

Structure and Dynamics of a Pennsylvanian-Age *Lepidodendron* Forest: Colonizers of a Disturbed Swamp Habitat in the Herrin (No.6) Coal of Illinois

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INTRODUCTION

*Tree stumps of arborescent lycopods were discovered in situ at the contact of the Herrin (No. 6) Coal and the Energy Shale Members, near the Walshville paleochannel, the major river channel running through and draining the Herrin coal swamp. The stumps are associated with, and in one case attached to, fallen trunks identified as a *Lepidodendron* similar to *L. aculeatum*. The stumps and trunks occur in a lower carbonaceous facies of the Energy Shale. The trees were rooted in the peat and represent the final vegetation at the site. Various lines of evidence suggest that the trees were of approximately the same age and formed a single stand that died as a consequence of completing a determinate life cycle, not as a result of mud accumulation or drowning. Distribution of the tree stumps is random. Consideration of tree habit and development, edaphic (soil) quality of this and similar swamp sites, and colonization dynamics suggests that these trees were opportunists within a milieu of stressful habitats. Vegetation structure probably was influenced only slightly or not at all by density-dependent (competitive) factors. Lycopods of this type are characteristic of clastic-compression (mineral-substrate) swamp vegetation, and occur in some coal-swamp (peat-substrate) communities, possibly in relatively higher nutrient areas. Their presence above the Herrin Coal appears restricted to near-channel sites, which they may have colonized as depositional and/or edaphic conditions changed from those typical of a peat-substrate swamp to those more similar to mineral substrates. There are a number of similarities between modern and ancient swamps in the ecological strategies of the dominant plants and the structure of the communities; however, there is little morphological "convergence" among the dominant species.*

The Pennsylvanian period in North America and Europe was a time in which extensive swamps developed in coastal and deltaic settings. These swamp habitats were a dominant part of the terrestrial landscape. Although the basic physical setting was the same as that of modern swamp environments, the plants that occupied them were completely different from those occupying post-Paleozoic swamps. These differences were not only taxonomic; reproductive biologies and architectures of the dominant trees differed greatly from those that came later. The nature of the diversity, spread among at least four classes of plants, contrasts with seed plant dominance (one class) in most post-Paleozoic, particularly modern, swamps. As a consequence of this combination of physical similarity and biological distinctiveness, Pennsylvanian-age swamp environments provide excellent opportunities to look for general patterns of community structure and dynamics that are independent of the particular species mix involved. They provide a natural "test case" to evaluate the generality of some ecological principles founded on studies of modern vegetation.

Swamps can be divided broadly into two major groups: peat-forming swamps and clastic swamps. In each case, but particularly for peat swamps, these habitats appear to be semi-closed, naturally bounded ecological islands. The physical conditions are extremely stressful to plants (*sensu* Grime, 1979) because of periodic flooding or high water tables and consequent low oxygen availability to roots, low pH, and frequently, low nutrient availability. Consequently, only a small subset of the total terrestrial flora can tolerate these conditions and grow in swamps, resulting in a sharp ecotone (vegetational boundary) between swamps and surrounding communities in "dry-land" habitats. One of the characteristic plant groups to dominate swamp environments during the early and middle Pennsylvanian in Euramerica was the arborescent lycopods. At

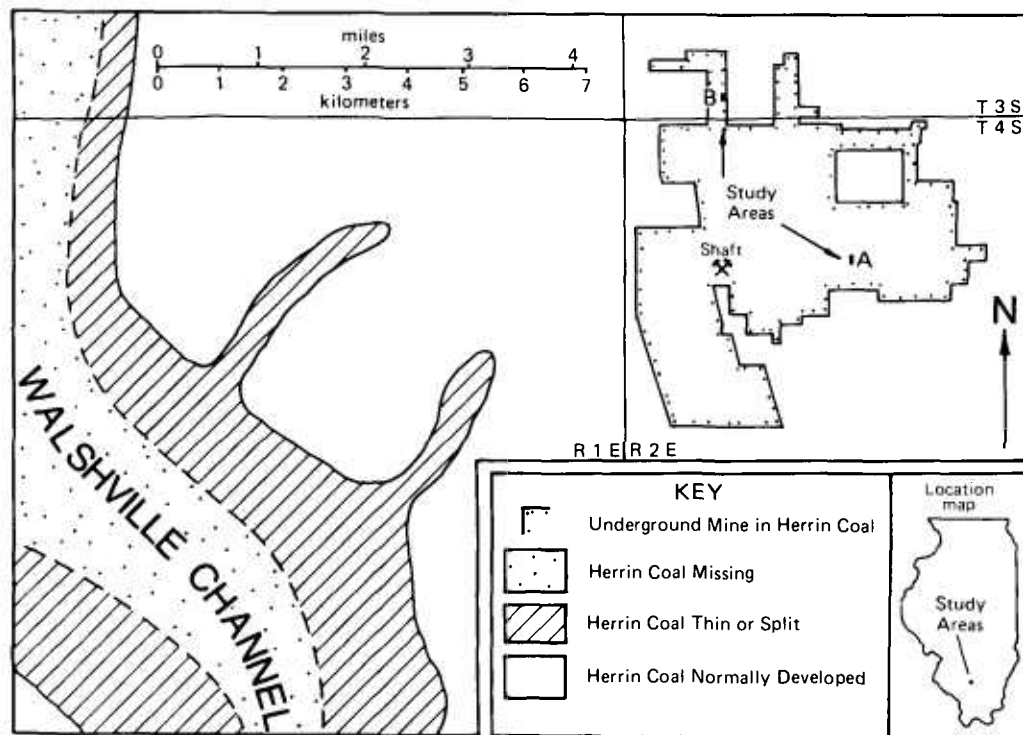


FIGURE 1—Study area located within Orient No. 6 Mine of Freeman United Coal Mining Company, Jefferson County, Illinois. (Walshville paleochannel and split coal information modified from Nelson, 1983.)

least seven genera and many species existed in a variety of ecological roles within the wet lowlands (DiMichele and Phillips, 1985; Wnuk, 1985; Gastaldo, 1986). The group as a whole appears to have been evolutionarily conservative, speciating relatively rarely, with species displaying long stratigraphic ranges.

This report concerns an occurrence of *Lepidodendron* tree stumps and trunks on the bedding interface of the Illinois Herrin (No. 6) Coal Member and the Energy Shale Member, the local roof rock of the coal in areas near the Walshville paleochannel, which is the site of a large river contemporaneous with peat deposition. The stumps appear to be rooted in the top of the Herrin Coal and represent the final forest of the area prior to inundation with fresh to brackish water. From a combined analysis of the preserved stumps and logs, the palynology of the coal, and the local and regional sedimentary environment, we are able to reconstruct the forest and its history, thus providing a basis to understand the dynamics of this particular kind of vegetation. *Lepidodendron* (*sensu* DiMichele, 1983, 1985) is found most commonly as compression-impression fossils in clastic rocks. The occurrence of a forest of these trees rooted in peat (coal) suggests local changes in the physical environment, perhaps conditions intermediate between peat and clastic swamps, combined with physical disturbance. This represents a lycopod forest with considerably different dynamics than those dominated by the lycopods *Lepidophloios* or *Diaphorodendron* (DiMichele and Phillips, 1985; Wnuk, 1985; Gastaldo, 1986), indicating the ecological diversity of arborescent

lycopods and pointing to both similarities and to differences from modern swamp forests.

GEOLOGICAL SETTING

The areas studied are within the Freeman Coal Company, Orient No. 6 Mine, an underground shaft mine in Jefferson County, Illinois: Waltonville 7-1/2' Quadrangle (shaft in sec. 7, T4S, R2E). Two areas within the mine were studied in detail (study areas A and B, Fig. 1). Area A is within a larger area mapped previously where upright stumps were reported (Krausse et al., 1979). The study areas are eight to ten kilometers from the Walshville paleochannel (Fig. 1), the major river channel running through the contemporaneous Herrin coal swamp (Johnson, 1972; Algaier and Hopkins, 1975; Nelson, 1979). The Herrin Coal in nearby mines is split by shales interpreted as having been deposited during floods from the channel.

Both study sites within the mine display the interface of the Herrin Coal and the Energy Shale of the Carbondale Formation (middle Pennsylvanian). Two major facies of the Energy Shale occur as immediate roof; the lower unit is a carbonaceous laminated medium-gray shale that is overlain by a coarser, less carbonaceous, silty, light-gray shale. Burk (1982) called the lower unit the non-marine bay-fill facies, and considered the upper, lighter facies to be either distal or proximal splay material.

Upright lycopod tree stumps and horizontal compressions of

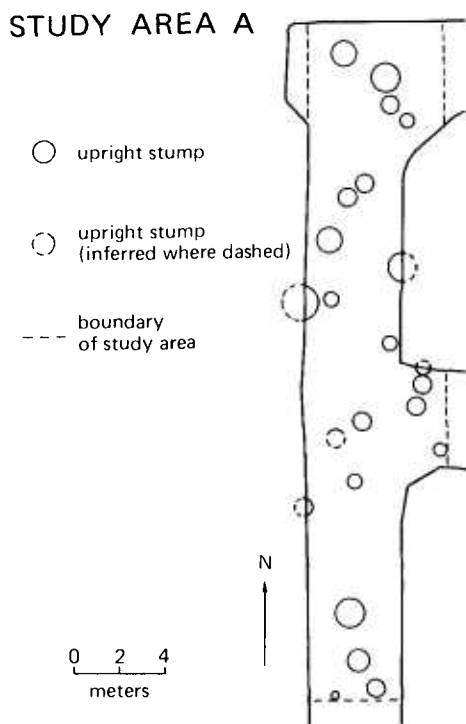


FIGURE 2—Map view of upright stumps in study area A. Stumps were mapped in an area of 130 square meters.

lycopod tree trunks are preserved within the lower laminated medium-gray shale. The lower facies is irregular in lateral distribution; maps of this distribution can be found in Krausse et al. (1979). Edwards et al. (1979) suggested that the patchiness of the older facies reflects original deposition; however, subsequent work by the authors and others (Nelson, unpubl. Illinois State Geological Survey field notes, 1979) indicates that the lower laminated facies was originally widespread and was eroded in places prior to deposition of the light-gray facies. Petrology of the lower facies near study area A (Edwards et al., 1979) indicates that it is finer grained than the upper light-gray facies and contains much finely dispersed organic matter as well as larger coalified-plant compressions. The carbonaceous matter was derived primarily from plants growing on the peat substrate, which gradually decayed and collapsed over a period of time. The lamination in this shale, where present, results from layers of clay and quartz silt alternating with more carbonaceous clay-rich layers, apparently due to pulsations of fresh water from the source area. We interpret this finely laminated shale as having been deposited in calm, slowly rising fresh to brackish water. Burk (1982) suggested that the depositional setting for this facies was a large shallow bay.

Animal fossils are uncommon in the lower facies. We found *Spirobia* attached to fallen trunks and scattered linguloid brachiopods in the shale. However, Krausse et al. (1979) reported some small pectinoid bivalves and Anthracosiididae in this lower shale unit, which is their "dark-gray shale facies". Burk (1982) also noted that the carbonaceous shale is poor in animal

fossils, especially at the base. The facies probably was deposited in fresh water at the base, grading upward into a brackish environment (John Utgaard, pers. comm.).

The upper silty light-gray facies of the Energy Shale unconformably overlies the lower facies and is the immediate roof to the Herrin Coal in areas where the lower facies is missing. The thick deposits of lighter-gray shale, which range up to 30 m thick, are interpreted as overbank flood deposits (Bauer and DeMaris, 1982; Edwards et al., 1979); the thicker deposits probably formed from channel avulsion in response to gradual marine transgression. Both east and west of the Walshville paleochannel the roof is a fissile marine black shale (Anna Shale Member) or a marine limestone (Brereton Limestone Member). Both overlap the Energy Shale over wide areas.

METHODS AND MATERIALS

In study area A, the main site of the analysis, upright tree stumps and horizontal trunks of lycopods were abundant (Fig. 2). A system of 1-m² grids was established on the roof in a portion of the site. We mapped all upright stumps within the grid area and recorded the following information for each: coordinate location; diameter or maximum and minimum cross-sectional dimensions (if the filling had fallen out, the diameter at the top of the resultant kettle bottom also was measured); direction of lean, if any; height of stump, where visible; identifying characteristics; and, if observable, the substrate in which the stump was rooted. We also recorded the directions and dimensions of some of the horizontal trunks. However, we were prevented from making a detailed survey of these because the study area was closed for ventilation purposes during the course of our investigation.

Stumps were too few and too scattered in study area B for us to establish a grid system. However, we recorded their dimensions and other data. We also noted dimensions and orientations for many horizontal trunks in this area.

We collected samples of coal from study area B for palynological and low-temperature ash determinations. We took samples from the upper 30 cm of the coal in three 10-cm increments, and later resampled the topmost three centimeters for separate analyses. Palynological analyses of previously collected channel samples in and near this mine were used for comparative purposes.

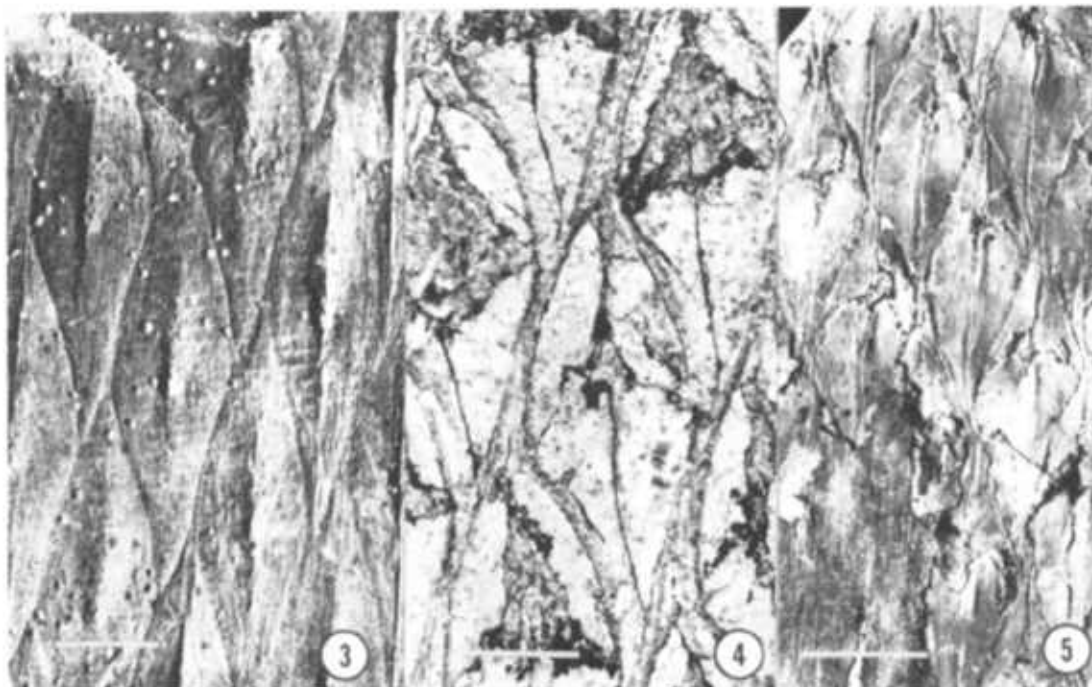
Analysis of Data

The distribution of tree stumps in study area A was evaluated using nearest neighbor analysis (Clark and Evans, 1954) to determine whether the distribution of stumps was uniform, random, or clustered. The nearest neighbor statistic, R , is a single number from 0 to 2.15: 0 = clustered, 1 = random, 2.15 = uniform.

Low-temperature ash analyses were performed at the Illinois State Geological Survey by Don Lowry according to the techniques of Gluskoter (1975).

Specimens

Compression-impression specimens of fossil plants and pyrite permineralizations of wood and primary xylem collected from a lycopod tree stump in the Orient No. 6 Mine are housed



FIGURES 3, 4, 5— Leaf cushions from fallen lycopod trunks. Cushions (diamond-shaped areas on trunks) shown in Fig. 3 are from partially decorticated (outer tissue layers lost) trunk. Note prominent upper and lower keels (vertical "ridge" lines), relatively small leaf scar, lack of well developed interareas (spaces between cushions) or fissures between adjacent leaf cushions. Radial protrusion in combination with these characters is typical of *Lepidodendron* of the *L. aculeatum*-type; however, infrafoliar parichnos prints (aerating strands) below the leaf scar are not clearly marked. (Scale bars = 1 cm).

in the paleobotanical collections, Smithsonian Institution, Washington, D.C. They bear the following catalog numbers: USNM 387496–387515.

Palynological analyses were performed by Dr. Russel A. Peppers of the Illinois State Geological Survey. Reference palynological slides prepared from coal macerations are housed in the paleobotanical collections of the Illinois State Geological Survey and bear the following reference numbers: 2765 (top 3 cm), 2731C (top 10 cm), 2731B (second 10 cm), 2731A (third 10 cm), all from area B, and 2730 (full seam reference maceration) from between areas A and B.

RESULTS

Identity of Stumps and Horizontal Trunks

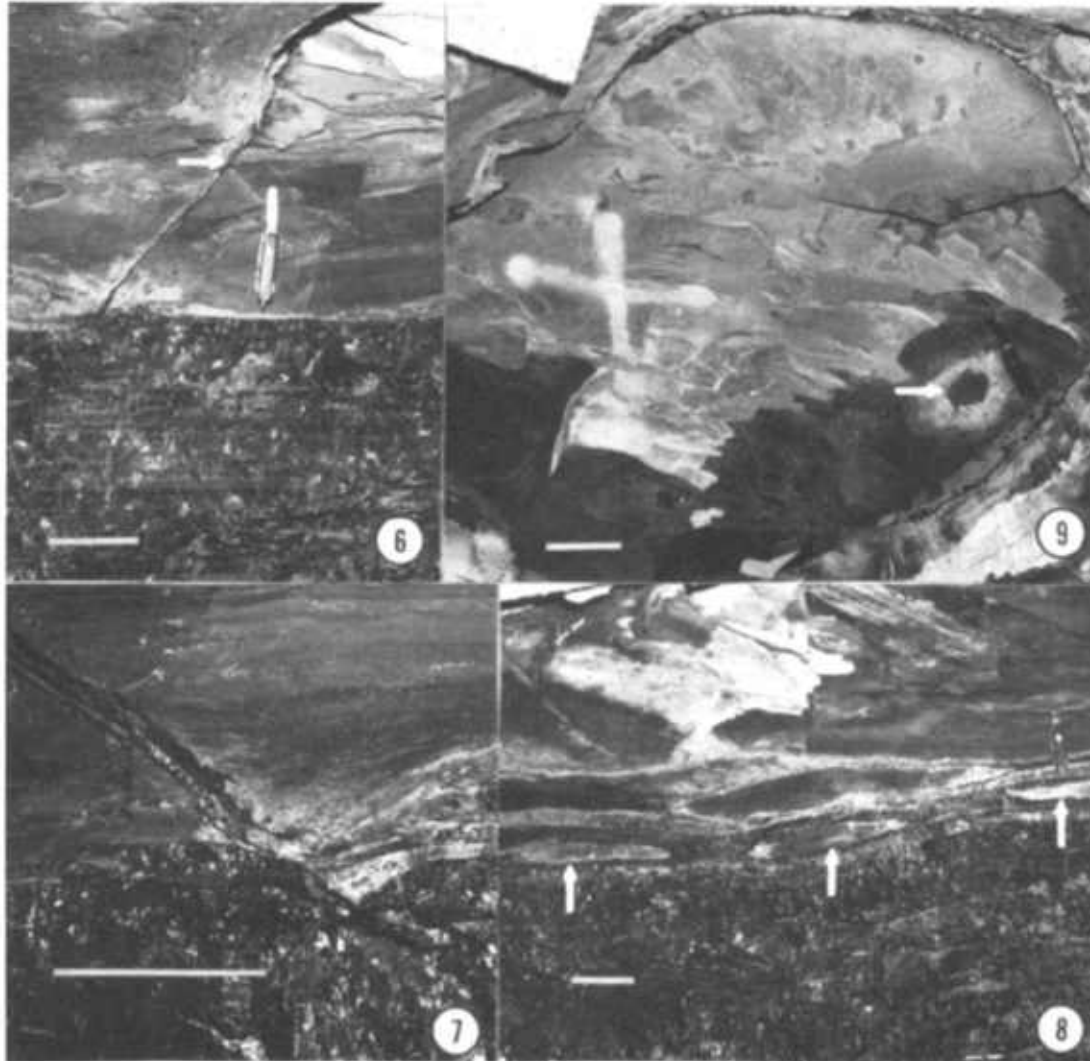
Most of the tree stumps and all of the horizontal trunks were identifiable as lepidodendrid lycopods. Their affinities appear to be with true *Lepidodendron*, in particular, forms similar to *L. aculeatum*. This identification is based on the following characteristics: leaf cushions higher than wide; distinct keel; evidence of limited development of leaf-cushion interareas; cushions radially protruding or "raised"; cushions apparently obliterated by gradual secondary stem expansion rather than being shed from the stem surfaces (Figs. 3, 4, 5). Cushion size and shape vary with stem diameter; height and width increase with stem diameter. This combination of leaf-cushion characteristics is known only in the species of true *Lepidodendron*, not *Diaphorodendron* (DiMichele, 1985), which also has higher than wide diamond-shaped leaf cushions. Infrafoliar parichnos (prints of

aerating strands below the leaf scar), one of the most conspicuous characteristics of true *Lepidodendron*, were not observed on any of the specimens collected. This may be a happenstance of preservation because infrafoliar parichnos were noted on a few specimens in the mine. However, these lycopods could belong to a sub-group of *Lepidodendron* not presently known from anatomical preservation. Features of the primary xylem from the one stump in which anatomy was recovered are similar to those of *L. hickii*, an anatomical species of true *Lepidodendron*.

Habit of Trees

The lycopod trees of this study appear to have had determinate growth (Eggert, 1961). A relatively short-lived, anisotomously branched (unequal "dichotomy"), determinate crown developed following a prolonged growth period during which trees were columnar, unbranched, and clothed in leaves.

Reconstructions of the developmental stages of trees with this habit are given by Andrews and Murdy (1958), Andrews (1961), DiMichele and Phillips (1985), and Wnuk (1985). We did not find leaves attached to trunk specimens, which suggests that all trees had reached the mature branched form. Evidence supporting this habit includes the lack of deciduous branch scars (ulodendroid scars) on any of the fallen trunks, unbranched fallen trunks over 15 m long, and branching observed only in stems less than 10 cm in diameter. These data are consistent with the habit described for *Lepidodendron aculeatum* by Thomas and Watson (1976).



FIGURES 6, 7, 8, 9—*In situ* *Lepidodendron* stumps and roots. **Fig. 6**) Cross section of contact between Herrin Coal and Energy Shale. Arrow indicates coalified rind (edge of tree stump), which contacts the upper surface of the coal. **Fig. 7**) Cross section of contact between Herrin Coal and Energy Shale. Coalified rind of tree stump surrounded by and infilled with shale joins coal. Note compactional deformation of coal and shale at contact. **Fig. 8**) Cross section of contact between Herrin Coal and Energy Shale. Oblique sections of axes (arrows) presumed to be *Stigmaria* occur several centimeters below coal-shale contact; these are filled with Energy Shale that probably filtered in through a continuous cavity from the tree trunks. **Fig. 9**) In-filled tree stump "kettle bottom" at base of Energy Shale (looking almost straight up). Note slickensided vitrain rind (especially lower right of photo) and off-center remnant of vascular bundle (at arrow). Stump averages 100 cm in diameter. (Scale bars in Figs. 6 to 9 = 10 cm).

Evidence for *In Situ* Rooting

We concluded that these lycopod trunks are *in situ* and not transported to the site from elsewhere. This conclusion is supported by several observations. Stumps visible in longitudinal section on the walls of cross cuts, where the coal face and the contact with roof shale were exposed, have coalified rinds that flare at the base and are confluent with the top of the coal (Figs. 6, 7). The flared base is typical of the basal part of lepidodendrid trees at the transition from stem to root. Confluence of the flared base with the top of the coal suggests that

the stumps were rooted in the peat. Undersides of stumps never were observed in the roof shale and many bedding surfaces within the shale were visible throughout the study area. This implies that trees did not establish on a mud surface, but on the peat itself. Lastly, a few shale-filled oval lenses occur in the upper 30 cm of the coal (Fig. 8). These lenses are the size of Stigmarian main roots and are filled with shale similar to the older facies of the Energy Shale in which the stumps are embedded. Such root axes indicate a continuous cavity for mud infiltration from the tree stumps on the swamp surface to the roots below.

STUDY AREA A

Stump diameters

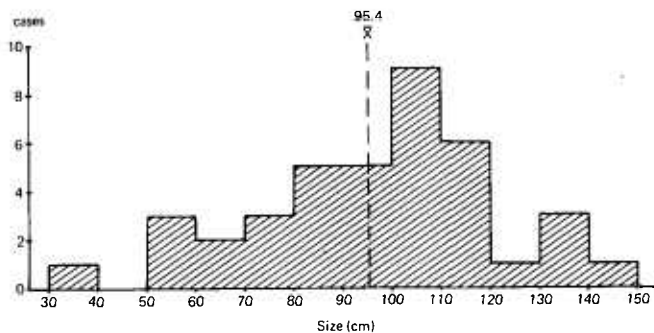


FIGURE 10—Distribution of diameters of upright stumps in and vicinity of study area A measured at or near coal-shale interface.

Nearest Neighbor Analysis

The nearest neighbor measure (R) for the stumps in study area A was 1.27, a distribution slightly to the uniform side of random (Fig. 2) and statistically distinguishable from random at the 5% confidence level using the c statistic of Clark and Evans (1954). Such a nearly random distribution is not unexpected in a group of plants that lacked clonal reproduction and appear to have been opportunistic, exploiting disturbed sites by rapid colonization. Opportunistic species invading an open site would establish initially more or less at random if the substrate and microhabitat were nearly uniform, as might be expected in a peat swamp. Minimal competitive interactions among the plants, as we will argue later, would result in only slight ordering of the vegetation.

Schmitz (1896), Beckett (1845), and Gastaldo (1986) also presented maps showing spatial distribution of large numbers of lycopod stumps. We calculated a nearest neighbor statistic for the data of Schmitz and Beckett. Schmitz diagrammed 33 stumps in a narrow east-west linear transect ($R = 1.69$). Although his sample size is comparable to ours, the narrowness of the exposure confines the distribution of neighbors with which comparisons are possible, producing an artificially high R value. Beckett mapped 74 stumps in a triangular area approximately one-fourth of an acre in areal extent; we calculated $R = 0.9$ for this array. Beckett has a very large exposure with the edge affecting few of the nearest neighbor comparisons, and although stump density was low, this does not affect the calculation. Gastaldo's three sites were intermediate in area between those of Schmitz and Beckett; using a different technique, he determined random stump placement for two of the three exposures. Our site, a relatively wide but linear exposure, also is intermediate in size between those of Schmitz and Beckett. Thus, the tendency toward a uniform distribution in our sample may have resulted from the relatively large number of stumps near the margin of the sample area.

Sizes and Areal Distribution of Stumps

Thirty-nine stumps in study area A and vicinity average 95 cm in diameter and range from 34 to 144 cm. The size

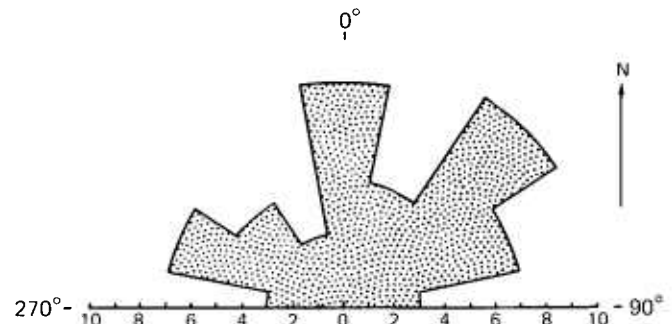


FIGURE 11—Orientations of fallen lycopod trunks from study area B. Data represent 49 tree trunks oriented by 22-1/2° sectors.

distribution of stumps, based on size class increments of 10 cm (Fig. 10) is unimodal but left-skewed and leptokurtic; therefore, it deviates somewhat from a normal distribution. This suggests that most trees were mature at the time of death, having achieved maximum size. Many stumps in study area A show a preferential southeast or east-southeast lean. The two stumps of smallest diameter did not lean, did not flare significantly at the base, and lacked a thick coalified rind. Although the definitive evidence was not preserved, these stumps may be calamites or pteridosperms rather than lycopods; their removal from the size-class curve (Fig. 10) would lead to a better approximation of normality. There were isolated occurrences of non-lycopod debris, mostly pteridosperm and calamite, in the lower part of the shale.

Determination of density (number of stems per hectare) and basal stem area per hectare was extrapolated from study area A (33 stems in 130 m²). Density was 1769 stems per hectare. Basal area was 992 m² per hectare, indicating that approximately 10% of the area in the lycopod forest was occupied by trees. This is likely to be inflated because our diameter measurements were made at the base of a tree, which was somewhat flared, rather than at breast height. Based on diameters of horizontal trunks and the amount of flaring of the tree bases where observable, we estimate that actual basal area may be as much as 30% below our calculation.

Horizontal Trunks

All horizontal trunks measured are from study area B. Although trunks were abundant in study area A, we were unable to complete our measurement of them because of mine operations. The 51 horizontal trunks that were measured had an average diameter of 46.2 cm (range 20 to 101 cm). Fragments of trunks, some up to 15 m long, showed no appreciable taper. Trunks were distributed throughout the lower 60 cm of the medium-gray laminated lower facies of the Energy Shale, diminishing upward in abundance within the shale. The mean distance of the trunks above the coal was 18.7 cm; local loss of the lower part of the shale in roof falls may have resulted in bias toward the higher end of the distribution. Trunks did not show preferential orientation (Fig. 11); Krausse et al. (1979) made a similar observation in another part of the same mine.

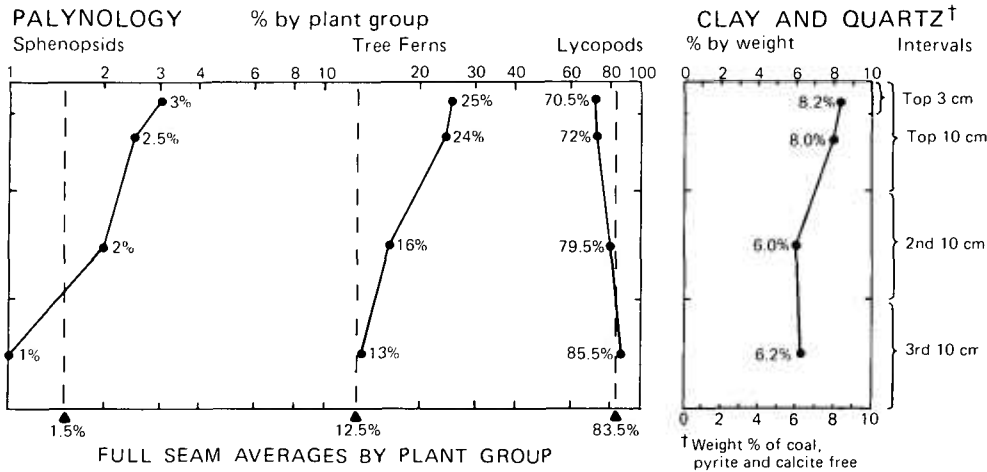


FIGURE 12—Palynology of the top 30 cm of the Herrin Coal in study area B compared with nearby full-seam data. Clay and quartz data from X-ray diffraction analyses of low-temperature ashes provide an index of the clastic component of the coal.

The distribution of fallen trunks throughout 60 cm of roof shale, their variable orientation, and the evidence for slow accumulation of the medium-gray laminated shale facies that entombs them, indicates that trees fell at different times. Many fallen trunks are not completely compressed and shale bedding can be followed throughout the cavity inside the coalified ring; the soft cortical tissues of the trees had decayed leaving a hollow cylinder of bark into which mud could filter. Large longitudinal cracks in some fallen trunks and in the walls of some stumps suggest that the trees twisted and buckled as they fell; they did not simply snap off or uproot. In places the sides of the mud-filled stumps were dented and deformed by other falling trees. In one case a mud-filled stump 112 cm in diameter was attached to a completely decorticated fallen trunk at a height of 30 cm into the roof shale. Trees may have fallen after enough longitudinal cracks had developed to weaken the shear strength of the supportive periderm. Mud began to filter into the trees well before they fell.

Palynology

Results of the palynological analysis by Dr. R. A. Peppers are shown in Figure 12 and Table 1. These results indicate a progressive change in the flora in the upper 30 cm of the coal, a pattern identified elsewhere in the Herrin Coal (Mahaffy, 1985; Peppers, 1970) and probably not related to or predictive of the final true *Lepidodendron* forest. In general, lycopods decrease from 85.5% in the lowest 10-cm bench (of the upper 30 cm) to 70.5% in the upper 3-cm increment. In this same interval there are progressive increases in tree ferns from 13% to 25%, in sphenopsids from 1% to 3%, and in filicalean ferns from 0.5% to 1%. Medullosans cannot be sampled directly because the large size of their pollen eliminates their inclusion in the fine fraction of the maceration used in spore analysis. The pattern that emerges is a relative drop in the spores of the group that dominated the coal swamp for most of its history (lycopods), and a rise in abundance of sphenopsid and fern spores. Whether this reflects vegetation change alone or has a strong taphonomic component is difficult to determine.

The floristic change (especially at the top of the seam) is actually more substantial than a survey of the major groups indicates. It is most marked in the top 3 cm of the seam where *Lycospora granulata*, probably from *Lepidophloios hallii*, is superseded by *Cappasporites distortus*, produced by *Diaphorodendron dicentricum* and *D. scleroticum* (Table 1). Thus, the drop in lycopods in the top 3 cm (Fig. 12) actually reflects a significant taxonomic change.

These floristic changes within the coal reflect patterns also detected by coal-ball sampling at other sites in the Herrin Coal (Phillips and DiMichele, 1981; DiMichele and Phillips, 1980). Thus, they indicate that conditions were changing late in swamp development, but that vegetational response involved species typically centered in coal swamps. The development of a more typical "compression" vegetation in the last phases of the swamp forest could not be predicted from these vegetational changes in the relative abundance of the typical coal-swamp plants.

Low-temperature Ash

Composition of low-temperature ash (clay and quartz content of the coal) is presented in Figure 12. There is a minor increase in clay-quartz abundance within the upper 30 cm of the 190-cm thick coal seam, from 6.2% in the lowermost 10-cm increment to 8.2% in the upper 3-cm increment. We interpret these results to indicate increasing clastic influx related to flooding activity from the channel.

DISCUSSION

The dominant trees of the Herrin coal swamp were lycopods, especially *Lepidophloios hallii*, *Diaphorodendron scleroticum*, and *D. dicentricum* (DiMichele and Phillips, 1985). True *Lepidodendron*, represented by the structurally-preserved stems of *L. hickii*, was abundant in a few places that appear to have been closer to channels or open water where nutrient levels were higher. The trees described here from the roof shales of the Herrin Coal appear to belong to the true *Lepidod-*

TABLE 1—Spore-Pollen Composition of Upper 3 cm of Herrin Coal, Study Area A (Percent abundance)

LYCOPODS	
Trees	
<i>Lycospora granulata</i>	44.0
<i>Cappasporites distortus</i>	20.5
<i>Crassispora kosankei</i>	0.5
Herbaceous	
<i>Endosporites globiformis</i>	1.0
<i>Anapiculatisporites spinosus</i>	4.5
FERNS	
Trees	
<i>Punctatosporites minutus</i>	15.5
<i>Laevigatosporites globosus</i>	0.5
<i>Thymospora pseudothiessenii</i>	1.5
<i>Punctatisporites minutus</i>	2.0
<i>Punctatisporites obliquus</i>	2.0
<i>Speciosporites minutus</i>	1.5
<i>Cyclogranisporites orbicularis</i>	2.0
Others	
<i>Verrucosporites microtuberosus</i>	0.5
<i>Triquitrites spinosus</i>	0.5
SPHENOPSIDS	
<i>Laevigatosporites ovalis</i>	2.5
<i>Laevigatosporites vulgaris</i>	0.5
CORDAITES	
<i>Florinites mediapudens</i>	0.5

endron evolutionary lineage and may be *L. hickii*. Their presence in an environment with rising clastic influx is consistent with what has been inferred about *L. hickii* from its occurrences in the Herrin Coal and elsewhere. What these exposures reveal is a short-lived flora growing under rather atypical coal-swamp conditions that were perhaps transitional between peat and clastic swamps.

We draw several conclusions about this forest and its component trees. The tree stumps and trunks in the roof shale of the Orient No. 6 Mine represent an *in situ* single, probably nearly even-aged, stand of trees that developed only in the vicinity of the Walshville paleochannel. There were few density-dependent (competitive) interactions among these trees. All died as a consequence of the natural completion of determinate growth. Re-establishment of the lycopod trees and other plants in the slowly accumulating muds of the lower facies of the Energy Shale occurred rarely or not at all, apparently due to water depth rather than to mud deposition.

The physical evidence supports the conclusion that the stumps are *in situ*. Transport of tree stumps in an upright position has been reported in volcanic mud flows (Fritz, 1980) and in lakes associated with mud flows (Coffin, 1983). However, in such cases the nature of the enclosing sediment, associated non-upright stumps, and the physical wear of stumps and other plant debris within the deposits are clear evidence of

transport. There is no evidence of such transport or of conditions that would permit such transport in any of the reports of tree stumps from Pennsylvanian-age sediments (Gastaldo, 1984; Stevenson, 1913). *In situ* stumps and associated trunks of *L. aculeatum* also occur in numerous exposures of the Dykersburg Shale Member above the Springfield (No. 5) Coal Member. This shale was deposited along the flanks of channels at the time of Springfield Coal deposition (Eggert, 1982; Hopkins, 1968). The distribution of tree stumps is analogous to that seen above the Herrin Coal. In addition, in areas of the Herrin Coal several kilometers from the Walshville paleochannel such as the Old Ben No. 24 Mine, the flora in the gray shale roof is limited to the lower few centimeters and is composed solely of species characteristic of coal-swamp assemblages, lacking a true *Lepidodendron* component (DeMaris, et al., 1983). These observations imply that *L. aculeatum* (or similar species) may have established preferentially in near-channel areas disturbed by flooding and clastic influx, perhaps in ephemeral riverine swamps.

Formation of the Orient No. 6 stand during a short time interval is an assertion critical to our argument. As a result all trees would have been of approximately the same age. Those trunks clearly identifiable as lycopods conform to a narrow, left-skewed, unimodal size distribution, which is an expected size distribution within a mature population of determinate trees. This does not rule out that they may have established at different times. However, there is no evidence of rooting in the base of the roof shale; all stumps appear to be rooted in the very top of the coal. This indicates a time of establishment between the last phase of the coal-swamp forest and the beginning of significant mud deposition. We found no evidence of peat erosion; the coal-shale contact appears to be gradational. The regional and local geology and data from coal-ash determinations suggest a brief hiatus at most between the final coal-swamp forest and the onset of Energy Shale deposition (Bauer and DeMaris, 1982; DeMaris et al., 1983; Kravits and Crelling, 1981). Thus, the period during which the trees could have established must have been short, probably less than the life span of a single tree.

New trees appear to have been unable to establish on the site once mud deposition began, but established trees appear to have been tolerant of the physiological stress induced by standing water and were able to complete their life cycles as mud deposition took place. The latter was suggested by the presence of a few lycopod strobili that were present in the lower facies of the gray shale. Lack of recruitment once mud deposition began is suggested by lack of rooting in the shale and by the absence of identifiably juvenile trees in the sample. The determinate habit of these trees leads to distinct differences in habit between "mature" reproductive trees and pre-reproductive "juveniles". The late stage architecture of mature trees consisted of a long unbranched trunk terminated by a branched leafy crown; juveniles were unbranched and had a trunk that bore long leaves.

The establishment of a stand of true *Lepidodendron* trees on the peat surface suggests considerable change in the edaphic qualities of the peat. Such changes may have been in pH, levels of substrate oxidation, and/or influx of clastics in fresh-water floods into the area with subsequent increase in nutrient levels.

This is consistent with the most common form of preservation of *L. aculeatum* and related species as compression-impression fossils in clastic-swamp deposits. Trees of the final lycopod forest probably were dependent on such changes in edaphic conditions that possibly coincided with disturbances such as floods in order for establishment to occur.

Proximity of this site to the Walshville paleochannel may have been the major factor influencing this specific transition from swamp flora to roof flora. The Walshville paleochannel was the major river running through and draining the Herrin coal swamp, and flooded the swamp on occasion (Bauer and DeMaris, 1982). As base level rose in response to marine transgression, the channel began to choke causing floods and deposition of clastics on the adjacent peat. This may have disturbed and created large openings in the swamp forest. Colonization of this kind of habitat by a low-diversity vegetation suggests that these lycopod trees were opportunistic, that is, capable of rapidly occupying recently disturbed low-competition environments.

Lycopod Forest Dynamics

The data from this study combined with the known features of lycopod morphology, growth, and development provide some insights into the dynamics of the forests formed by true *Lepidodendron*. Starting points for comparison are Schlesinger's (1978) study of the Okefenokee Swamp forest, an ombrotrophic (rain-fed) peat swamp dominated by *Taxodium* (bald cypress), and the study of Gibson and Good (1986) on *Chamaecyparis thyooides* (Atlantic white cedar) swamps. Schlesinger described several general attributes of swamp forests, particularly those in ombrotrophic settings: low taxonomic diversity, high basal stem area per hectare, random tree spacing, low crown volumes, and an abundance of species with evergreen-sclerophyllous habit. Such forests show low levels of intraspecific and interspecific competition and are structured primarily by the interaction of disturbance (fire, in the case of the Okefenokee) and environmental stress (*sensu* Grime, 1979). Gibson and Good, also studying a simple conifer-dominated system, found a distinct relationship between self-thinning of the stand, presumably due to intraspecific competition and site quality. The most dense stands were those of low quality sites where the onset of self-thinning was delayed. They also found stands to be even-aged, establishing themselves after disturbance of the site by clear cutting.

Although the gymnosperms *Taxodium* and *Chamaecyparis* differ enormously in gross anatomy and morphology from *Lepidodendron*, the parallels and consistencies between Schlesinger's observations and conclusions and the patterns described by Gibson and Good and our study are striking. The lycopod forests we describe are low in diversity and have high basal areas per hectare; the trees are spaced essentially randomly and disturbance appears to be a key element in initiating forest stands. Lycopods had low crown volumes for most of their growth period (DiMichele and Phillips, 1985; Wnuk, 1985) and their sclerophyllous leaves were probably evergreen. The latter trait has been related to plants tolerant of low-nutrient conditions. This certainly seems to have been the case with lycopod trees growing on peat or flooded fresh clastic substrates.

Lepidodendron sp. seems to have been more opportunistic than *Taxodium disticum*, but like *Chamaecyparis thyooides* could establish in even-aged stands after disturbance. *Lepidodendron* trees were cheaply constructed with little wood and thick, but non-lignified, supportive bark. Combined with a single short interval of massive reproduction late in tree growth, cheap construction allowed the trees to disperse to sites that were recently disturbed but intrinsically stressful, then grow quickly and repeat the cycle. The data suggest limited intraspecific interaction and subsequent self-thinning, probably a consequence of the very low nutrient conditions in the swamps. In a patchy landscape, as in swamp forests surrounding channel systems, many local stands of such trees may have existed with each stand in a different phase of development. Lycopod forests of this kind may be an extreme in forest dynamics within stressful environments.

In his review of lycopod forests, Gastaldo (1986) noted that lycopod forests of clastic swamp settings grew mostly in sediment-accumulating environments and may represent the rapid colonization of a single surface following disturbance. However, Gastaldo (pers. comm.) and Wnuk (1985) also have discovered stands of lycopod trees of different ages. These assemblages are dominated by *Lepidophloios* and *Diaphorodendron*, which implies that there are a number of kinds of lepidodendrid-dominated forests with different dynamics.

Analyses of tree distribution at the Orient No. 6 Mine and sites detailed in Schmitz (1896), Beckett (1845), and Gastaldo (1986) suggest random or only slightly ordered distributions of the trees. Several pairs of trees in the largest size classes at Orient No. 6 were nearly abutted. Thus, close spacing does not seem to have influenced the ability of trees to achieve maximal size under the local conditions. Furthermore, these lycopods show an exceptionally high basal area per hectare indicating dense stands of large trees. Allowing for our overestimation, this is still greater than that reported by Schlesinger (1978) for the Okefenokee forests. Taken together, these observations suggest few competitive interactions among the trees. We suggest that tree interactions were limited mostly to simple physical space expropriation. This, again, is consistent with observations of low competitive interactions among plants in abiotically stressful peat swamps.

As far as is currently understood, lycopod trees that had dendritic dichotomously or anisotomously branched crowns were determinate (Andrews and Murdy, 1958; Eggert, 1961); *Lepidodendron* trees had this kind of habit (Thomas and Watson, 1976). Juvenile trees were unbranched and columnar in shape, clothed with linear lanceolate leaves that formed the "crown". In *L. aculeatum* branching began when the trunk reached approximately 30 m in height (Thomas and Watson, 1976). Thus, a branched crown was present only in the final phases of determinate growth. This is a short period relative to the total life of the tree. Cones were borne laterally in the crown, which confined reproduction to the final growth phases and made the tree essentially monocarpic. Canopy interactions among juvenile trees would have been minimal, thus leading to little competition for sunlight. This would have been especially significant where lycopod trees could establish, rapidly forming an approximately even-aged stand. The branched crowns do not appear to have formed a dense canopy; branching was

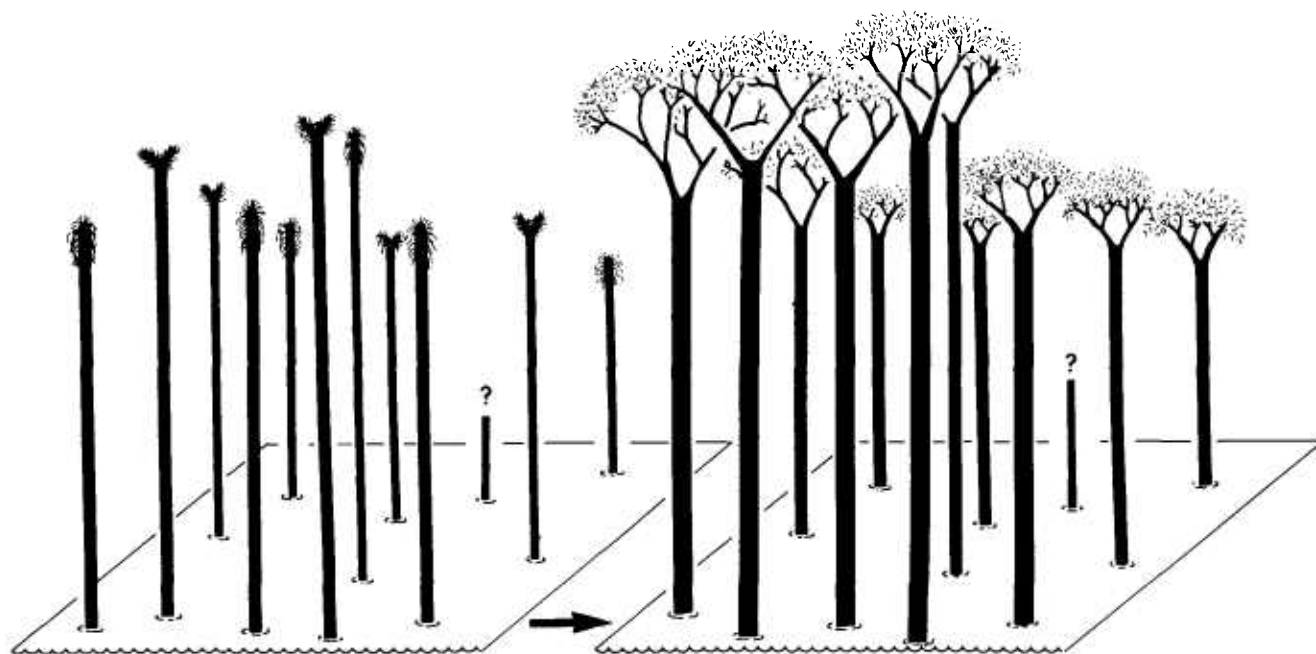


FIGURE 13—Schematic reconstruction of lycopod forest stand in two stages of tree development. Stage 1 (left) shows trees in pre-reproductive phases just as branching is beginning in some individuals; note extreme openness of canopy. Stage 2 (right) illustrates the forest in its final developmental stage when trees are reaching or have reached reproductive maturity; these trees had one period of reproduction before death (monocarpic). Stem of indeterminate affinity marked by (?), possibly calamite or pteridosperm.

sparse and leaves were short, closely investing crown branches, and were abscised from all but the termini of the branches (Chaloner and Meyer-Berthaud, 1983). The major adaptive advantage conferred by the crown was probably reproductive; it provided an elevated site for cone production with greater area than an unbranched trunk, which facilitated dispersal of spores and seed-like propagules. We have reconstructed the forest as it may have appeared when trees were in the pre-reproductive stage and again at a later stage when growth and reproduction were in terminal phases (Fig. 13).

The Orient No. 6 stand appears to have had a relatively narrow age structure. There is no evidence of successive generations, although this does not mean that this type of tree was incapable of self-replacement on sites. Changing local conditions at the Orient No. 6 sites probably prevented the successful establishment of new individuals, but allowed standing individuals to persist.

CONCLUSIONS

As a group, the lepidodendrids were able to exploit sites of low nutrient availability better than most contemporaneous plant groups. They frequently dominated coal-swamp forests, often developing as nearly monotypic stands and probably under conditions stressful to most other plant species. In compression preservation, lepidodendrids are common as stumps in sandstones and shales and on sites with little evidence of soil development or with weakly gleyed soils, again suggesting low-nutrient substrates. The close placement of

stumps and the general random distribution of trees on a site suggest little competition for light or substrate nutrients. The columnar shape of juveniles and the open late-developing branched crown of the sexually mature plants would have formed a very open canopy that would not have severely attenuated light penetration. Because of nutrient chelation by organic acids in the substrate and low oxygen availability to roots in flooded areas, lepidodendrids may have removed nutrients primarily from the water column rather than relying on release from the substrate. This condition also is found in some modern swamps (Schlesinger, 1978). The forests formed by these lycopod trees probably were short-lived and structured primarily by responses to abiotic factors with limited density-dependent effects.

Comparison of modern intrinsically stressful swamp environment with those of the Pennsylvanian suggests that the organization and structure of the communities is generally very similar. Diversity is low, competitive interactions among plants appears to be low despite high stem densities, and complexity of the forests is low as measured in number of stories, number and diversity of epiphytes, and diversity of life forms and plant habits. In other words, the system is simple in structure and controls compared to non-swamp vegetation. In addition, the geological record of swamp forests suggests that these species associations may persist for long periods of time, even though a given swamp may be short-lived locally, and that they are terminated by catastrophic disturbances that disrupt the associations and displace or eliminate many species. Following these disruptions, new stratigraphically long-ranging species

associations are established (Knoll, 1985; DiMichele, Phillips and Olmstead, 1987). Despite similarities between some modern and ancient swamps in the ecological strategies of the dominant plants and in community structure, the plants of the Pennsylvanian swamp described here have few modern analogs. Similarities in morphology, such as evergreen habit, sclerophylly, and low crown volumes reflect only very general "convergence" and suggest that certain aspects of morphology confer an advantage under swamp conditions. However, there is little evidence of phenotypic convergence at the level of specific morphological traits when lycopods are compared to modern gymnospermous or angiospermous swamp trees.

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The whole system of human culture is based fundamentally on a mechanism of communication and transmission that requires people to be brought up in such a way that they develop a mental setup which leads them to be ready to believe others. . . . A frequent result of the process seems to be that people believe too much and believe it too strongly. The process that evolution has provided us for doing the job seems often to lead to considerable exaggeration of the ability to believe.

—C. H. Waddington