A drowned lycopsid forest above the Mahoning coal (Conemaugh Group, Upper Pennsylvanian) in eastern Ohio, U.S.A.

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Abstract

Over 800 mud-filled casts of upright lycopsid tree stumps have been documented immediately above the Mahoning coal in an active underground mine located in northwestern Jefferson County, Ohio. The coal body originated as a pod-shaped peat body of ~ 60 km². Trees are rooted at several levels within a thin (15–40 cm) bone coal directly above the banded coal; they extend upward up to 15 cm into overlying, flat-bedded, carbonaceous mudstones that coarsen up. From a maximum basal diameter of 1.2 m, stumps taper upward to diameters no less than 0.3 m. Within single-entry transects, < 6 m wide that total 2585 m in length, stumps are randomly distributed. The trees are identified as lepidodendrids on the basis of gross morphology, external stem patterns, and attached stigmarian root systems, and provisionally as Lepidophloios or Lepidodendron by associated palynology of the enclosing matrix. Palynological analyses of incremental seam samples indicate an initial dominance of lycopsid spores with lepidodendracean affinities (Lycospora granulata from Lepidophloios hallii), replaced upwards by tree-fern spores, with a reoccurrence of lepidodendracean spores in the upper benches; spores of Sigillaria (Crassispora) are abundant only at the base of the coal. Petrographic analyses indicate a parallel trend from vitrinite-rich to inertinite- and liptinite-rich upward in the coal body. All data indicate that the peat represented by the Mahoning coal was drowned slowly. During the earliest stages of inundation, a lycopsid forest was re-established, only to be subsequently drowned.

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1. Introduction

Forest ecosystems have existed in the tropics since the Late Devonian, when a tree habit first evolved in woody progymnosperms and lycopsids. During the Carboniferous, a greater variety of forest types emerged as dominant tree forms diversified taxonomically and segregated ecologically (DiMichele and Hook, 1992). Among the most common forests of the Pennsylvanian were those dominated by arboreous lycopsids, which are particularly well known from coal-bearing rocks in North America and Europe. Although recognition of such "fossil forests" extends back to the early 1800s (Gastaldo, 1986a), the number of trees reported within any one deposit generally has been few, and documentation of their areal distribution limited.

The 1992 discovery of upright lycopsid tree stumps in the roof of the Sterling Mine, a newly opened drift mine in the Mahoning coal (Conemaugh Group, Upper Pennsylvanian Series) of northwestern Jefferson County, Ohio, provided an opportunity to map the distribution of many trees over a considerable area. Because tree stumps often contribute to major roof-control problems in underground mines, stump locations were mapped initially in the main entries to determine their size and abundance. As the mine advanced, tree stumps proved to be ubiquitous in all headings. Stumps also were observed in abandoned entries south of the present mine and in photographs of old works to the west, both in the same coal body. We here present four mapping transects that recorded 814 tree stumps, as well as palynological, petrographic and geochemical analyses of the coal, the geology of the coal and immediately adjacent rocks, and the paleoecological implications of these data.

Our understanding of the biology, taxonomy, and ecology of Pennsylvanian lycopsids has increased substantially over the past 20 years. For the most part, these plants were confined to nutrient poor, frequently disturbed, swampy habitats (Phillips and DiMichele, 1992). Tropical wet lowlands of the time were populated by several genera of trees (Diaphorodendron, Lepidodendron, Lepidophloios, Sigillaria, among numerous others) that overlapped minimally within areas of peat accumulation, but shared opportunistic or colonizing life-histories (Phillips and Peppers, 1984). Some taxa (Lepidophloios, Lepidodendron, Synchysidendron) were monocarpic, with reproduction confined to the final stage of tree life (DiMichele and Phillips, 1985), and some reproductive strategies are known to have involved water dispersal (Phillips, 1979). The biologies of virtually all of these Carboniferous lycopsids suggest short-lived forests with limited local recruitment. Certain taxa (e.g., Lepidodendron, some species of Diaphorodendron and Synchysidendron) flourished in near-channel settings that were subjected to frequent sediment influx or burial, and consequently are dominant elements in compression-impression assemblages (DiMichele and Phillips, 1994); others (e.g., Lepidophloios) are found less commonly as compressions but dominate many coal-ball assemblages, suggesting centers of distribution on peat or organic-rich muds.

The remarkable number of upright lycopsid occurrences in the Pennsylvanian of North America and Upper Carboniferous of Europe was made possible by the peculiar morphology of lycopsid-tree architecture, which allowed wholesale fossilization. These trees were supported by a thick rind of water-resistant bark; woody tissues were limited to a small central cylinder of little structural integrity. Following inundation and death,
the soft parenchymous tissues of the main trunk rotted, leaving a hollow defined by the still-intact bark. Sediment-laden waters infilled the resulting cylinder either by overflowing its edges after emergent portions fell or by infiltrating longitudinal fissures in the bark (Rex, 1985; Gastaldo, 1986b; DiMichele and DeMaris, 1987; Gastaldo et al., 1989).

Lycopsids are known to have dominated tropical wetland environments of Euramerica throughout the Westphalian (Phillips et al., 1985). At approximately the Westphalian–Stephanian boundary, however, most lycopsid tree genera became extinct in areas of North America west of the modern Appalachian Mountain chain. Palynologic data show that in the Appalachians, and more specifically within our study area of northeastern Ohio (Phillips et al., 1985; Kosanke, 1988), the Mahoning coal is the youngest mineable coal known to be dominated or co-dominated by lycopsids.

2. Location and geologic setting

The Sterling Mine is located on the southeastern side of a ~60-km² deposit of southeastwardly dipping Mahoning coal that is centered at the junction of Jefferson, Columbiana, and Carroll Counties, Ohio (Caudill and Slucher, 1990) (Fig. 1). Drift entries were opened in the northern portion of this deposit during the 1870s, and surface mines have operated in the area since the 1940s. Underground mining proceeded southward until 1961, when the Sterling Coal Company closed its large underground mine in the face of increased operating costs. The remaining southern reserve has been developed by the East Fairfield Coal Company, which organized the Sterling Mining Corporation in 1991.

The Mahoning coal is the lowermost mineable coal in the Upper Pennsylvanian Conemaugh Group (Fig. 2). Within the Appalachian coalfield, other significant deposits of mineable Mahoning coal are restricted to northeastern Ohio, mainly Columbiana County, and very small adjoining areas of Pennsylvania, West Virginia, and Maryland. The upper Allegheny and lower Conemaugh rocks of this region are interpreted to have been deposited by a large, northwestwardly prograding, fluvial–deltaic system (Ferm and Cavaroc, 1969; Ferm, 1970; Donaldson, 1974).

3. Methods and materials

"Kettlebottom" is a term used by miners for a sediment-filled cast of a tree stump that is exposed underground at or near the contact of the coal bed and overlying roof rock. Depending on burial conditions, such trees may extend upward for a few centimeters or for many meters into the overlying clastic rocks (Gastaldo, 1986a; DiMichele and DeMaris, 1987; Scott and Calder, 1994). Kettlebottoms usually are defined by a thin (< 1 cm) rind of vitrinized material that represents the coalified outer bark of the original tree. The contact between the vitrinized rind and host mudrocks
Fig. 1. Mahoning coal body of Jefferson, Carroll, and Columbiana Counties, Ohio, and location of the Sterling Mine. Extent of abandoned underground mines based upon mine maps (Ohio Geological Survey open files). Modified from map supplied by T.R. Miller and R.W. Hook.

Fig. 2. Regional stratigraphy of northern Appalachian Basin and comparison with North American midcontinent and European terminology.
usually is slickensided to a glassy, mirror-like surface. Because of the natural flaring at the base of a tree, kettlebottoms have a distinctive, downward-opening, bell shape, which is accentuated in more highly compactible mudstones. The Sterling kettlebottoms occur in a bone coal that directly overlies the bright-banded Mahoning coal. Bone coal is a widely used term applied to an impure non-banded bituminous coal that breaks with a splintery fracture, like that of a fractured limb bone. Bone coals commonly grade both vertically and laterally into organic-rich mudstones.

3.1. Measurement of tree stumps

The locations, diameters, and, in some cases, vertical extent of kettlebottoms within parts of the Sterling Mine were recorded on four separate transects (Fig. 3). In each transect, an intersection of a specific entry (an opening that leads into the coal body) and crosscut (an opening that links parallel entries) was established as an origin; these points were plotted later on 1:600-scale and 1:2400-scale mine maps. Because variations in
entry and crosscut dimensions are not depicted accurately on the mine maps, the
distance between successive crosscuts within each transect was measured in-mine so as
to minimize compound error. Kettlebottoms were recorded within entry segments
bounded by successive cross-cuts: X- and Y-coordinates for each kettlebottom were
determined by tape-measured distance down the entry from the corner and by distance
perpendicular to the side of the entry. These data were transferred subsequently to a grid
system, as well as to the 1:600-scale mine maps.

Data from all four transects were combined into a composite transect for statistical
analysis of tree-stump distribution. Although entry widths varied somewhat, a standard
width of 5.5 m was imposed when locations were transferred to a map grid; therefore,
the number of kettlebottoms used in calculations reliant on transect area is slightly less
than the total number observed in-mine. Distribution patterns were evaluated by two
techniques. In the first, adapted from Hayek and Buzas (1996), the composite transect
was subdivided four times, each time using quadrats of different length: 3, 6.1, 9.1, and
12.2 m. Means and variances of stump occurrences for each of the quadrat lengths were
plotted, with the means on the abscissa and the variances on the ordinate. In the second
statistical analysis, adapted from Haining (1993), the number of stumps per 3-m quadrat
and the average number of stumps in the two adjacent 3-m quadrats were recorded.
Quadrats then were grouped according to the number of stumps they contained (0–5
stumps per quadrat), and for each group the mean number of stumps in adjacent quadrats
was determined. Further statistical analyses are described with results.

Several factors influenced measurement of stump diameters. Because of the grada-
tional contact between the bright-banded coal and overlying, stump-bearing bone coal,
the bone-coal roof had been removed over short distances (< 3.5 m) by the continuous
miner in parts of each transect. This decreased the completeness, basal diameters, and
possibly the frequency of observed stumps. Maximum diameters also could not be
determined in cases where a kettlebottom was exposed partially at the side of an entry
adjacent to a coal pillar. In most cases, however, maximum and minimum trunk
diameters were measured at the basal-most exposed edge. If stigmarian-root lobes were
preserved, these were not included in diameter measurements, although dimensions
including root lobes were noted. The vertical extent and basal and uppermost diameters
were measured for a few "hollow" stumps, the infillings of which had been pried-down
by roof-bolting crews. An even smaller number of prostrate trunks were observed and
measured, none of which could be associated with a particular upright stump.

In addition to tree stumps, other plant remains were sought in the Sterling Mine. No
identifiable compression fossils were found during examination of considerable amounts
of roof rock that had either fallen or had been dropped intentionally for belt entries.

3.2. Palynological and petrographic methods

In order to examine the relationship between plants of the peat body represented by
the Mahoning coal and the tree stumps themselves, incremental coal and roof samples
were analyzed palynologically. Four columns of coal were collected (Fig. 3) in
increments using natural breaks, such as megascopic changes or fusain partings or
bands. In the laboratory, coal samples first were crushed to -1 mm size (-18 mesh)
and then riffled to obtain a representative sample of ~ 50 g. From this, 5 g were removed for maceration. To isolate spores and pollen, samples were oxidized in Schulze’s solution (KMnO₄ + HNO₃), digested in 5% KOH, screened at ~60 mesh to remove coarse material, and concentrated in an acidified, concentrated solution of ZnCl₂. Two hundred and fifty spores and pollen were counted to determine the relative percent of taxa in each sample. Spore affinities are based on reports by Ravn (1986) and Eble (1988). Strew-mounted slides, prepared using Crystal Mount (a water-soluble adhesive) and Permount are stored at the Kentucky Geological Survey, and the Department of Paleobiology, National Museum of Natural History.

Ash yields were determined using a Leco Mac 400 automated proximate analyzer. Ashing was done at 750°C in an oxygen-enriched environment. Total sulfur contents were determined using a Leco SC-132 sulfur/carbon analyzer. Ash and sulfur values are reported on a dry basis.

Coal petrographic analyses were carried out for each incremental coal sample. Particulate pellets were prepared using 5–7 g of 1 mm coal, and maceral percentages are based on a count of 500 points in incident light (ISO, 1984). All samples were etched in an acidified potassium permanganate (KMnO₄) solution prior to microscopical analysis to make macerals of the vitrinite group more discernable (Mackowsky, 1974). Vitrinite macerals represent coalified stem and root tissues (mainly wood and bark), and may be subdivided into a number of types of "structured" and "unstructured" varieties, depending on the degree of cellular preservation. Telinite and telocollinite represent large (generally > 50 μm) pieces of structured vitrinite; vitrodetrinite, gelocollinite, and desmocollinite (gelocollinite and vitrodetrinite undifferentiated) are unstructured vitrinites indicative of elevated levels of biodegradation. Liptinite macerals represent hydrogen-rich plant parts, such as spores and pollen, cuticles, and resins. Inertinite macerals represent previtrinite plant components that were oxidized by either fire or the activities of microorganisms; fusinite and semifusinite are the most common of the inertinites.

4. Results

4.1. Characteristics of the coal body and overlying rock interval

The Sterling Mine is located in a pod-shaped body of Mahoning coal that ranges in thicknesses from 0 to 1.42 m (Fig. 1). Throughout the areas of the Sterling Mine examined in this study a clastic-rich bone coal up to 25 cm thick is present at the top of the coal bed. Thin (< 1 cm thick) fusain bands occur locally within the bone coal. The bone coal grades upward to carbonaceous mudstone. These mudstones show no evidence of bioturbation, either in the form of rooting or burrows, and coarsen-upward into fine-grained sandstones. Gray to light-gray, rooted mudstones, some of which are mottled red or red-green, are developed above the tabular sand deposits. On the Sterling property, the erratic Brush Creek coal and accompanying marine zone occur 16–24 m above the Mahoning coal.
4.2. Spatial and dimensional data on stump occurrences

A total of 814 stumps occur within the transects, which total 2585.2 m in length. At the standard width of 5.5 m, the area of the composite transect is 1.42 ha. Both analyses of stump occurrences indicate a random distribution. The plot of mean and variance of stump distributions within quadrats 3, 6.1, 9.1, and 12.2 m in length (Fig. 4; Table 1) deviated slightly from a line described by the power function $y = ax^b$. Determination of the values of $a$ and $b$ was simplified by log transformation of the data, which converted the curve to a straight line described by the equation $y = a + bx$ (Hayek and Buzas, 1996). In this method, if kettlebottoms were randomly distributed, the mean and variance of stump occurrences would be equal at all quadrat sizes, resulting in a line with slope of 1. If stumps were ordered in distribution, as in an orchard, variance would change little as quadrat size varied, resulting in a line of low slope (in the extreme, for any given quadrat size, the number of stumps per quadrat would be expected to be about the same, resulting in low variance). If stumps were clumped, variance in stump number

Table 1
Summary statistics for repeated quadrat analysis of average stump number per quadrat in subset of transect area of the Sterling Mine

<table>
<thead>
<tr>
<th>Quadrat size (m X m)</th>
<th>Total stumps</th>
<th>(stumps per quadrat)</th>
<th>Mean</th>
<th>Variance</th>
<th>Standard deviation</th>
<th>Coefficient of variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>3 X 5.5</td>
<td>445</td>
<td></td>
<td>1.15</td>
<td>1.46</td>
<td>1.21</td>
<td>0.83</td>
</tr>
<tr>
<td>6 X 5.5</td>
<td>445</td>
<td></td>
<td>2.30</td>
<td>3.31</td>
<td>1.82</td>
<td>0.55</td>
</tr>
<tr>
<td>9 X 5.5</td>
<td>445</td>
<td></td>
<td>3.45</td>
<td>5.27</td>
<td>2.30</td>
<td>0.44</td>
</tr>
<tr>
<td>12 X 5.5</td>
<td>445</td>
<td></td>
<td>4.59</td>
<td>7.25</td>
<td>2.69</td>
<td>0.37</td>
</tr>
</tbody>
</table>
Table 2
Total number of stumps in a given quadrat of the 3-m length class vs. the average number of stumps in the two adjacent quadrats in the transect

<table>
<thead>
<tr>
<th>Average number of stumps in two adjacent quadrats</th>
<th>Number of stumps in sample quadrat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td>---------------------</td>
<td>-----</td>
</tr>
<tr>
<td>0</td>
<td>36</td>
</tr>
<tr>
<td>0.5</td>
<td>27</td>
</tr>
<tr>
<td>1</td>
<td>38</td>
</tr>
<tr>
<td>1.5</td>
<td>27</td>
</tr>
<tr>
<td>2</td>
<td>15</td>
</tr>
<tr>
<td>2.5</td>
<td>14</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>3.5</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>4.5</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total sample quadrats</strong></td>
<td><strong>159</strong></td>
</tr>
</tbody>
</table>

Average number of stumps in adjacent quadrat pair

|                     | 1.02 | 1.1  | 1.4  | 1.25 | 1.26 | 0.9 |

See text for explanation 3 m × 5.5 m quadrats.

would change more rapidly than the mean as quadrat size changed, resulting in a line of high slope (as quadrat size increased fewer quadrats would encompass most of the stumps in a clump, whereas other quadrats would have few or no trees, resulting in increasing variance). By means of the computer software program Mathematica, an equation was determined for the line described by these points (Fig. 4):

\[ y = 0.22 + 1.16x \]

For log-transformed data, 1.16 is the slope, which is equivalent to the exponent of the function that describes a power curve fit to the raw data before log transformation. This line shows that change in the relationship between mean and variance remains approximately proportional as the quadrat size changed. Allowing for the displaced y-intercept, the data essentially describe a 1:1 line, which supports the inference of a random distribution.

Another way of examining these data is presented in Table 2; for each of the 3-m quadrats, number of stumps per quadrat is plotted against average number of stumps in the two adjacent 3-m quadrats. Note that the largest group of quadrats had no stumps with frequency decreasing to only three quadrats with five stumps. The number of stumps in adjacent quadrats does not show any relationship to number of stumps in the target quadrat, indicating a random spatial distribution.

Basal diameters were measured for 662 kettlebottoms. The average minimum diameter was 72.4 cm. Trunk diameters measured several centimeters above the flared bases indicated a rapid tapering just above the roots. Based upon measurements of 17 hollow stumps and prostrate trunks, average stem diameter above the basal flare was 60.2 cm (lycopside trunks were pole-like and diminished only slightly in diameter along the
vertical extent of the trunk, prior to crown branching). Although these average diameters differ, their relative similarity confirms our observation that the upper few centimeters of roof had been cut in some cases, thereby lessening the effect of basal flaring. Flared bases of enormous diameters, some exceeding 120 cm, occur in the western half of the Sterling mine, towards the center of the coal body itself, but have not been mapped.

From transect data, the number of stumps per hectare is 573.2. Minimum tree basal area was 163.8 m²/ha, and maximum basal area was 235 m²/ha. These numbers are based upon the mean estimates of the minimum and maximum stump diameter multiplied by the number of stumps per hectare (minimum estimate from horizontal trunks and stump subset that permitted measurement above the flared base; maximum estimate from basal-most measurements of all stumps).

4.3. Palynology, geochemistry, and petrography of the Mahoning coal bed

Palynofloras recovered from the Mahoning coal bed are typical of upper Middle and lower Upper Pennsylvanian coals of the Appalachian Basin (Fig. 5; Appendix A). These coals correlate approximately with the late Westphalian D of European stratigraphy (Phillips et al., 1985). Collectively, arborescent lycopsid spores (mainly *Lycospora*) are most abundant in the lower benches of the main coal body, and decrease upward to the top of the bed, where they are replaced by tree-fern spores. In three of the four profiles, lycopsid spores increase again in the uppermost coal samples and in the bone coal. The dominant lycopsid spore is *Lycospora granulata* (from *Lepidophloios hallii*); other common *Lycospora* species include *L. pusilla* (from *Lepidodendron hickii*), *L. pellicida* (from *Lepidophloios harcourtii*), *L. micropapillata* and *L. orbicula* (from *Paralycopodites brevifolius*). *Granisporites medius* (from *Diaphorodendron* and *Synchysidendron*) and *Crassispora kosankei* (from *Sigillaria*) also are present, the latter being most abundant in samples of a thin “leader” bench of ash-rich coal that underlies the main bench and in basal parts of the main coal body. The minor increase in lycopsid spores in the top of the coal bed and in the bone coal is composed almost entirely of *Lycospora* species, especially *Lycospora granulata* produced by members of the Lepidodendraceae (*Lepidophloios* and *Lepidodendron*).

Tree-fern spores are both abundant and diverse. “Thin-walled” forms are represented by *Punctatisporites minutus*, *Punctatosporites rotundus*, *Apiculatisporites saetiger*, *Laevigatosporites minutus*, and *Spinatosporites exigus*. “Thick-walled” forms are represented by *Laevigatosporites globosus* and *Punctatosporites granifer*. *Thymospora pseudothiessenii* also is present. Thin-walled species are the most common tree-fern spores in the leader samples and in the benches of the main coal body. Thick-walled spores increase in abundance towards the top of the bed and dominate the bone-coal samples. Small-fern spores are present but are minor in occurrence (< 1%).

Spores and pollen of other plant groups, especially calamites (*Calamospora*, *Laevigatosporites minor*, and *L. vulgaris*) and cordaites (*Florinites*), are present in minor amounts throughout the seam profiles.

The Mahoning coal bed can be divided into three geochemical zones (Appendix A). A lowermost “leader” zone contains moderate ash (avg. 17.3%) and high sulfur (avg. 3%); this zone is not present everywhere in the mine and varies from 12.5 to 27 cm
Fig. 5. Palynological composition of coal columns 1–4; see mine map for locations. For detailed composition see Appendix A.
thick where sampled. The main coal bed averages 96.2 cm where sampled and averages 8.1% ash and 2.2% sulfur. The uppermost bone coal varied from 10 to 25 cm within the mapping transects and averages 46.9% ash and 2.4% sulfur (see Appendix A).

Petrographic trends in all four columns of coal are essentially the same (Fig. 6). Benches in the bottom and middle parts of the main coal bed typically contain high percentages of vitrinite, especially structured vitrinites (telinite and telocollinite). High-ash leader coals and thin basal benches of the main coal body (e.g., samples 2413, 2415 in column 4), where present, contain decreased percentages of vitrinite and higher percentages of liptinite and inertinite. The proportion of desmocollinite, relative to telinite and telocollinite, is higher in these layers as well. Upper parts of the main coal bed, in contrast to the lower and middle portions of the bed, contain much higher amounts of liptinite and inertinite macerals, and a higher proportion of desmocollinite relative to telinite and telocollinite. In column 4, these benches contain high total sulfur, much of which appears as pyrite infilling of cellular or structural voids in the inertinite.

4.4. Identity of the tree stumps

Megascopic data on the taxonomic identity of the kettlebottoms are meager and equivocal. Although stumps were identified as lycopsids on the basis of size, flared bases with stigmarian axes or the four lobes typical of stigmarian systems, vitrinized rinds, and irregular, vertically fissured external surfaces, external leaf cushions or other features characteristic of specific lycopsid taxa were lacking in all cases. Rarely exposed prostrate trunks usually had the deep, irregular, longitudinal fissures typical of large, "decorticated" lycopsid stems.

Palynological data provide the strongest evidence for identity of the trees. Spores of the Lepidodendraceae are the most abundant lycopsid spores in the top bench of the coal and in the bone, indicative of Lepidophloios, Lepidodendron, or both as the source; spores of other lycopsid genera are virtually absent in these upper layers. Tree-fern spores are the dominant elements in the upper bench of the coal and bone coal, but no tree-fern macrofossils were recognized in any part of the mine examined in this study.

4.5. Taphonomy of the stump-bearing interval

Stumps intersected by pillars at the side of an entry indicate that trees are rooted within an interval that ranges from the top of the coal to ~ 18 cm higher in the bone coal. Because such examples are few, it is not possible to determine if this variation is related to the thickness of the bright coal or the bone coal, or if there are any patterns spatially or topographically within the mine. Nonetheless, only fifteen examples of stigmarian axes or lobed stigmarian bases were identified in clastic roof rock. Unequivocal examples of trees rooted at the coal–bone interface, combined with the fact mentioned previously that the expanded basal portion of numerous stumps within the bone coal had been cut during mining, indicate that most of the lycopsid forest was rooted in peat and originated just before or during the earliest phase of inundation.

Aerial parts of lycopsid trees, including trunks, leaves, and reproductive organs borne in the tree crowns are extremely rare as compression fossils in the bone coal and
immediately overlying mudstones. No prostrate trunks can be associated with an in situ stump. Identifiable compression fossils of other kinds of plants are virtually absent. The lack of such data suggests that the forest was drowned prior to the abscission of leaves and reproductive organs and that fallen trees macerated in standing water and contributed only highly degraded organic matter to the muck represented by the bone coal.

5. Discussion

The palynology of the Mahoning coal samples from the Sterling Mine is typical of upper Allegheny coals. The palynoflora of the initial stages of peat formation, which resulted in the thin and discontinuous "leader" coal, is compositionally diverse, with roughly equal proportions of lycopsid and tree-fern spores. Crassispora kosankei, from Sigillaria, reaches its highest abundance in these basal coal layers. In contrast, the main coal body was originally dominated by arborescent lycopsids, in particular Lepidodloios hallii (Lycospora granulata). Paralycopodites brevifolius (Lycospora micropapillata and L. orbicula) also reaches its highest abundances in the lower parts of the main coal body, and is patchy in distribution, a pattern similar to other coals in which P. brevifolius occurs (DiMichele and Phillips, 1988; Calder, 1993). In all four of the coal columns there is a progressive vertical diminishment of lycopsid spores and a concomitant increase in tree-fern spores.

Palynological patterns similar to those found in the Mahoning typify other Westphalian-equivalent coals of the Appalachians, and have been interpreted as a response to changing edaphic conditions, possibly from ombrogenous peat development (Eble and Grady, 1990, 1993; Eble et al., 1994). The relatively low ash yields, and low sulfur contents of the lower part of the main coal bench are consistent with a domed, ombrogenous interpretation; domed peats are characteristically low in ash (< 5%) and sulfur (< 1%) (Neuzil et al., 1993).

Physical data from the Mahoning coal make the picture for this coal less clear, and even suggest that the mire may have been largely planar throughout its development. The lower portion of the bed, dominated by lycopsid trees, contains high percentages of vitrinite macerals, especially telinite and telocollinite, and is low in overall ash yield. These traits are also suggestive of wet conditions; acid, anoxic water cover of the surficial peat is conducive to the formation of high vitrinite coal (Teichmüller, 1989). The low ash yields indicate that sediment influx was kept in check. Middle and upper-middle portions of the bed, in which tree ferns begin to increase in abundance, remain low in ash and vitrinite-rich, much the same as the lycopsid-dominated, lower portions of the bed. The terminal layers of the coal bed, those directly adjacent to the bone-coal roof lithology, contain higher ash yields, desmocollinite (relative to telinite + telocollinite), and higher percentages of liptinite and inertinite macerals. These data indicate that the terminal peat layers of the mire were subjected to higher rates of degradation than older layers. An influx of extra-mire waters, which most likely had a more neutral pH, would allow for more extensive microbial decay of the plant litter, and effectively increase the amount of desmocollinite in the resultant coal. Likewise, extra-mire waters are likely to have carried sediment, which would lead to higher ash
yields. Some portion of the increased inertinite fraction in these layers may also have been brought in as water-borne detritus, although more basic conditions upon immediate burial also have been cited as contributing to the non-pyrolytic formation of inertinite in coal (Taylor, 1926, 1927). It also is possible that the aerenchymatous root, stem, and leaf tissues of tree ferns, dominant during this period in mire development, were more easily degradable than the bark and root tissues of lycopsid trees. If so, then the increased percentages of desmocollinite, and possibly inertinite, in the terminal portions of the coal bed are at least partially due to a floristic change. The increased percentage of liptinites in terminal layers probably is a result of concentration due to their natural resistance to decay, although an allochthonous origin for some part of the liptinitic fraction in these layers cannot be ruled out.

Low-ash peats also can develop in predominantly planar mires, as evidenced by the Okefenokee swamp of southeastern Georgia, U.S.A. Data from Cohen et al. (1984) on 72 samples of peat from the Okefenokee swamp indicate an average ash yield of 8.8% (dry basis), with 21 of these samples (29%) being < 5% ash (dry basis). Factors that inhibit widespread sediment influx into planar mires include sediment flocculation and fallout when neutral extra-mire waters contact more acid mire waters (Staub and Cohen, 1979), and vegetation baffling along mire margins (White and Tiessen, 1913; Kravitts and Crelling, 1981; Staub and Richards, 1993).

The combination of palynological and geochemical analysis, in light of actualistic studies, suggests that a drop(s) in water table, and frequent exposure of the peat surface, was not responsible for the vertical change in the Mahoning flora. Rather, it is probable that the peat surface was covered most of the time by acidic, anoxic water, and can be broadly characterized as planar throughout its history. The low ash yields in this part of the bed also indicate that widespread flooding by extra-mire waters (e.g., crevasse splay) was minimal, or did not occur. A change in nutrient levels within the mire may have been the primary cause for the change in flora, but unfortunately, the effects of nutrient loading or deprivation on Pennsylvanian plants are largely unknown.

The lycopsid forest immediately above the Mahoning coal represents the final forest of the mire, and the rocks immediately above the Mahoning coal in the Sterling Mine record the drowning of the peat-forming ecosystem. Biotic changes associated with this terminal environmental shift are indicated by the rise of thick-walled tree-fern spores, which become increasingly prominent compared to thin-walled species in the uppermost parts of the coal and bone in association with increases in ash content and Lycospora abundance. The clastic-rich bone in which the stumps occur represents a muck (sensu Kearns and Davison, 1983) that accumulated in the standing waters that inundated the original mire. Although fusain bands are present in the bone coal, the demise of the mire cannot be correlated with catastrophic fire; the carbon rings of tree stumps are not fusinized and macroscopic fusain is not particularly abundant in the uppermost parts of the bone-coal layer. An absence of identifiable foliar material in the bone coal and overlying dark-gray mudstones, as well as the geochemical characteristics of the bone coal, suggest that plant remains (other than the stumps of drowned trees) underwent maceration in waters of neutral to alkaline pH. Moreover, a general lack of trees rooted exclusively in the bone coal suggests that water cover was long lasting and deep enough to prevent the establishment of new trees except in the earliest phases of inundation. In a
Table 3
Comparison of published spatial analyses of lycopsid forests

<table>
<thead>
<tr>
<th>Study</th>
<th>Area (m²)</th>
<th>Distribution</th>
<th>Stems/ha</th>
<th>Biomass/ha (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DiMichele and DeMaris (1987)</td>
<td>130</td>
<td>random</td>
<td>1769</td>
<td>992</td>
</tr>
<tr>
<td>Beckett (1845)</td>
<td>1005</td>
<td>random</td>
<td>763</td>
<td>215 (estimate)</td>
</tr>
<tr>
<td>Gastaldo (1986a)</td>
<td>4250</td>
<td>random</td>
<td>87</td>
<td>38</td>
</tr>
<tr>
<td>This study</td>
<td>14200</td>
<td>random</td>
<td>573</td>
<td>160</td>
</tr>
</tbody>
</table>

restricted sense, this assemblage is an "autochthonous, non-catastrophically preserved" roof shale flora (Gastaldo et al., 1995).

The disparity between composition of the lycopsid forest and palynomorph composition of the final increments of coal and bone is problematic. The buried lycopsid forest undoubtedly represented a short time increment relative to the overall history of peat accumulation. Its palynological signature, assuming that it attained reproductive maturity, would probably be enclosed in a relatively thin layer of sediment, and if preserved would be averaged into the analysis of the bone-coal layers. Additionally, the clastic content of the bone indicates at least some transport of sedimentary particles into the mire, doubtless including spores and pollen. Thus, the palynological makeup of the bone layers probably includes a greater proportion of allochthonous elements than found in the main coal bed. Thick-walled tree-fern spores, in particular, are indicative of a clastic-swamp to terrestrial source and may have come in from the areas surrounding the peat body.

The tree stumps in the roof rocks of the Mahoning are not an exceptional occurrence. Fossil trees and tree stumps of lycopsids are common in the roof rocks and intercoal mudstones of Pennsylvanian and Upper Carboniferous coals throughout Euramerica. However, of the numerous reports and descriptions of these ancient trees and forests, few actually provide two-dimensional spatial data (for literature summary see Gastaldo, 1986a). Three studies that mapped stump distributions are compared with the present study in Table 3, and contribute to several generalities.

In situ lycopsid fossil forests most commonly are of low diversity, often consisting of one identifiable species. In situ co-occurrences of species from other plant groups are rare, and usually are reported to be calamites, although Wnuk and Pfefferkorn (1987) report clumps of pteridosperms occurring within a stand of mixed lycopsid trees. Taphonomic factors, particularly the unique structural configuration of lycopsid trees, may favor their differential preservation. However, peat-clastic transitional environments are a narrow ecological opportunity, given their association with disturbance and rising water tables, thus excluding many groups of plants not tolerant of standing water and high light influx. It is clear that the lycopsids could tolerate a wide range of stressful physical conditions, most marked by disturbance, low nutrient levels, and minimal competition for light. There also is ample evidence that lycopsid tree species were ecologically segregated, using different resources (Phillips and DiMichele, 1992; Calder,
Where spatial patterns of coal-clastic transitional forests have been studied, tree distributions are not distinguishable from random, which has several implications. Most importantly, random distribution implies little or no intraspecific competition for resources. This inference is supported by several other observations. Trees were growing in a substrate with limited available mineral resources; essentially their rooting systems were bathed in a periodically replenished nutrient solution. In addition, tree lycopsids of the Lepidodendraceae were monocarpic, growing for most of their individual lives as unbranched poles, with crown formation and cone production limited to the final phases of growth (DiMichele and Phillips, 1985). Thus, light competition was probably minimal, especially where tree densities were low.

The number of stems and biomass per hectare vary greatly among the few studies in which such numbers can be estimated. This may reflect sampling problems as well as natural variation. For example, high densities in the study of DiMichele and DeMaris (1987) were projected from study of a small area, which may have been a clump of trees within a larger random pattern. Gastaldo (1986a) reported low tree densities, but notes that erosion may have removed some stumps from the sampling area. However, a study by C. Wnuk and H.W. Pfefferkorn (pers. commun., 1995) finds very high densities of lycopsids in a mixed stand of polycarpic and monocarpic species, mixed with other groups of plants, and indicates that the natural variance may have been considerable.

In conclusion, although understanding of the structure and dynamics of ancient lowland forests, such as that described here, has increased greatly in the past decade, interpretations are based on a small number of cases. Apparently conflicting patterns may point to natural diversity in forest structure, dependent on local environmental conditions and the taxonomic composition of the forest. This is to be expected. As additional data accrue, we expect that the wetlands of the late Paleozoic will prove to be as structurally and dynamically complex as those of many modern tropical regions.

Acknowledgements

We are indebted to numerous people of the Sterling Mining Corporation, including Timothy R. Miller, who assisted in all aspects of field work and primary data collection and provided information about the distribution of stumps in areas of the mine not examined in this study, and W.T. Mackall, for allowing us to conduct this investigation. Robert Hook, Austin, Texas, assisted in all aspects of field work, provided geological interpretations, and made extensive contributions to and comments on earlier versions of the manuscript. Maps of abandoned underground coal mines within the study area were compiled by R.M. DeLong (retired, Ohio Geological Survey). M.A. Buzas helped with statistical methods. We thank John H. Calder and Robert A. Gastaldo for numerous helpful comments on the manuscript. This is contribution No. 32 from the Evolution of Terrestrial Ecosystems Program at the Smithsonian Institution, which provided partial support.
Appendix A. Summary palynological composition, ash and sulfur for sampling increments of coal columns 1–4. Locations of coal columns is shown in Fig. 1

A.1. Mahoning Coal Column 1

<table>
<thead>
<tr>
<th>SW Corner X2</th>
<th>Bone 2053</th>
<th>Bone 2054</th>
<th>Top of bed 2055</th>
<th>2056</th>
<th>2057</th>
<th>Base of bed 2058</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thickness (in)</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>10</td>
<td>9</td>
<td>14</td>
</tr>
<tr>
<td>Ash yield (% dry)</td>
<td>48.5</td>
<td>56.7</td>
<td>32.9</td>
<td>6.6</td>
<td>3.7</td>
<td>10.8</td>
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<tr>
<td>Sulfur content (% dry)</td>
<td>1.76</td>
<td>0.7</td>
<td>1.49</td>
<td>2.81</td>
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<td>1.85</td>
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<td>Telinite</td>
<td>27.4</td>
<td>35</td>
<td>41.6</td>
<td>51.8</td>
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</tr>
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<td>Telocollinite</td>
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<td>24.6</td>
<td>24</td>
<td>16.6</td>
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<td>Corpocollinite</td>
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<td>Desmocollinite</td>
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<td>19.8</td>
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<td>15.2</td>
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<td>Total vitrinite</td>
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<td>82.2</td>
<td>85.4</td>
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<td>Sporinite</td>
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<td>6.8</td>
<td>6.6</td>
<td>4.2</td>
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<td>Cutinite</td>
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<td>Resininite</td>
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<td>0.8</td>
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<tr>
<td>Liptodetrinite</td>
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<td>4.4</td>
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<td>5.2</td>
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<tr>
<td>Total liptinite</td>
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<td>12.4</td>
<td>10.2</td>
<td>11.2</td>
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<td>Fusinite</td>
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<td>3.2</td>
<td>1.8</td>
<td>1.2</td>
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<td>Semifusinite</td>
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<td>0.4</td>
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<td>1</td>
<td>1.8</td>
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<td>Total inertinite</td>
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<td>5.4</td>
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<td>L. granulata</td>
<td>8</td>
<td>3.6</td>
<td>12</td>
<td>28.8</td>
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<td>68.8</td>
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<td>Total lycopsid trees</td>
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<td>SW Corner X2</td>
<td>Bone 2053</td>
<td>Bone 2054</td>
<td>Top of bed 2055</td>
<td>Base of bed 2058</td>
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<tr>
<td>---------------------</td>
<td>-----------</td>
<td>-----------</td>
<td>-----------------</td>
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<tr>
<td><em>Laevigatosporites globosus</em></td>
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<td>72</td>
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<td>5.2</td>
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<td>Total small ferns</td>
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<td>Total calamites</td>
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<td><em>Florinites florini</em></td>
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<td><em>F. similis</em></td>
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<td><em>Vesicaspora wilsonii</em></td>
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<td>Total cordaites</td>
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### A.2. Mahoning Coal Column 2

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<th>2383</th>
<th>2384</th>
<th>Top</th>
<th>2385</th>
<th>Roof</th>
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<td></td>
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</tr>
<tr>
<td>Thickness (in)</td>
<td>3</td>
<td>7</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>3</td>
<td>45.87</td>
<td>12.55</td>
<td>5.1</td>
<td>5.44</td>
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<td>1.19</td>
<td>1.54</td>
<td>1.34</td>
<td>2.47</td>
<td>1.64</td>
<td>2.06</td>
<td>1.37</td>
<td>1.06</td>
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**Total Lycopsid Trees**

19.6

**Total Small Lycopsids**

0.8

**P. minutus**

25.6

**P. granifer**

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1 in = 1 inch = 2.54 cm.
References


ISO (International Organization of Standardization). 1984. Methods for the petrographic analysis of bitumi-


