin vegetation is buried. In the organic shale that constitutes the lower part of the coaly interval, however, fossil plants were found, mostly as highly detrital debris. These included calamitean stems, indeterminate lycopsid stem remains, and isolated pinnules of the pteridosperm *Neuropteris*. Perhaps like modern dense stands of *Equisetum*—the closest living relative of the ancient calamiteans—or bamboo thickets—which have a similar growth aspect—the calamiteans might have been so densely packed together as to choke out all the ground cover and prevent juveniles of larger trees establishing. Thus the only large trees might be those that began their growth before the calamites were established in the area.

Does Vegetation Rich in Lycopsid Trees Have Modern Analogues?

Generalizations about the terrestrial, wetland tropical forests of the Pennsylvanian have been based on a wide variety of sources of data. They often refer back to modern vegetation, however, as the model for interpreting the generally limited areas of autochthonous or, more commonly, parautochthonous fossil assemblages. There is little question that the vegetation of Pennsylvanian tropical peat-forming habitats was subject to high rainfall nearly continuously throughout the year, what Cecil and Dulong (2003) describe as humid or perhumid climates. Peat will not form in tropical regions if there is an extended dry season during which decay will exceed annual accumulation of organic matter (Cecil, 1990).

The term forest, and even the term rain forest (e.g., Falcon-Lang, 2004; DiMichele et al., 2007), has been applied to Pennsylvanian-age peat-forming vegetation. *In situ*, autochthonous assemblages, such as those reported here and elsewhere (e.g., Gastaldo, 1986a; DiMichele and DeMaris, 1987; DiMichele et al., 1996, 2007; Gastaldo et al., 2004), clearly raise questions about the use of these terms. Most of these Early–Middle Pennsylvanian plant assemblages did not have dense, light-attenuating canopies. There is a remarkable amount of variation in this, however. Gastaldo et al. (2004), for example, convincingly showed that an Early Pennsylvanian peat-forming forest could consist of widely spaced, large lycopsid trees, scattered patches of smaller-statured tree ferns, and vast areas of open space filled with dense thickets of low-lying lianas, almost like a wet savannah. In contrast, Wnuk and Pfefferkorn (1984, 1987) documented a blown-down stand of Middle Pennsylvanian trees in which there were many large, mature lycopsids, reaching heights >20 m with an understory of significantly smaller pteridosperms of two types; one type was self supporting and <5 m in height, and the other formed a thicket with individuals <10 m tall. This latter forest may have

been open throughout much of its existence, before crowns appeared on the lycopsids during the final, reproductive phases of their growth (DiMichele and Phillips, 1985; Bateman, 1994). A recently reported, Middle Pennsylvanian assemblage (DiMichele et al., 2007) documents a change across a gradient in substrate moisture, from a variety of large lycopsids emergent through a likely much lower canopy of tree ferns (wetter substrate), into lycopsids within a mixed, low canopy of tree ferns, pteridosperms, calamiteans, and cordaitaleans (less wet). In this vegetation, the uppermost story of lycopsid trees, once again, was too widely spaced to form a closed canopy, although there may have been a lower canopy formed of the tree ferns with an admixture of other species in some areas. In what may be one of the earliest records of an extensive *in situ* fossil forest, Taylor (1845) provides diagrams of a dense accumulation of mixed lycopsid trunks, mainly *Sigillaria*, which are >10 m in length, over an area of 170×2.3 m (391 m^2) from within an underground coal mine in southeastern Pennsylvania. This assemblage included only small numbers of tree ferns and pteridosperms and thus was mainly a forest of large, polelike lycopsids.

Stands of *in situ* lycopsid tree stumps, effectively of a monotypic character, have been recorded over many years (see Gastaldo, 1986a, 1986b, for a historical summary). Recent studies of these assemblages (Gastaldo, 1986a; DiMichele and DeMaris, 1987; DiMichele et al., 1996), some including as many as 800 stumps, indicate that the trees were randomly distributed spatially, effectively not interacting with one another in terms of the controls on their spacing. Such distributions may derive from the growth habits of these trees—that is, the lack of large, spreading, shade-generating canopies for most of the life history of any one tree—and the fact that these trees appear to have favored very wet to mostly flooded habitats with soft substrates, where nutrients would have been available in dissolved form in the water. The question that always arises about these kinds of assemblages is this: Were there any other plants present that were removed by decay before the lycopsid stumps were filled in and buried by clastic sediment? This is why more emphasis has been placed on data from mixed-species assemblages as representative of original vegetation. There is considerable evidence from other sources, however, particularly coal balls (e.g., Phillips and DiMichele, 1981), for stands consisting exclusively or almost exclusively of lycopsids, which supports the data from compression-impression and mold-cast forms of preservation for the existence of large areas covered by nothing but lycopsid trees. Once again, were these forests the way we traditionally characterize forest vegetation? That is to say, Were they composed of large trees forming closed canopies of touching or even interlocking branches? They may have had the appearance of fields of utility poles and allowed enormous amounts of light to reach the ground. These lycopsid trees likely were rapidly growing (e.g., Phillips and DiMichele, 1992), and their height may have reflected, not a design to support a light-intercepting canopy per se, but rather one to facilitate wide dispersal of propagules in ecosystems with high levels of intrinsic disturbance. We conclude this based on the inference from many lines of evidence that those large lycopsids with terminal, determinate crowns spent most of their lives as unbranched poles, the crowns appearing only in the final phases of life (Eggert, 1961; DiMichele and Phillips, 1985; Wnuk and Pfefferkorn, 1987; Bateman, 1994). Furthermore, they produced the majority or all of their reproductive organs in those crowns, located tens of meters above the ground (e.g., DiMichele and Phillips, 1985; Bateman and DiMichele, 1991). Thus, it does not seem likely that their crowns were primarily light-interception devices; rather, height could be closely correlated with the distribution of wind-dispersed reproductive units. This is well documented for pollen and spores (Traverse, 1988, chap. 17), and similar correlations should be expected for wind-dispersed propagules. The seedlike reproductive units of the large lycopsids appear to have been initially wind-dispersed and then further dispersed by flotation (Phillips, 1979; Phillips and DiMichele, 1992).

The Jenlin assemblage appears to have had a strikingly vertical above-ground aspect with limited or no light-intercepting canopy (as occurs in

a modern tropical rain forest). The bulk of the biomass appears to have been in calamitean stems forming dense, if somewhat dispersed, clumps of sticklike, photosynthetic axes. The height of these plants was >3 m, and they likely bore foliage, although direct evidence of lateral branches and leaves is lacking. The *Sigillaria* population, in contrast, consisted of widely dispersed trunks that were ~1 m in diameter at the base at maturity and probably >10 m in height, given what is known of sigillarian stems from other deposits. Like many of the arborescent lycopsids, these trunks appear to have been unbranched until the final phases of growth, with branches heralding the physiological shutdown of the tree and termination of its life (Eggert, 1961). Consequently, the sigillarians can be visualized as widely spaced emergents, towering over the thickets of calamiteans.

What terms should be used to describe these various kinds of vegetation? Retallack (1992) addressed the problem of describing past vegetation types that lack modern analogues, in this case, Devonian floras. The lycopsid-rich vegetation of the Early and Middle Pennsylvanian, in particular, may be seen as equally peculiar when compared to modern kinds of vegetation. With fundamentally polelike vertical construction, a forest like the one preserved at Jenlin, or other kinds of lycopsid- and calamitean-rich forests, might be called pole forests, given that such forms were their dominant aspect, or wetland savannahs, where the pole trees were widely spaced and large areas of ground cover and small clumps of understory intervened (e.g., Gastaldo et al., 2004).

Burial and Preservation

This small patch of forest preserved in the Jenlin pit was buried rapidly by waterborne sediment, accounting for the upright posture and excellent preservation of the plants. The matter for consideration in this case is one of accommodation space for the sediments—where did such space come from? The plants are buried in ~3 m of sediment that lacks fine sedimentary structures and appears to have only a few large trough or scour surfaces, suggesting rapid emplacement beneath water level (Rubin, 1987). This deposit was then subjected to further scour. Thus, it is not likely that compaction of the peat bed on which the forest was growing alone could have accounted for the necessary space; peat compaction ratios are subject to some debate, and estimates vary from as low as 2:1 (Nadon, 1998) to more than 20:1 (Winston, 1986). A considerable difference in water table and sedimentary conditions is indicated by a peat bed—which can be flooded, but not more deeply or for a longer period than vegetation can tolerate—versus coarse clastic material, which will accumulate in moving water at least as deep as the deposit itself. Consequently, we suggest that rapid change in base level took place, accompanying climate changes from nearly year-round wetness to wet-dry seasonality. This was expressed locally by transgression of shallow seas into this coastal habitat through local drainages, resulted in drowning of the forest accompanied by building of sediment into the drowned area.

Climate and sediment transport models (e.g., Cecil, 1990; Cecil and Dulong, 2003) suggest that peat formation is fundamentally a high rainfall rather than a groundwater-table phenomenon. Furthermore, during periods of high rainfall, sediment movement is considerably inhibited by plant rooting in and stabilization of clastic soils. Sea-level rise, probably accompanying glacial melting (the Pennsylvanian was an interval of polar glaciations; see Gastaldo et al., 1996; Falcon-Lang, 2004), is coincident with the development of rainfall seasonality in tropical areas, which reduces plant cover and enhances the movement of clastic sediment (see Cecil et al., 2003, for an example and application in Pennsylvanian rocks). It is plausible that the Jenlin forest may have been drowned and could have persisted in standing water for some time prior to burial by sediment. The initial input of finer-grained material, followed by coarser sediment, is consistent with such a model, even if not definitive. The sediment documents initial burial in a wedge of increasingly coarse and

high-energy siltstone and sandstone, followed by scours and more sandstone deposition. Such sedimentation suggests deposition in a high constructive environment, perhaps a deltaic setting, built out into a flooded coastal area.

In summary, this area was steadily sinking as a result of regional basin subsidence. A eustatic rise of sea level inundated the peat swamp. Although some of the plants could tolerate standing water, peat formation was greatly diminished. With a change from an ever-wet environment to a seasonally dry climate, runoff and sediment load into the area increased. A small delta prograded into the area (with sediments coarsening upward), burying and compacting the peat and underlying organic-rich clays, further deepening the water and making room for more sediment. Thus the trees were encased in mud <2 m deep within a few years at most, and the entire 4–5-meter-thick deposit was laid down in not much more time, perhaps considerably less. The trees died, and their upper portions, or what remained of them, were removed by further scouring.

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