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ARBORESCENT LYCOPOD REPRODUCTION AND PALEOECOLOGY IN A COAL-SWAMP ENVIRONMENT OF LATE MIDDLE PENNSYLVANIAN AGE (HERRIN COAL, ILLINOIS, U.S.A.)

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ABSTRACT

DiMichele, W.A. and Phillips, T.L., 1985. Arborescent lycopod reproduction and paleoecology in a coal-swamp environment of late Middle Pennsylvanian age (Herrin Coal, Illinois, U.S.A.) Rev. Palaeobot. Palynol., 44: 1—26.

The arborescent lycopods dominated many coal-swamp plant communities of the Middle Pennsylvanian. A relatively small number of important species occurred in coal swamps, each with distinctive ecological requirements reflected in their reproductive biology. The major genera in the late Middle Pennsylvanian age Herrin Coal of the Illinois Basin were *Lepidophloios*, *Lepidodendron* sensu *L. scleroticum* and *L dicentricum*, and *Paralycopodites*, which are dealt with in this study. *Sigillaria*, and *Lepidodendron* sensu *L. hickii* (true *Lepidodendron*), were minor parts of the vegetation. The species of these genera conform to three ecological strategies. Opportunists include *Lepidophloios hallii*, *Lepidodendron dicentricum*, and *Lepidodendron hickii*. These species had determinate, dendritic crowns and each tree apparently reproduced during a short, unrepeated interval late in determinate growth. They grew in areas that were disturbed or with high abiotic stress. *Paralycopodites brevifolius* was a colonizing species, rapidly occupying sites where peat formation was irregular, and perhaps locally disturbed by clastic influx. *Paralycopodites* had straight trunks with rows of deciduous lateral branches; cones were borne at the tips of the branches conferring individuals with continuous, high levels of reproduction. Displacement from sites occurred as edaphic conditions changed. *Lepidodendron scleroticum* and *Sigillaria* were site occupiers. *Lepidodendron scleroticum* trees individually produced the most massive wood and periderm of coal-swamp lycopod species, and also had deciduous lateral branches and low but continuous reproductive output. Locally, *L. scleroticum* was very abundant, and such areas occurred irregularly. None of the lycopod trees had vegetative reproduction. Some *Sigillaria* may have been apomictic, although the major circumstantial evidence supporting this is from Upper Pennsylvanian specimens of *Mazocarpon oedipternum*.

INTRODUCTION

Arborescent lycopods dominated the vegetation of most Euramerican coal swamps during the Early and Middle Pennsylvanian. Such abundance was due to vegetative and reproductive traits that allowed lycopods to exploit low-nutrient coal swamps more effectively than other contemporaneous

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plant groups (DiMichele et al., in press). The coal swamps of the late Middle Pennsylvanian, including that represented by the Herrin Coal of the Illinois Basin, were the most diverse floristically of the entire Pennsylvanian. They included many of the important species of lycopods in a variety of ecological settings. Morphological studies of anatomically preserved lycopods from coal swamps provide the basis for correlation of sexual reproductive cycles, reproductive outputs, and modes of dispersal, with growth and cone-bearing habits of lycopod trees. In combination with community analyses, we can deduce ecological amplitudes and the relationships of ecology to evolution, migration and extinction, which mediated the changing abundance patterns of lycopods during the Middle Pennsylvanian.

The principal lycopods that we discuss from the Herrin Coal are *Lepidophloios*, *Lepidodendron*, and *Paralycopodites*. These, and other Pennsylvanian age, lycopod trees had no detectable means of vegetative reproduction, with the possible exception of apomixis. Therefore, potentially sexual megaspores were the principal means for production and dispersal of new sporophytes. In the most abundant arborescent lycopods of coal swamps megaspores were part of a complex sporangium—sporophyll unit, specialized for various modes of wind and aquatic dispersal (Phillips, 1979). Because of the reliance on sexual reproductive structures in a spore-to-spore life history, details of reproductive biology are highly correlated with ecological roles of the plants in coal-swamp ecosystems.

The vegetational history of the Herrin Coal apparently was controlled largely by site-specific variation in abiotic factors. No clear evidence of directional whole-seam succession has been detected. There are some large-scale patterns of vegetational change that suggest fairly synchronous floristic shifts across much of the coal swamp (Phillips et al., 1977; Phillips and DiMichele, 1981). The general similarity of vegetation from one site to another emphasizes the relative uniformity of the swamp throughout much of its vast extent (Phillips and Peppers, 1984). This vegetational uniformity makes the Herrin Coal ideal for a general study of lycopod reproductive biology. There also are some known paleogeographic changes within the Herrin Coal related to wetter—drier gradients with which reproductive biology can be compared.

GEOLOGICAL SETTING

The Herrin (No. 6) Coal Member of the Illinois Basin Coal Field is in the Carbondale Formation, Kewanee Group and is Middle Pennsylvanian (Desmoinesian) in age. It is equivalent to the Kentucky No. 11 Coal in western Kentucky.

The Herrin is a widespread, thick coal, covering much of the Illinois Basin Coal Field, particularly the southern two-thirds (Smith and Stall, 1975). It overlies a thick sequence of deltaic sediments and was derived from a low-lying, fresh-water, peat swamp (Wanless et al., 1969). Brackish waters did not invade the swamp until late in its development. A marine transgression is indicated in the peat by local occurrences of mixed, marine faunal—plant coal balls at the top of the coal (DiMichele, 1978, 1979b), and by marine muds deposited in paleochannels at the top of the coal (DeMaris et al., 1983).

A large meandering river, the Walshville Channel (Johnson, 1972; Algaier and Hopkins, 1975), flowed southward through the Herrin coal swamp for over 270 km (Nelson, 1979). The coal thickens markedly in proximity to the channel in places, and frequently contains clastic splits deposited during floods. Thick wedges of a non-marine gray mudstone, the Energy Shale, overlie the Herrin Coal along the Walshville Channel; these are interpreted as crevasse splay deposits (Bauer and DeMaris, 1982). Overlying the Energy Shale are marine deposits, the black, fissile Anna Shale and the Brereton Limestone. Farther away from the Walshville Channel, where the Energy Shale was eroded or not deposited, these marine rocks directly overlie the coal.

Natural outcrops of the Herrin Coal are practically non-existent, so our sampling was restricted to active mines, both surface and underground. This biases our sampling because active mines generally are located where coal is thickest and most accessible. Active mines in Herrin Coal lie along an arc extending southward from Springfield, Illinois to East St. Louis, and then eastward across the southern part of the state into western Kentucky. Most of the coal-ball sites are in the southern part of the basin (Fig.1), through a transect of approximately 185 km. The closest sample sites to the Walshville Channel are those from the Old Ben No. 24 Mine, 15 km away.

MATERIALS

Coal-ball vertical sections were analyzed from the following localities:

1. Sahara Coal Company No.6 Mine, west of Harrisburg, Saline County, Illinois, Vertical Section (VS) 2 — Harrisburg 7 1/2′ Quad. (Sec. 30, T9S, R5E), and VS 5 — Harrisburg 7 1/2′ Quad. (SE, Sec. 24, T9S, R4E)
2. AMAX Coal Company, Delta Mine, Pit 5 1/2, Crab Orchard, Williamson County, Illinois, VS 2 — Marion 15′ Quad. (Sec. 28, T9S, R4E)
3. Old Ben Coal Company No. 24 Mine, Benton, Franklin County, Illinois, VS 3 and 5, and 4 — Ina 15′ Quad. (Sec. 11, T6S, R2E)
4. Peabody Coal Company, Eagle Surface Mine No.2, Shawneetown, Gallatin County, Illinois, Core of coal balls (“Shawneetown Core”) — Shawneetown 7 1/2′ Quad. (Sec. 9, T10S, R4E)
5. Peabody Coal Company, Ken Mine, Ohio County, Kentucky, VS 2 and Random Sample — Paradise Quad. (37° 16′33″N, 86° 57′42″W)

Random samples were examined from fourteen additional mines in the Illinois Basin (Fig.1). All specimens are housed in the Paleobotanical Collections, Department of Plant Biology, University of Illinois, Urbana, Illinois.

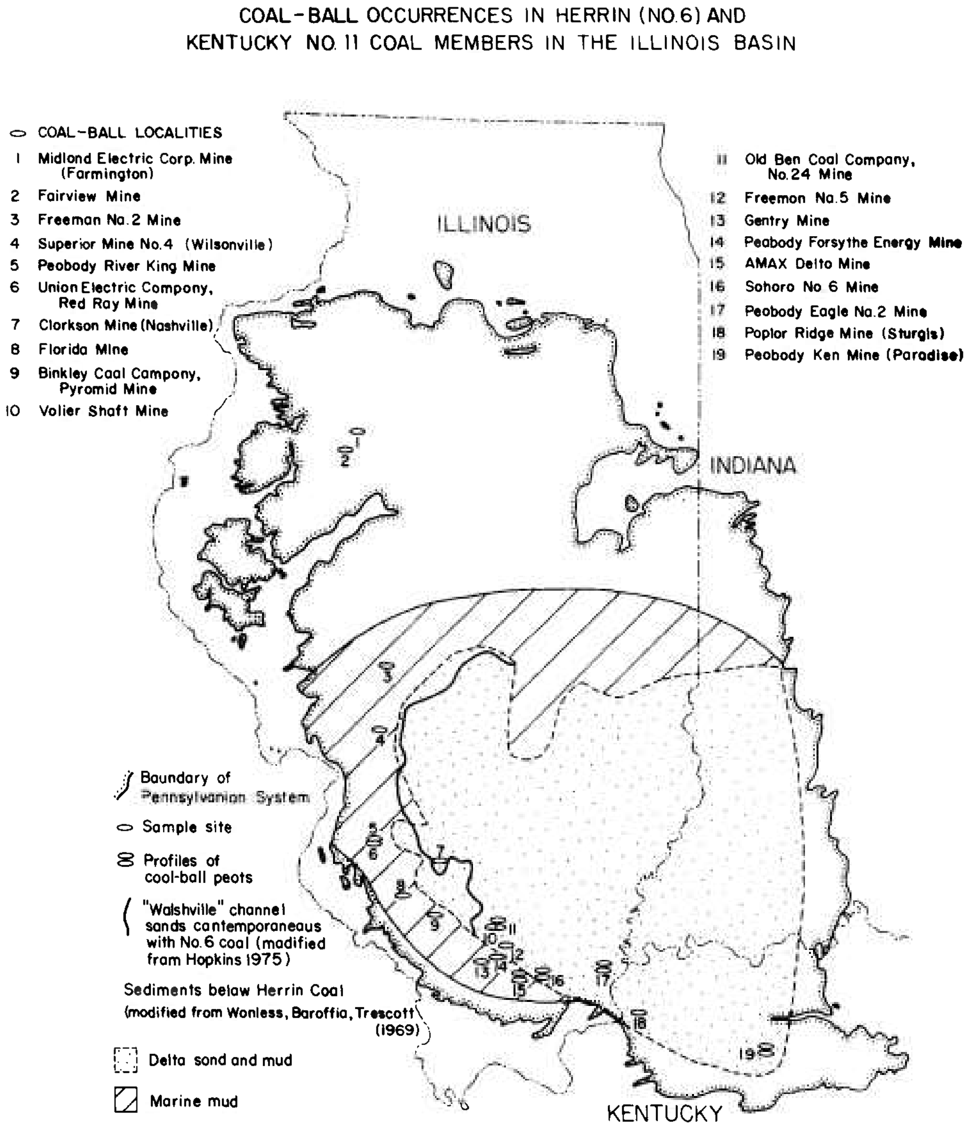

Fig.1. Coal-ball localities in the Herrin (No.6) Coal and its equivalents in the Illinois Basin. The coal swamp developed over a platform of marine sediments deposited prior to a marine regression. The Walshville channel is a sandstone and shale deposit contemporaneous with the coal; the direction of flow was southward.

METHODS

Coal balls were collected as random samples from active mine areas or tipples, or as profiles directly from the coal seam. Techniques for collection and processing of vertical sections are those of Phillips et al. (1977), modified by quantifying a peel from each saw cut in the coal ball. Cellulose acetate peel preparations follow the techniques of Joy et al. (1956). The percentages given for identified plant material have been normalized to 100% taxonomically identifiable plants. The amount of unidentifiable material in coal balls from the Herrin Coal is typically 10—20%. Percentages given for the abundance of lycopod aerial tissues are based on the whole peat volume of a profile or random sample. Roots have not been factored out of these calculations, as we have done for ecological analyses of communities (Phillips and DiMichele, 1981). However, lycopod root systems are not reported as part of the contribution of each species to the total peat volume because not all of the roots can be assigned with consistency to specific stem taxa.

LYCOPOD COMPOSITION OF THE HERRIN COAL SWAMP

Quantitative analyses of structural-peat deposits in coal balls from the Herrin Coal indicate that lycopods account for 69—75% of the total peat volume at the sites sampled (Phillips et al., 1977; Phillips and DiMichele, 1981) (Table I). Lycopod cones and sporangium—sporophyll units account for only 1—2% of the total lycopod biomass; other aerial vegetative tissue, mostly bark, accounts for 20—56%, and *Stigmaria* root systems of lycopod trees account for 11—36%.

Six species of arborescent lycopods have been identified in the Herrin Coal. Three of these species account for 97% of the total lycopod biomass:

TABLE I

Lycopod abundance in the Herrin (No.6) Coal Member: percent volume of total peat profile

Coal-Ball Profiles	Lycopods	Lycopod stems	*Lepidophloios hallii*	*Lepidodendron scleroticum*	*Lepidodendron dicentricum*	*Paralycopodites brevifolius*	*Sigillaria* sp.	*Lepidodendron hickii*
Delta VS 2	72.1	55.6	49.2	2.7	1.0	2.6	0.08	0.0
Shawneetown Core	74.9	21.8	19.4	8.1	0.3	0.3	0.0	0.0
Old Ben VS 3—5	77.8	36.0	28.2	2.6	2.5	2.5	0.2	0.0
Old Ben VS 4	68.9	33.1	19.7	3.4	7.7	0.0	1.3	0.0
Sahara VS 2	72.2	21.6	5.6	11.9	1.1	0.7	2.3	0.0
Sahara VS 5	63.4	21.6	7.3	8.2	4.0	2.0	0.02	0.0
Sahara VS 4	64.9	26.7	20.6	1.6	3.0	0.2	1.0	0.3
Paradise VS 2	75.1	50.0	—	—	—	—	—	—

Lepidophloios hallii, *Lepidodendron scleroticum*, and *L. dicentricum*. The others are *Paralycopodites brevifolius*, *Sigillaria* sp., and *Lepidodendron hickii*. *Lepidophloios hallii* is the most abundant plant in the Herrin Coal; its aerial tissues and organs account for 20—50% of the total peat volume at sites we have sampled. *Lepidodendron scleroticum* (3—11%) and *L. dicentricum* (1—8%), although less abundant than *Lepidophloios* overall, were very important in some parts of the coal swamp. *Lepidodendron scleroticum* and *L. dicentricum* are treated here as belonging to the genus *Lepidodendron*; however, they differ substantially from *Lepidodendron hickii*, which belongs to the same phyletic lineage as the type species of *Lepidodendron* (L. *aculeatum*, see Thomas, 1970). *Lepidodendron scleroticum*, *L. dicentricum*, and related forms found in other coal swamps, should be considered as part of a distinct genus (see DiMichele, 1983, for discussion). *Paralycopodites* is usually rare (<2%) and appears to be an indicator of environments transitional from clastic to peat substrates. *Sigillaria* (<2%) and *Lepidodendron hickii* were quite rare, and may indicate drier or higher-nutrient parts of the coal swamp. Non-arborescent lycopods in the Herrin coal swamp were *Chaloneria* (Pigg and Rothwell, 1983), *Selaginella* (Phillips and Leisman, 1965), and *Spencerites* (Leisman and Stidd, 1967).

MORPHOLOGY, REPRODUCTIVE BIOLOGY AND DISTRIBUTION

All of the Pennsylvanian age lycopod trees were heterosporous. The sexual phases were a large endosporic female gametophyte and a small endosporic male gametophyte. Reproductive differences among the species were found in growth habit, timing of cone production, and cone architecture. *Paralycopodites brevifolius* was the only species with bisporangiate cones. All others produced separate microsporangiate and megasporangiate strobili. Despite differences in habit, individual trees of all species apparently had determinate vegetative growth (Andrews and Murdy, 1958; Eggert, 1961). This is one of the more unusual aspects of lycopod trees and an important controlling factor in their ecology.

Each of the lycopod tree species had a distinct ecological strategy in coal-swamp ecosystems. Reproductive traits were an important part of the strategy, in particular the architecture of dispersal units and the timing of reproduction in each species. Dendritic, synchronously determinate crowns developed in *Lepidophloios hallii*, *Lepidodendron dicentricum*, *Lepidodendron hickii* and *Sigillaria* spp. (Lemoigne, 1960; DiMichele, 1979a, b, 1983; Wnuk, in press). *Lepidophloios hallii* and *Lepidodendron hickii* produced their cones laterally on crown branches late in determinate growth, in one relatively short period of reproduction. *Lepidodendron dicentricum* bore its cones at or near tips of crown branches, probably in a short, unrepeated period of reproduction (DiMichele, 1979b, 1981; Wnuk, in press). Cones of *Sigillaria* were borne in whorls on the main trunk and crown branches, in repeated, but discrete, periods of reproduction (Schopf, 1941a).

Paralycopodites brevifolius and *Lepidodendron scleroticum* had main trunks that appear to have been determinate. The crown was formed by two or more rows of deciduous lateral branches borne along the trunk (DiMichele, 1980, 1981; Wnuk, in press). Cones were produced at the tips of the deciduous branches, resulting in nearly continuous reproduction in sexually mature plants.

Reconstructions of some of these trees in reproductive phases are shown in Fig.2.

Lepidophloios hallii (Evers) DiMichele

Lepidophloios hallii is estimated to have been a small tree with a maximum height of 10—15 m (Hirmer, 1927; DiMichele, 1979a). Formation of a dendritic, dichotomously branched crown in the later phases of growth coincided with the onset of reproduction (Fig.2). During most of the vegetative development the trees grew as unbranched cylinders clothed with leaves (Andrews and Murdy, 1958).

Lepidophloios hallii produced megasporangiate cones, *Lepidocarpon*, and microsporangiate cones, *Lepidostrobus oldhamius* (Schopf, 1941a; Felix, 1954; Crookall, 1964; Balbach, 1967; Phillips, 1979). Cones were borne on short, lateral, halonial branches in two or more rows, on stem segments (>3 cm in diameter) located in the middle and upper crown. Cones also may have been borne at the tips of terminal branches (Weiss, 1903; Thomas, 1978; DiMichele, 1979a). Evidence supporting the cone-bearing function of halonial branches, a long-standing controversy (Jonker, 1976), includes the anatomical similarity of *Lepidocarpon* and *Lepidostrobus oldhamius* axes to halonial branches, and the disruption of halonial vascular systems by periderm formation. The latter is consistent with the vascularization of deciduous structures (DiMichele, 1979a). Relative positional relationships of microsporangiate and megasporangiate cones are not known. However, confinement of cone-bearing branches to the middle and upper crown regions indicates a sustained, but relatively short, and unrepeated period of cone production late in the determinate growth of the trees.

Lepidophloios hallii produced very large numbers of *Lycospora granulata* microspores. Where *L. hallii* is present, even in small numbers, this spore tends to dominate the coal-spore flora (Peppers, 1970, 1982). *Lepidocarpon* cones disaggregated at maturity, releasing large numbers of megasporangium-sporophyll units, which were very seed-like in their construction. The lateral laminae, or "integument", enveloped the megasporangium, which contained a single functional megaspore and a massive female gametophyte. Phillips (1979) suggested that these units were dispersed by water, and that fertilization occurred following cone disaggregation and release of the *Lepidocarpon* units into the swamp. Embryos, some with secondary xylem (Phillips et al., 1975; Phillips, 1979), and the massive, nutritive female gametophytes suggest that floating *Lepidocarpon* could remain viable for long periods. It is the most common, and uniformly distributed of any swamp-plant reproductive structure (Table II), despite its large size, occur-

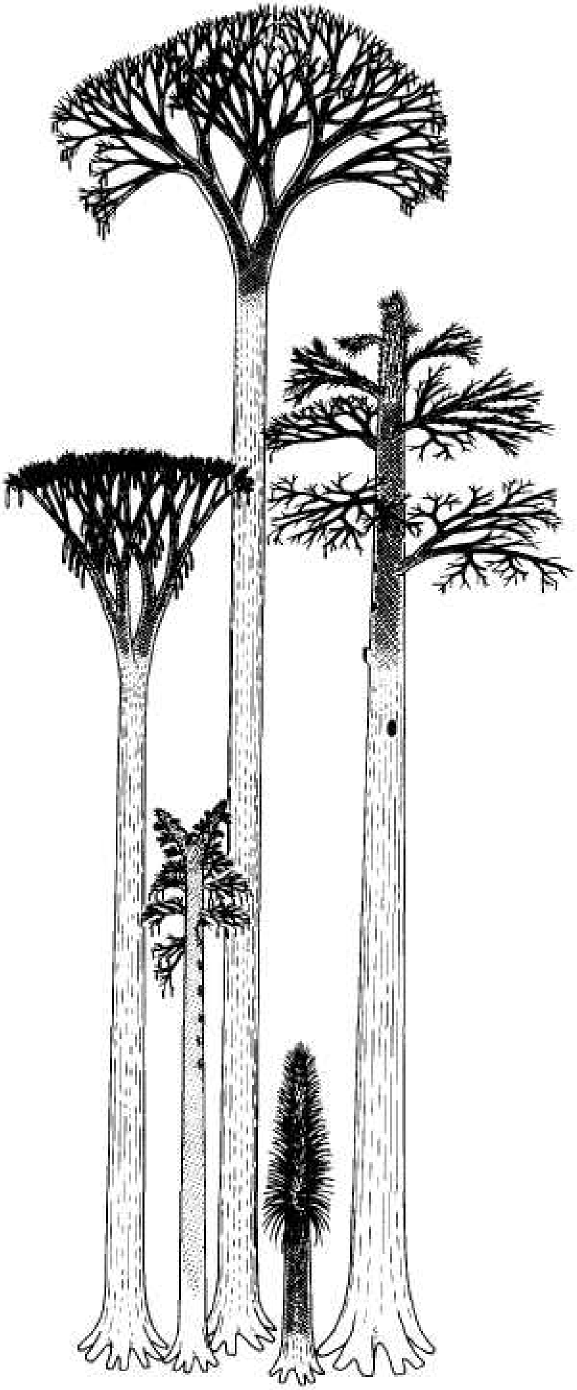

Fig. 2. Reconstructions of the major arborescent lycopods of the Herrin Coal. Left to right: *Lepidophloios hallii*, *Paralycopodites brevifolius*, *Lepidodendron dicentricum*, young pre-reproductive tree of general form, *Lepidodendron scleroticum*. All trees, except juvenile, shown in reproductive phases of growth. See text for further details.

TABLE II

Distribution of lycopod fructifications in coal-ball profiles: percent of total peat volume by zone (zone 1 is bottom-most in each profile)

	Zone number												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Old Ben VS 4													
Lepidocarpon lomaxii	0	0.2	1.5	0.4	0.7	0.4	0.3	2.2	1.1	0.8	0.44	0.45	
Lepidostrobus oldhamius	1.2	0	0.27	0	0	0	0	2.6	2.5	0	0.02	0	
Lepidostrobus diversus	0	0	0	0	0	0	0	0	0	0	0	0	
Achlamydocarpon varius	0	0	0	1.1	1.5	0.18	0	0.97	3.1	0	0.02	0.3	
Delta VS 2													
Lepidocarpon lomaxii	1.55	0.4	0.52	1.27	0.49	0.96	1.15	0.31	0				
Lepidostrobus oldhamius	0.25	0	0.12	0.99	0.01	0.24	0	0	0				
Lepidostrobus diversus	0	0.05	0	0	0	0	0	0	0				
Achlamydocarpon varius	0	0	0.01	0.17	0.01	0.87	0.01	0	0				
Sahara VS 5													
Lepidocarpon lomaxii	1.3	1.7	0.9	5.6	1.1	2.5	1.6	3.0	2.9	1.9	4.7	1.6	2.6
Lepidostrobus oldhamius	0	0.13	0.37	1.5	0.02	0.2	0.48	3.9	0	0.1	0	0	0.31
Lepidostrobus diversus	0	0	0	8.5	0	0.02	0.04	0	0	0.25	0	0	0
Achlamydocarpon varius	0	0.04	0.37	0.41	0.31	0.5	0.63	0.4	3.8	2.05	0.15	0.04	0
Sahara VS 2													
Lepidocarpon lomaxii	0.4	0	0.4	1.5	0	0.5	0.1	0.1	0.16				
Lepidostrobus oldhamius	0.2	0	0	0.4	0	0	0	0.8	0				
Lepidostrobus diversus	0	0	0.3	0.4	0	0	0	0.05	0.04				
Achlamydocarpon varius	0	0	0.1	0	0	0	0	0.12	0.29				

ring in almost all zones of a coal-ball profile, even those where *Lepidophloios* vegetative tissues are rare or absent.

Lepidophloios hallii was the most common lycopod of the Herrin coal swamp; its tissues account for as much as 50% of the peat at some sites (Table I). The distribution of *L. hallii* on a site through time, based on coal-ball profiles, conforms to one of several patterns. Frequently *L. hallii* is the most common plant in several consecutive coal-ball zones and is also common throughout the entire profile (Delta VS 2, Old Ben VS 4, Fig.3; Old Ben VS 3–5, Fig.5; Shawneetown Core, Fig.6). Less commonly, *L. hallii* occurs in low numbers throughout the entire thickness of the profile with great abundance in only a few zones (Sahara VS 2, VS 5, Fig.4). Rarely, *L. hallii* will be absent in several successive zones; this is illustrated by Sahara VS 5 (Fig.4) above a large fusain accumulation in zone 5. Zones above the fusain band are dominated by *Psaronius* and *Medullosa*.

Community analyses (DiMichele and Phillips, 1980; Phillips and DiMichele, 1981) indicate that *L. hallii* reached its maximal abundance in communities of low diversity, with as few as four species. These assemblages usually had few or no homosporous plants or ground-cover plants, such as *Psaronius*, sphenopsids, or coenopterid ferns. This suggests high levels of abiotic stress that excluded many kinds of plants. A long standing-water regime was probably the major abiotic factor controlling the composition of

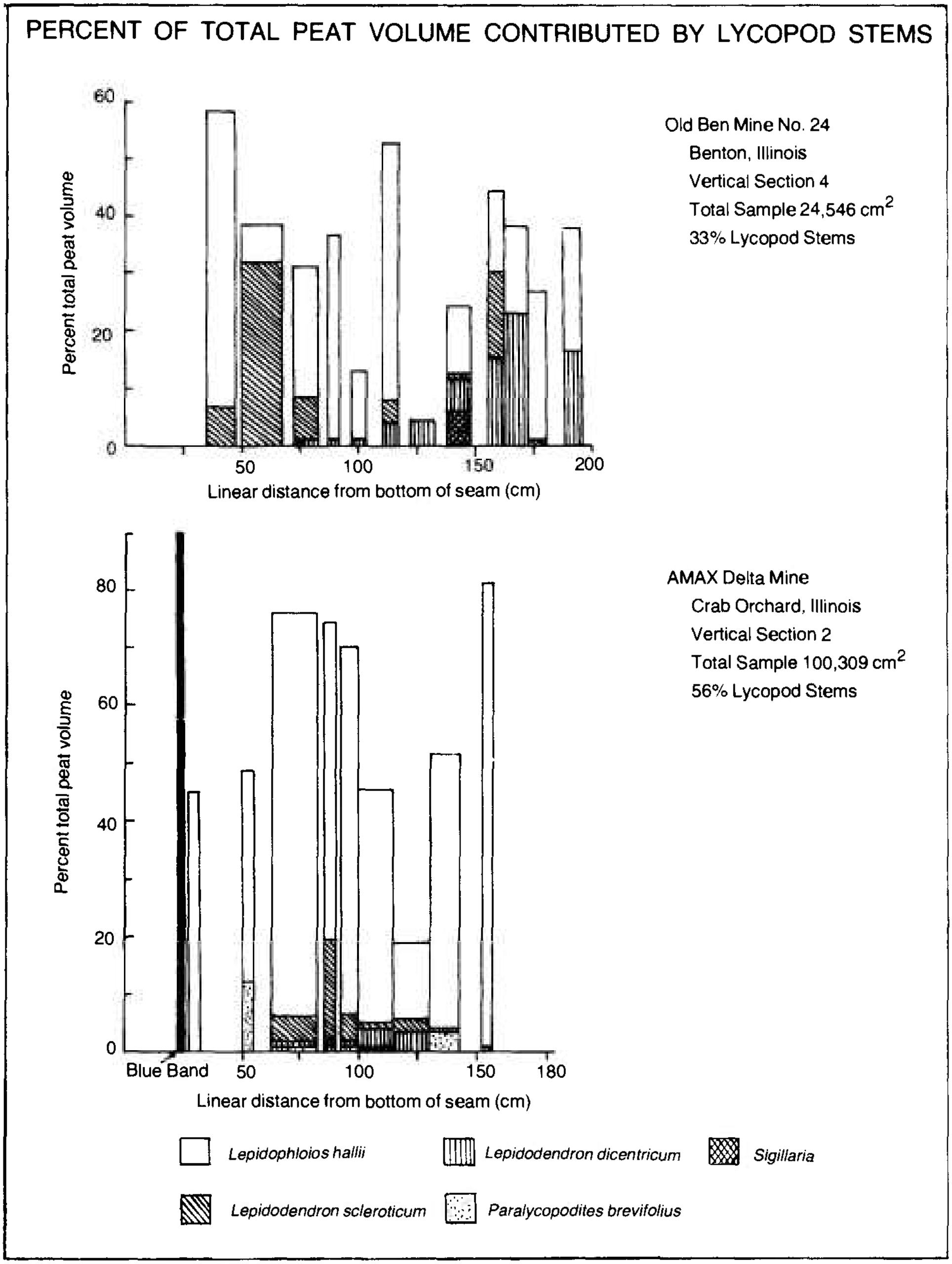

Fig. 3. Percent of total peat volume contributed by lycopod stems in coal-ball profiles from Old Ben Coal Company No. 24 Mine Vertical Section 4, and AMAX Delta Mine Vertical Section 2. Each bar of histogram represents one coal-ball zone in the vertical seam thickness (horizontal axis).

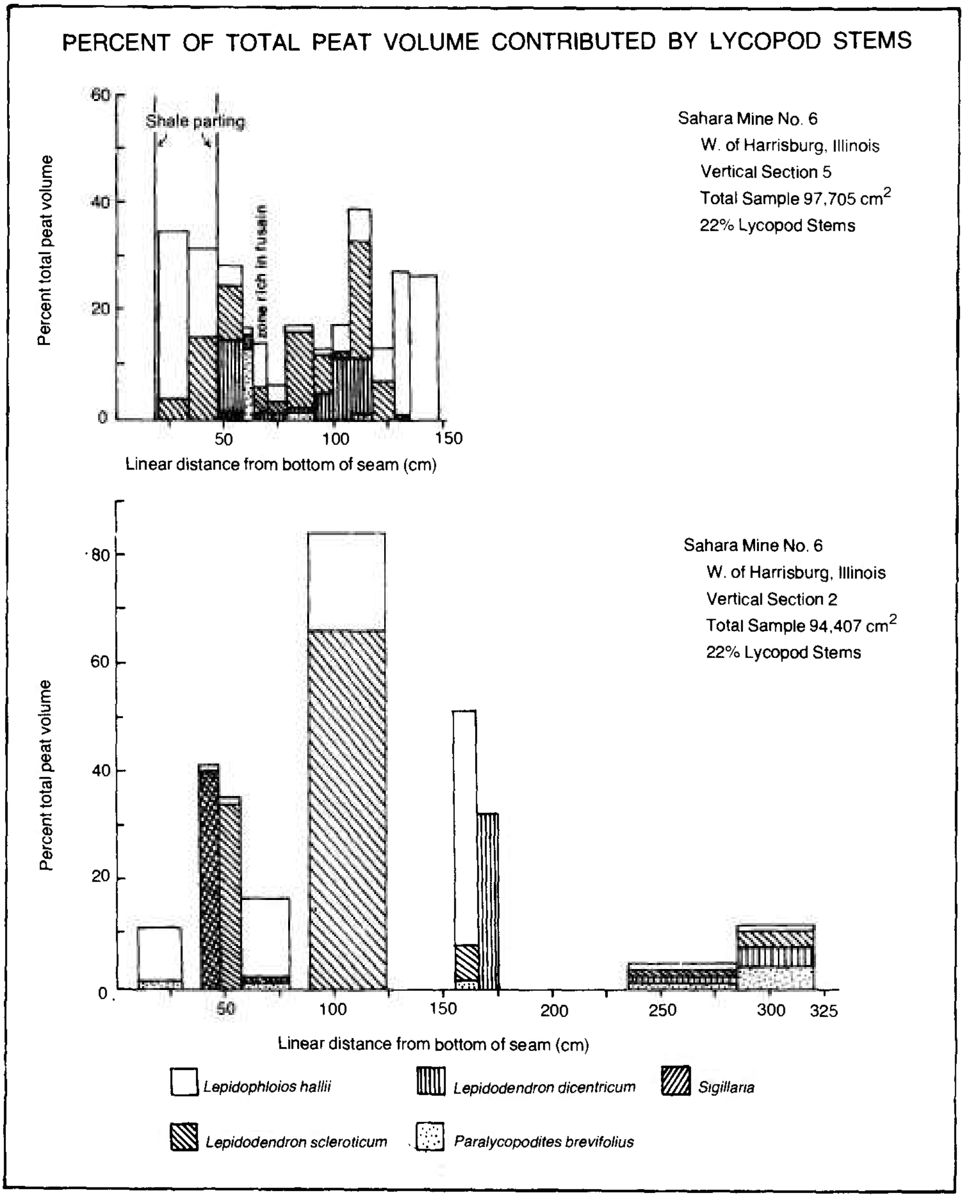

Fig.4. Percent of total peat volume contributed by lycopod stems in coal-ball profiles from Sahara Coal Company Mine No.6 Vertical Sections 5 and 2. Each bar of histogram represents one coal-ball zone in the seam thickness (horizontal axis).

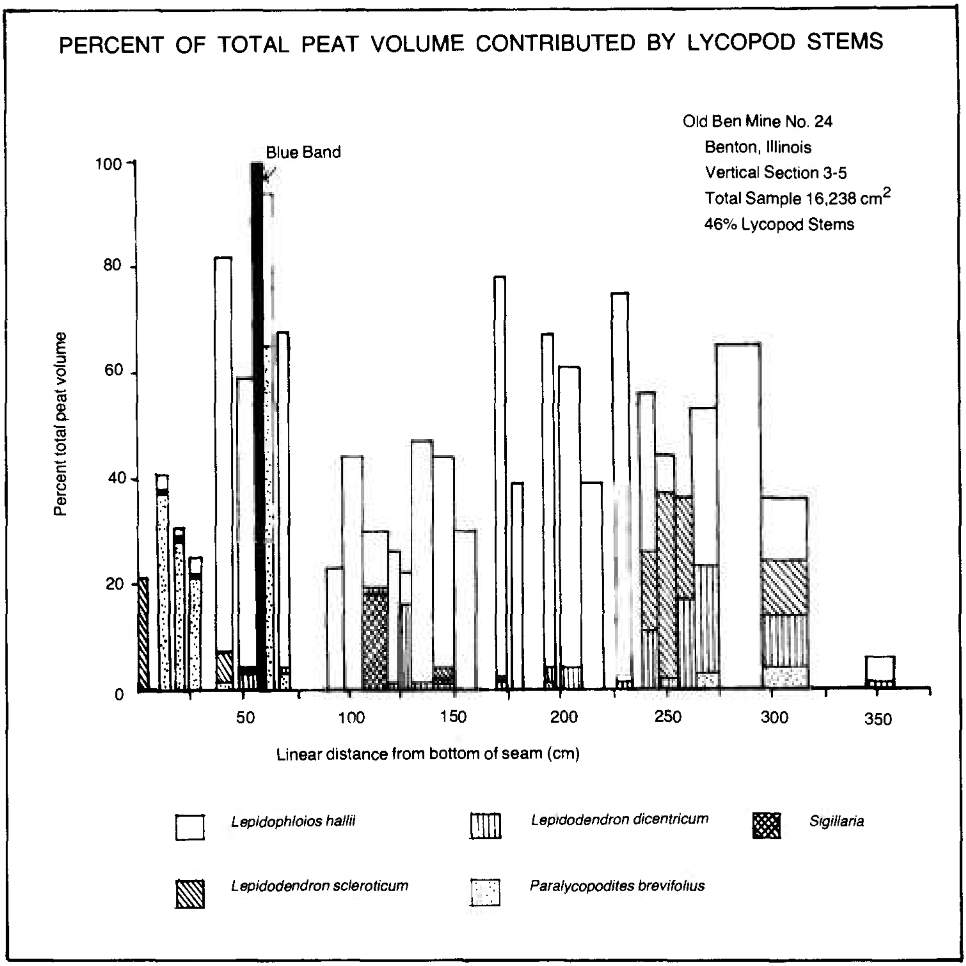

Fig.5. Percent of total peat volume contributed by lycopod stems in coal-ball profiles from the Old Ben Coal Company No.24 Mine, combined Vertical Sections 3 and 5. Each bar of the histogram represents one coal-ball zone in the vertical seam thickness (horizontal axis).

Lepidophloios-dominated assemblages. Under such conditions ground-cover and homosporous plants would have had difficulty becoming established. The morphology and distribution of the organs of *L. hallii* (Phillips, 1979; DiMichele, 1979a) are consistent with this interpretation. *Lepidophloios* is very rare outside of coal-swamp deposits in the Middle Pennsylvanian.

Lepidodendron dicentricum C. Felix

Lepidodendron dicentricum trees were large. Wnuk (in press) describes compression specimens 30—40 m tall; the trees may have been smaller on peat substrates. An anisotomously branched, determinate crown formed late

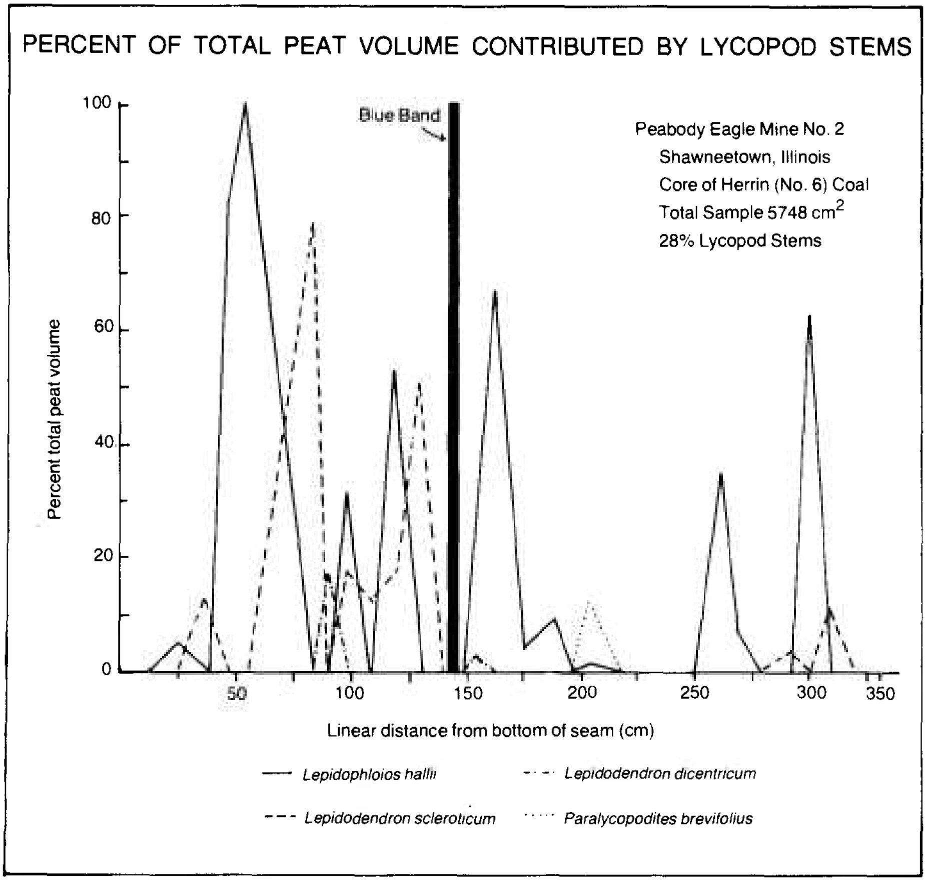

Fig.6. Percent of total peat volume contributed by lycopod stems in core of coal balls from Peabody Coal Company Eagle Surface Mine No.2.

in growth (Fig.2) (DiMichele, 1979b, 1981; Wnuk, in press). As with *Lepidophloios hallii*, a *L. dicentricum* tree was a cylinder with an apical clothing of leaves during most of its growth.

Cones and cone fragments of *Achlamydocarpon varius* are associated consistently with *Lepidodendron dicentricum*. Cones probably were borne just proximal to the tips of the branches in the determinate crown. Small, protostelic lateral branches, 5—8 mm in diameter, are found only on stems 2—3 cm in diameter. These protostelic branches have anatomy similar to that of cone axes of *A. varius*. The occurrence of cone branches only on stems from the uppermost parts of a determinate crown suggest a relatively short and almost synchronous period of reproduction during the final phase of tree growth.

Achlamydocarpon varius cones were monosporangiate (Taylor and Brack-Hanes, 1976; Leisman and Phillips, 1979). The megasporangiate cones disaggregated at maturity to release numerous sporangium—sporophyll units, which were seed-like in containing a single functional megaspore. These dispersal units are by far the most common identifiable remains of *Achlamydocarpon varius*. The megasporangium opened proximally. The functional megaspore was covered on the proximal face by a large, fibrous massa (Taylor and Brack-Hanes, 1976) that effectively prevented exposure of the female gametophyte even after opening of the spore. Leisman and Phillips (1979) noted that the massa contains numerous pores approximately 65 μm in diameter, about the size of the microspore of *A. varius*, *Cappasporites*. These pores perhaps acted to entrap spores. Microsporangiate cones are much less common than megasporangiate cones or the dispersal units. Similarly, when quantitative studies of peat and palynology are compared, there is usually a far larger percentage of *Lepidodendron* in the coal-ball flora than its microspore *Cappasporites* in the coal-spore flora (Peppers, 1982). This pattern of microspore under-representation in the fossil record of *A. varius* is a sharp contrast with the reproductive patterns in *Lepidophloios* and other *Lycospora*-producing lycopods. It has been noted that *Cappasporites distortus* microspores are commonly in tetrads in the sporangia (Leisman and Phillips, 1979, p.110) and in the dispersed state (Chadwick, 1983, p.206). This may reflect some specializations functionally linking the microspores and megaspores (Leisman and Phillips, 1979; Phillips, 1979), perhaps a more precise mode of fertilization. The dispersal potential of megasporangium-sporophyll units of *A. varius* was limited (Table II). Propagules occur most often in association with *Lepidodendron dicentricum*, although they also occur with its relative, *L. scleroticum*, and probably were produced by the entire evolutionary lineage to which these species belong, also including *L. vasculare* and *L. phillipsii* (DiMichele, 1981).

Lepidodendron dicentricum is a minor component of most random coal-ball collections from the Herrin Coal and other upper Middle Pennsylvanian coals of the mid-continent. Its abundance on a site through time was variable, based on occurrences in coal-ball profiles. In most profiles, *L. dicentricum* occurs in most zones, but at <10% of the biomass. One or two zones with 10—30% of whole peat biomass usually occur in each profile, often in zones from the upper 1/2 to 1/3 of the seam (Figs.3 and 4). Community analyses indicated that zones with peak abundances of *L. dicentricum* have high diversity. Included are usually rare plants, such as *Sutcliffia*, *Heterangium*, *Zygopteris*, *Lepidodendron hickii*, and many herbaceous forms. This may be an early successional assemblage, or one resulting from moderate levels of disturbance, maintaining a non-equilibrium setting and high diversity. The occurrence of *L. dicentricum* in most kinds of coal-swamp communities, its determinate habit, relatively short period of reproduction, and maximal abundance in highly diverse assemblages suggest a fugitive ecological role: *Lepidodendron dicentricum* apparently occupied sites for short periods, rarely formed extensive stands, and exploited the randomly occurring openings that characterize a tropical forest.

Lepidodendron scleroticum Pannell

Lepidodendron scleroticum trees were of moderate height. Compressions studied by Wnuk (in press) reached heights of 20–25 m. Most of the close relatives of *L. scleroticum* had straight trunks with opposite rows of deciduous lateral branches. Evidence from coal balls and compression fossils suggests a similar habit for *L. scleroticum* (DiMichele, 1981; Wnuk, in press), resulting in a crown that was not synchronously determinate (Fig.2). Branches probably abscised after the cones they bore had dispersed their units.

Lepidodendron scleroticum and *Achlamydocarpon varius* are associated in coal-ball profiles, but the association is not as great as that between *L. dicentricum* and *A. varius*. However, occurrences of *A. varius* with *L. vasculare* and *L. phillipsii* have been documented from sites in which no other lycopod trees occurred, indicating that the same kinds of reproductive organs were produced by all members of this closely related group of species (DiMichele, 1981).

Cones probably were borne at or near the tips of determinate lateral branches. The continuous production of these branches would have conferred upon *L. scleroticum* a nearly constant reproduction. However, all three *Lepidodendron* species with this growth habit are associated with low numbers of *A. varius* cones or propagules. This suggests low reproductive output at any one time, even though reproduction was temporally extended. Megasporangiate cones and disseminules are much more common than microsporangiate cones; this was apparently the case for all *A. varius* producing lycopods.

The distribution of *L. scleroticum* was more variable in both time and space than that of the other major lycopods in the Herrin coal swamp. In most profiles, *L. scleroticum* dominates several successive coal-ball zones in one or more parts of the profile, and is a minor component, <20% of the biomass, in the remaining zones. Occasionally, it is the major lycopod of an entire profile. Community analyses indicate that *L. scleroticum*-dominated zones are floristically heterogeneous (Phillips and DiMichele, 1981). This is perhaps the most difficult of the lycopods for which to deduce a specific ecological role. The frequent dominance of several successive zones, a capacity for essentially continuous, low-level reproduction, and the relatively thick wood and thick periderm, suggest that individual plants occupied sites for long periods and perhaps in large stands. Variability of associated vegetation and low fusain levels suggest that sites may have been variable in quality and perhaps were perturbated irregularly, favoring dominance of a plant that was literally always in a reproductive phase. *Lepidodendron vasculare*, the closest morphological parallel to *L. scleroticum*, reached its zenith in Illinois Basin coal swamps in the early Desmoinesian. Such coal swamps were irregular in areal extent, quite variable in peat thickness, and frequently split by marine clastic partings (Eggert and Phillips, 1982). The physical characteristics of the coals indicate that the coal swamps were severely disturbed sporadically. Thus, a large part of the success of

L. vasculare may be tied to continuous reproduction, which would provide a constant local background of propagules to re-establish stands following disturbance.

Paralycopodites brevifolius (Williamson) DiMichele

Paralycopodites appears to have been a small tree, probably <10 m tall (DiMichele, 1980). A straight, columnar trunk bore two opposite rows of small, deciduous lateral branches. Both trunk and deciduous branches were determinate; the trunk diminished in size through a limited number of dichotomies. The lateral branches reached maximum diameters of 6—8 cm and lacked wood and periderm, suggesting limited size; secondary tissues were present in the trunk. Leaves remained attached to lateral branches and to most of the trunk (Fig.2; and see reconstruction of *Ulodendron* in Hirmer, 1927).

Paralycopodites is associated with small, bisporangiate cones, which Brack-Hanes and Thomas (1983) have recently transferred from *Lepidostrobus* to *Flemingites*. In the Middle Pennsylvanian *Paralycopodites* is associated with *Flemingites diversus* (Felix, 1954), or *F. schopfii* (Brack, 1970). A similar association with *F. scottii* (Jongmans, 1930) has been noted for Lower Carboniferous specimens (Williamson, 1872, 1893; Scott, 1920; Jongmans, 1930). Cones were produced in abundance. They probably were borne at the tips of the deciduous branches; this connection is suggested by the close similarity in size and anatomy of the smallest branchlets and bases of cone axes. This morphology insured relatively continuous, high levels of reproduction following attainment of reproductive maturity.

Flemingites diversus cones were free-sporing and bisporangiate (Felix, 1954). Abundant *Lycospora micropapillata* microspores were produced in the upper one-half of the cone (Phillips and Peppers, 1984), and megaspores were produced in the lower one-half, 12—16 per sporangium. The megaspores were the dissemination units. They were not part of a sporangium—sporophyll complex, as in *Lepidocarpon* or *Achlamydocarpon*. Endosporic gametophytes were reported by Gordon (1910), Brack-Hanes (1978), and Phillips (1979). Despite the abundance in which they were produced, *Flemingites diversus* cones and dispersed megaspores occur almost exclusively in coal-ball zones where *Paralycopodites* is present. This implies limited dispersal potential for the megaspores.

Paralycopodites is less abundant than most of the other lycopod trees in the Herrin Coal, but is more frequent in occurrence than *Sigillaria*. *Paralycopodites* frequently dominates or is very abundant in a few zones, but is usually absent from the rest of a profile. High abundances in upper Middle Pennsylvanian coals, particularly in the Herrin and Springfield Coals of the Illinois Basin, occur immediately above the underclay, above clastic bands, or in mixed clastic—coal intervals, particularly in the lower parts of the seam. This suggests that *Paralycopodites* may have colonized wet, clastic substrates and been important in the early phases of peat development, both in the initial phases of the swamp and after subsequent disturbances associated with high clastic influx. *Paralycopodites* thus seems to have been part of a colonizing vegetation that also contained abundant medullosan pteridosperms as a dominant or sub-dominant element.

DISCUSSION

The broad spectrum of lycopod ecological strategies is reflected in reproductive traits specific to each. In most instances, ecological parallels can be drawn between lycopod trees and seed-plant trees in modern ecosystems, even though similarities in morphology and ecology clearly have evolved independently. This implies that the number of evolutionary "solutions" to many ecological "problems" may be rather limited — the variations being derived mainly from the underlying architectural distinctions among different plant groups. For the lycopods, the evolution of the tree habit, even with limited wood and phloem, the development of nutrient-rich, highly dispersible propagules, and the ability to exploit low-nutrient, flooded, peat substrates were major factors allowing their success in coal swamps.

One of the most unusual aspects of these trees was determinate vegetative growth. In species with dendritic, synchronously determinate crowns, such as *Lepidophloios hallii*, *Lepidodendron dicentricum*, and *Lepidodendron hickii* (DiMichele, 1983), the trees were unbranched cylinders, partially clothed with leaves for most of their growth period. A sparsely branched crown of limited extent appeared in the later phases of growth; this was associated with diminution in primary body size, smaller leaf cushions and leaves (Chaloner and Meyer-Berthaud, 1983), and ultimately, with cones. This mode of growth is discussed in detail by Eggert (1961), and growth stages are illustrated by Andrews and Murdy (1958), Andrews (1961), DiMichele (1979a, 1981), and, most notably, by Wnuk (in press). Trees with deciduous lateral branches had small crowns; the lateral branch systems were determinate and closely associated with the production of cones. Reconstructions of this type of lycopod crown can be found in Hirmer (1927), in DiMichele (1981), and in Wnuk (in press), who presents developmental states.

The lycopod trees with deciduous lateral-branch crowns parallel modern seed plants in some aspects of crown architecture and function. As in seed plants, crown volume was constantly in flux; the crown was present for most of the tree's life span, and served to markedly increase photosynthetic area. Branch abscission also occurs in some seed plants (Millington and Chaney, 1973).

The synchronously determinate crown, often reconstructed as the typical lycopod growth form, was not functionally analogous to crowns of most other trees. The terminal branching system did not markedly increase the photosynthetic area. It was not densely branched, was associated with diminution in leaf size, and was present for a short time relative to the life of a tree. A major adaptive consequence of the determinate crown was to increase the physical area for cone production, in conjunction with elevation and separation of the cones. This presumably increased the effectiveness of wind dispersal. In essence, such a crown can be considered analogous to an inflorescence. Trees of this form would have cast little shade, and probably had relatively little impact on sub-canopy wind velocities during any stage in their development. Consequently, most lycopod-dominated forests were probably very open, not the dense, dark tropical forests of reconstructions that usually show trees of a forest in a last phase of determinate growth.

Cones of nearly all the arborescent lycopods were similar to shoot systems of the parent plants. Sporophylls usually had a greatly expanded distal lamina that would have significantly augmented the photosynthetic capacity of the fertile branches. In view of the small primary phloem zone and lack of secondary phloem in the stems of lycopod trees (Arnold, 1960; Eggert and Kanemoto, 1979), photosynthesis in the cone itself was probably quite important in its development. Energy allocation studies of numerous extant plants have revealed that both flowers and fruits produce a significant proportion of the photosynthate needed in their development (Bazzaz and Carlson, 1979; Bazzaz et al., 1979; Bazzaz, 1984). This suggests the possibility that reproduction in many plants may be largely energetically independent of vegetative growth. If this is correct, it should significantly change our concept of "reproductive allocation" in plants. For the many lycopod trees with large, short-term reproductive outputs and limited food-translocation systems, the photosynthetic sporophylls were of considerable importance. The distal laminae of these sporophylls potentially had other important functions, at least in some species, in wind and water dispersal of disseminules following disaggregation of megasporangiate cones (Phillips, 1979).

Reproductive strategy and growth form

The ecological distribution of lycopod trees was very much controlled by tree habit and timing of cone production. Determinate trees could occupy sites for limited periods of time. For a population of trees to remain on a site for long periods, replacement in kind would have to occur as individuals matured and died. Anatomical studies indicate a general positive correlation between the thickness of wood and periderm and the habit of the tree. Species with dendritic, determinate crowns, such as *Lepidophloios*, *Lepidodendron hickii*, and *Lepidodendron dicentricum*, lacked, or had only small amounts of wood and periderm in crown branches (final phases of determinate growth), with thicker periderm in the trunk (DiMichele, 1979a, b, 1983; Wnuk, in press). Such trees were "inexpensive" in their construction, and probably grew rapidly with large primary bodies and minimal support tissue.

The species with excurrent trunks and deciduous lateral branches could occupy sites for relatively long periods of time because of extended growth of the main stem, even if ultimately determinate. In *Lepidodendron* *scleroticum* the wood and periderm extended acropetally into relatively small branches and were quite thick in the trunk. Similarly, *L. vasculare*, *L. phillipsii*, and *Paralycopodites brevifolius* had relatively thick wood and periderm in the trunk (DiMichele, 1980, 1981), suggesting extended growth and greater allocation to support tissues.

Plants with determinate crowns and one relatively short period of reproduction would have been most successful in environments where severe disturbances were infrequent, and where completion of the final, reproductive phase of growth was not compromised. However, frequent changes in vegetation within most coal-ball profiles indicate local changes in environment and vegetation, which would have placed a selective premium on rapid growth and reproduction, even in the most stable environments.

Species with extended cone production on deciduous lateral branches, represent a broader spectrum of ecological strategies than the "determinate-crown" species. They range from colonizers to forms that evidently occupied sites for considerable periods, even in the midst of minor vegetational change. As a group, these species appear to have been able to grow and maintain continuity of populations in irregularly and often frequently disturbed areas.

Sigillaria represents a strategy in determinate growth and reproduction different from those found in the other lycopod trees. The crowns were not well developed. Cones were borne on short peduncles, in whorls, repeated in acropetal progression on the trunk and crown branches. *Sigillaria* is more abundant in clastic than in peat-forming environments, and the genus frequently is associated with high fusain in coal-ball profiles. Its probable tolerance of drier sites fits with repeated episodes of reproduction Significant reproductive changes may have occurred between Westphalian and Stephanian age sigillarians, further accentuating adaptation to drier environments, namely by the occurrence of apomixis.

The best circumstantial evidence for apomixis is found in some of the cone specimens of *Sigillaria*, *Mazocarpon oedipternum*, from the Upper Pennsylvanian. Schopf (1941a) reported intact cones with megaspores embedded in intrasporangial parenchyma within the megasporangium. Small, multicellular spherical bodies are present within archegonia of the megagametophytes; these are interpreted as embryos (Schopf, 1941a; Phillips, 1979). With the proximal faces of the megaspores still embedded in the parenchymatous, columellar dome within the sporangium, origin of the putative embryos by fertilization seems unlikely. In his explanation of the functional morphology of *M. oedipternum*, Schopf proposed a series of steps in which sporophylls, bearing sporangia, abscised from the cone axis, and mechanically degraded, releasing the spores. If correct, this sequence of events does not reflect synchroneity of microspore-sperm release and megaspore receptivity, necessary for successful syngamy. It also has been noted that the persistence of intrasporangial parenchyma bound to the megaspore surface (including the proximal face) appears to protect the spore from damage and dehydration (Phillips, 1979). Apomixis has been reported in many extant heterosporous plants, including *Selaginella* and *Isoetes* (Lyon, 1901, 1904; Bruchmann, 1912, 1920; Hieronymous, 1913; Geiger, 1934; Steil, 1939; Horner and Arnott, 1963; Pant and Srivastava, 1965; Webster, 1974; Webster and Steeves, 1974).

Paleoecology

Reproductive biology was an integral part of the ecological strategies displayed by lycopod trees. Reproductive patterns and those of species distribution and abundance correlate closely. These lead to a better understanding of the roles played by lycopod trees in the coal-swamp ecosystem. The lepidodendrids can be classified very generally into three groups, opportunists, colonizers, and site occupiers. Opportunists exploited disturbed sites, sites with high abiotic stress and reduced competition, favoring rapid completion of the life cycle. All were forms with determinate, dendritic crowns. The only colonizer, *Paralycopodites*, was similar to an opportunist, but was capable of rapidly occupying relatively extensive areas, probably on decayed peat or transitional clastic-peat substrates. It dominated such areas for variable periods, and probably was eliminated by edaphic changes favoring other species. Site occupiers were capable of remaining on sites for extended periods due to a functionally, almost indeterminate growth and by extended or repeated periods of reproduction. These trees were favored in irregularly disturbed areas that were relatively stable and equable between disturbances. The random nature of disturbances may have resulted in either extended, stable, forest stands, or variable to relatively short stand life. Most opportunists were selected against such environments.

Opportunistic species in the Herrin Coal were *Lepidodendron dicentricum*, *Lepidophloios hallii*, and *Lepidodendron hickii*. *Lepidodendron dicentricum* is probably the closest parallel to a modern opportunist (fugitive). It occurred in many different kinds of assemblages, but usually at low levels (<10%). This suggests that *L. dicentricum* was capable of invading even established stands in areas with minor disturbance. The determinate crown and relatively short interval of reproduction are consistent with a fugitive life history. Individual plants did not occupy sites for long periods, but the single, large reproductive effort insured dispersal to nearby available sites.

Lepidophloios hallii lacks a good modern analog. Plants occurred in almost all coal-swamp assemblages of the Herrin Coal, probably as a consequence of the great dispersal potential of *Lepidocarpon*. However, *L. hallii* reached its maximum abundances (>70% of total peat volume) in communities of very low diversity, often with as few as four species. Ground-cover and free-sporing plants were rarely part of such assemblages. These factors suggest that *L. hallii* was dominant in flooded areas where high levels of abiotic stress excluded most other plants. Such assemblages occur in most Herrin Coal profiles, sometimes in many consecutive zones (Fig.3), indicating that populations of *L. hallii* could maintain dominance of a site. We consider *L. hallii* to be an opportunist because it occurred in most parts of the Herrin coal swamp and dominated areas of high abiotic stress.

Lepidodendron hickii was rare in late Middle Pennsylvanian coal swamps of the Illinois Basin. It occurred most often in pteridosperm-dominated vegetation from areas near fresh-water channels. The closest relatives of *L. hickii* were *L. aculeatum* and similar compression forms of clastic depositional environments. Areas of abundant *L. hickii* in coal swamps may have been higher in nutrients than was typical for most of the coal swamp.

Paralycopodites brevifolius was the most obvious colonizing species of lycopod tree in late Middle Pennsylvanian coal swamps. It apparently was rather specific in its ecological requirements. Parts of swamps disturbed by heavy clastic influx, or parts of clastic substrates where a peat-swamp flora was just becoming established often supported *Paralycopodites*. Vegetation in such areas may have been patchy or hummocky with irregular and discontinuous peat formation. Johnson's (1979) evaluation of the petrography of a *Paralycopodites*-dominated interval of the Herrin Coal supports this interpretation. In such transitional environments, the continuous reproduction of *P. brevifolius* would provide a constant background of spores and young plants, maintaining continuity of populations in an area that was not ameliorated by a peat substrate. The high reproductive output of the plants insured rapid colonization of local sites, and both microspores and megaspores were provided by the bisporangiate cones. *Paralycopodites brevifolius* appears to have been eliminated from such sites by edaphic conditions that favored dominance by other, coal-swamp-centered trees, especially *Lepidophloios*.

The major site occupier in the Herrin coal swamp was *Lepidodendron scleroticum*. The long-term growth of the main trunk and sustained reproduction would have allowed single trees to grow and propagate for extended periods. Low reproductive output, relatively thick wood and periderm, and the variable plant composition of assemblages dominated by *L. scleroticum* further support this deduction. Once again, much can be understood about *L. scleroticum* in a swamp as complex as the Herrin by examining the morphologically similar *L. vasculare* in simpler coal swamps of the Early Desmoinesian. *Lepidodendron vasculare* dominated coal swamps of lower deltaic-plain regions subject to irregular disturbance, possibly related to brackish water influx. In these environments, the continuous, low levels of reproduction were favored because of the irregularity and frequency of disturbance; this pattern probably would have selected against "determinate-crown" trees with a short reproductive period by repeatedly destroying pre-reproductive individuals. Local parts of the Herrin coal swamp were subject to irregularly occurring, but frequent, variation in the environment; fluctuations in water depth or the standing-water period may have favored development of *L. scleroticum* stands. *Sigillaria* also may have been a site occupier in the late Middle Pennsylvanian. These relatively large trees with thick periderm, had repeated periods of reproduction. *Sigillaria* was relatively rare in most coal-swamp assemblages, but was common in clastic-swamp and other lowland environments. This implies that a number of species of *Sigillaria* were probably more tolerant of drier environments than were most other lycopod trees. The evidence for apomixis in *Mazocarpon oedipternum* further suggests such dry-site tolerance. The need for water-mediated fertilization in heterospory would eliminate non-apomictic forms in most non-aquatic environments because of the crucial nature of timing spore-release relative to favorable conditions. With repeated reproductions, some megaspores may have reached sites moist enough for sporophyte establishment during the life-span of a tree. This seems most likely in areas where abiotic stress was high and success of any individual reproductive event was low.

SUMMARY

Key elements in the reproductive biology of the arborescent lycopods were the timing of cone production relative to the habit of the tree, the morphology and dispersal potential of disseminules, and duration of time for which one tree could occupy a site in the forest. Other important factors, such as the ratio of male to female reproductive effort, can only be inferred very tentatively from the relative abundance of cone and spore types, except for *Flemingites diversus*, which was bisporangiate. Reproductive patterns correlate well with general paleoecological strategies of the trees that are inferred largely from community ecology. Each species was highly specialized in one or more aspects of its reproduction and growth. This is not unexpected in a group of evolutionarily related species, most of which were ecologically centered in coal swamps. Possibly because of the limited resources and edaphic constraints of coal swamps, reflected in low diversity, only forms that effectively exploited one kind of sub-environment would be likely to survive in the face of long-term resource competition with other lycopod trees. In fact, all contemporaneous species represent very different ecological roles. Where species appear to be very closely related, with similar habit and reproduction, e.g., *Lepidodendron vasculare*, *L. phillipsii*, and *L. scleroticum*, there is minimal geographic or stratigraphic overlap. This is not to imply that there has been niche differentiation by competitive exclusion. It is equally or more likely that the only new species able to establish within coal swamps were those that had ecological requirements somewhat different from the ancestors. Selection by elimination of new forms that significantly overlapped ancestral populations in resource requirements would allow only more divergent forms to persist. Niche differentiation would then result from a more-or-less acompetitive historical process.

The consideration of reproductive biology and vegetative form along with detailed ecological assessment of fossil plants can provide considerable insight into the similarities and differences between modern and extinct vegetation. Lower vascular plants from many different evolutionary lineages appear to have evolved independently very similar ecological roles to those found in angiosperms today. Within such biotic similarities may lie generalities about ecological and evolutionary processes that can not be obtained from studying modern plants alone; the role of architectural constraint, the nature of the interaction between selective filters and evolving lineages, the temporal duration of congeneric ecological overlap, and the relationship between directional environmental changes and community structure. Within the framework of paleoecological studies of evolution these represent added dimensions that amplify our recognition of the similarities and significant differences between Pennsylvanian age and modern ecosystems.

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