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A WOODY LYCOPSID STEM FROM THE NEW ALBANY SHALE (LOWER MISSISSIPPIAN) OF KENTUCKY[1]

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ABSTRACT

A lycopsid axis from the New Albany Shale (Sanderson Formation) of Kentucky is described. The stem, which branches dichotomously, is 45 mm in diameter and is characterized by a relatively narrow parenchymatized protostele, a 3.0 mm-thick cylinder of secondary xylem, a tripartite cortex, and a periderm that is more than 5.0 mm thick. The secondary xylem is composed of uniseriate and biseriate vascular rays and narrow tracheids with scalariform wall thickenings on both radial and tangential walls. The periderm is characterized by elongate, thick-walled cells, some of which broaden tangentially in the outer part of the tissue forming zones that appear wedge-shaped in cross section. Surface features of the axis, including leaf bases, are not preserved. The stem is tentatively regarded as a member of the Lepidodendrales in accordance with the numerous anatomical characters that it shares with more recent representatives of the order. Because the external morphology is not known, however, the possibility exists that the axis corresponds to a protolepidodendralean taxon currently known only from compression and/or impression remains or some other nonlepidodendralean plant that produced secondary xylem. The extremely narrow profile of the secondary xylem tracheids (relative to other arborescent lycopsids) is interpreted as evidence that the plants grew in a habitat that was substantially drier than the Upper Carboniferous coal swamps.

THE LEPIDODENDRALES is an extinct order of arborescent lycopsids known primarily from Carboniferous fossils. Stems included within this order exhibit unique, helically arranged leaf cushions and histologically distinct secondary xylem and periderm. Coincident with the formation of coastal peat swamps during the early part of the late Carboniferous, the lepidodendraleans underwent a period of extensive diversification, becoming one of the dominant vascular plant groups of the Upper Paleozoic. The plants were exceptional in size, number, and morphology and occupied a variety of ecological zones within the coal swamps (DiMichele and Phillips, 1985); the obvious evolutionary success of the group has been attributed to the presence of a suite of unusual vegetative (DiMichele and Phillips, 1985; Cichan, 1985, 1986) and reproductive (Phillips, 1979; Thomas, 1981) features.

Despite the fact that the Lepidodendrales is one of the best-understood plant taxa of the Carboniferous, relatively little is known about the early evolutionary history of the group, in particular the phylogenetic events that occurred prior to the invasion of the coal swamps. The group reputedly arose during the late Devonian from plants with a *Lepidodendropsis*-type morphology (Thomas, 1978), and it has been suggested that *Valmeyerodendron, Cyclostigma,* and *Lepidosigillaria* represent morphological intermediates between the Upper Devonian plants and the more massive Upper Carboniferous representatives (Stewart, 1983). Most of the uncertainty surrounding the early evolution of the Lepidodendrales can be attributed to the scarcity of anatomically preserved fossils from the late Devonian and earliest Carboniferous. Although compression and impression material from these times is known in some detail (Jennings, 1972; Chitaley, 1982) and has provided important information relative to stem morphology, anatomically preserved axes are generally required to unequivocally determine the presence of secondary tissues and thus establish lepidodendralean affinities (Thomas, 1978; DiMichele, 1983).

In this contribution, a permineralized lycopsid stem from the New Albany Shale (Lower Mississippian) of Kentucky is described. The axis exhibits relatively thick zones of secondary xylem and periderm, both of which are histologically similar to tissues found in significantly younger members of the Lepidodendrales. In this respect, the axes represent the oldest, certifiably woody lycopsid fossils

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about which published information currently exists (but see Cai and Qin, 1986) and, thus, are likely to be important in understanding the early evolution of lepidodendralean lycopsids. The fossils are also significant in that the secondary xylem tracheids are three to four times smaller than those in woody lycopsids from the Upper Carboniferous. Based on the relationship that seems to exist between tracheid size and edaphic conditions at the growth site, this distinction is likely to be important in evaluating the ecological characteristics of the source region of the New Albany Shale flora.

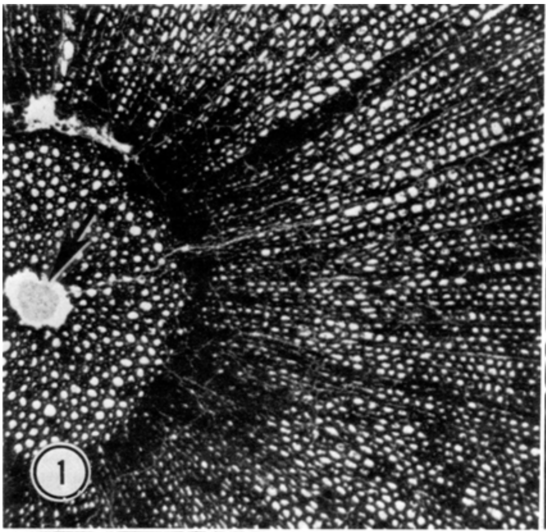
MATERIALS AND METHODS—The description is based on five calcium phosphate permineralizations collected from the Falling Run Member of the Sanderson Formation, New Albany Shale (Lower Mississippian) near Boston, KY (Nelson County, Mercator grid coordinates—85°38′50″ by 37°45′). The beds have been tentatively dated as early Tournaisian (?Tn1b) (Scott, Galtier, and Clayton, 1984), and, as such, the flora from these deposits is slightly older than that from the Montagne Noire locality of France (mid- to late Tournaisian Tn2b–Tn3c). Two of the fossils (P-1783, P-1784), which apparently represent parts of the same axis, are roughly cylindrical and measure ca. 4.5 cm in both length and diameter. At the macroscopic level, the axes consist of a xylem core surrounded by several concentric layers of tissue. The other specimens are smaller pieces of a fragment that had previously been cut into three parts (P-1788, P-1789, P-1790); each piece measures ca. 1.5 × 2.0 × 2.5 cm. The original fragment consisted of a xylem cylinder and some extraxylary tissue at the level of an apparent isotomous dichotomy. Cross- and longitudinal sections of the material were prepared using the technique described by Stein, Wight, and Beck (1982). Tracheid and periderm cell widths were measured at the widest part of the individual cells in tangential, longitudinal sections. All slides and fossil fragments are currently housed in the Paleobotanical Collections, Cleveland Museum of Natural History, Cleveland, OH.

DESCRIPTION—*Stele*—The axis is characterized by a parenchymatized protostele, with a primary xylem cylinder that measures ca. 1.2 mm in diameter (Fig. 1). A central cavity, which presumably represents the remains of the pith, is present and measures ca. 0.3 mm in diameter. The primary xylem cylinder (Fig. 1) is ca. 0.5 mm thick and is characterized by tracheids with scalariform thickenings on radial and tangential walls. The tracheids are polygonal in cross section, with a mean diameter of 42 μm (SD = 10 μm, N = 75). Tracheids near the periphery of the xylem cylinder are noticeably smaller and presumably represent the protoxylem elements. There is no evidence of a protoxylem corona (Fig. 1).

Secondary xylem—The secondary xylem cylinder (Fig. 1, 2) is ca. 3.0 mm thick and is characterized by elongate tracheids, thin-walled ray cells, and leaf traces that are terete in tangential sections (Fig. 3, 4). The mean tangential width of tracheids in the middle and outer parts of the wood is 39 μm (SD = 6.0 μm, N = 75); tracheids in the innermost wood are substantially narrower. Scalariform thickenings occur on both the radial and tangential walls of the elements (Fig. 3, 5). In general, the preservation of the wood is poor, and "Williamson striations" could not be resolved in either primary xylem or secondary xylem tracheids. Vascular rays are mostly uniseriate and biseriate and range from one- to ca. eight-cells high (Fig. 3). Within the wood, leaf traces follow a horizontal or slightly inclined radial course and are arranged in a low helix about the axis. At one site the leaf traces appear to be whorled.

Branching—In one of the specimens, two xylem cylinders are present, characterized by both primary and secondary xylem. The two cylinders are essentially equal in diameter (ca. 6.0 mm) and diverge from one another at an angle of approximately 40 degrees. The specimen is interpreted as a region of the stem at a level where the vascular tissue divided in association with branch formation. The nearly equal size of the two xylem cylinders suggests that the branching pattern of the stem was isotomous.

Cortex and periderm—Most of the tissue just peripheral to the secondary xylem cylinder, a zone ca. 3.0 mm broad and conforming positionally to the phloem and inner cortex, is not preserved. As such, a description of this tissue is not possible with the material at hand. A broader zone ca. 7.0 mm thick surrounds the vacuous region and presumably represents the middle cortex. The cells of this zone are relatively large (mean tangential width = 144 μm, SD = 47 μm, N = 75), parenchymatous, and irregular in shape (Fig. 6). Beyond this is the outer cortex, a narrow (3–5 cell layers) band of tissue contiguous with the inner margin of the periderm (Fig. 7). The cells that comprise this region are parenchymatous in appearance and more or less rectangular in shape (mean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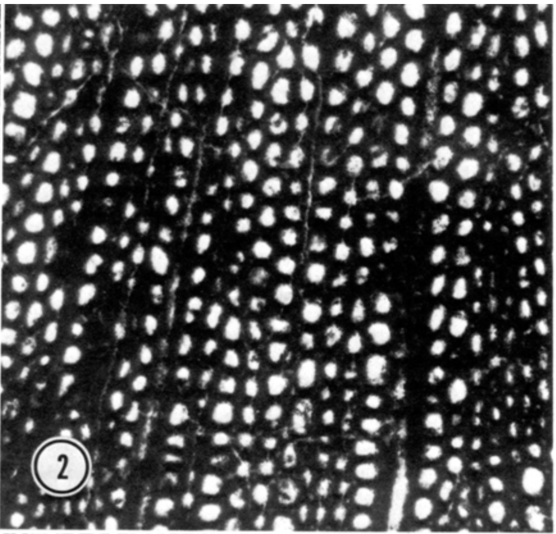
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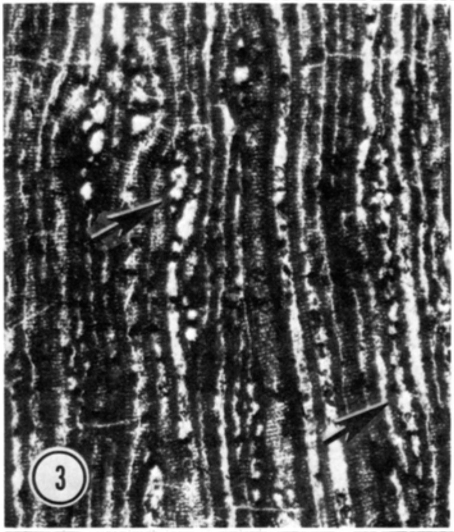
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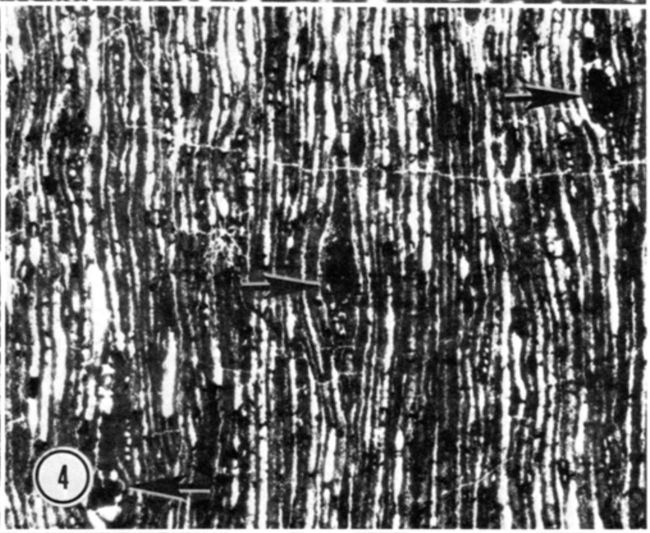
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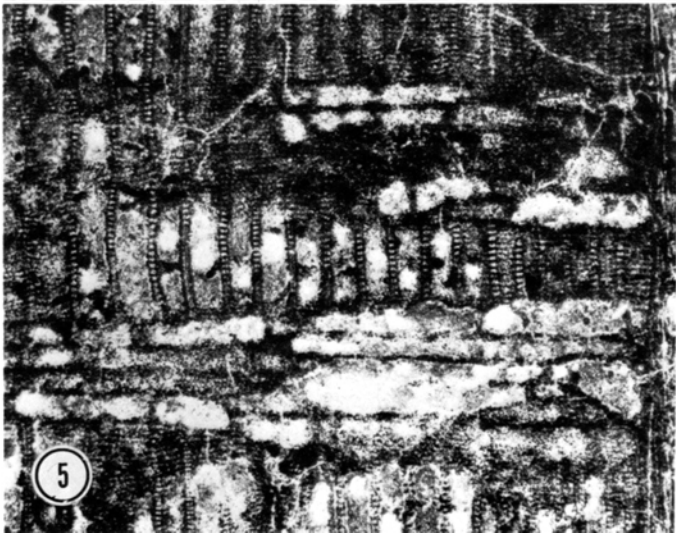
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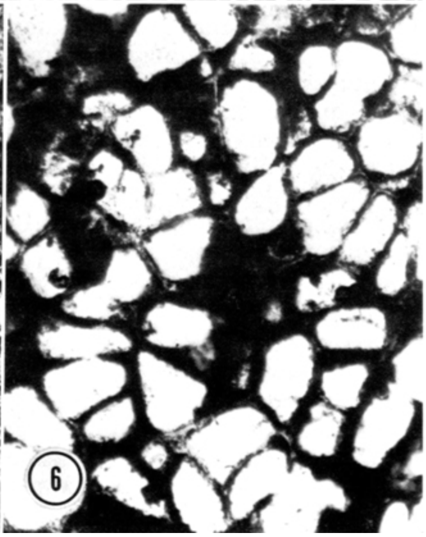
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tangential width = 93 μm, SD = 29 μm, N = 75). The long dimension of most of the cells is oriented longitudinally.

The well-developed periderm (ca. 6.0 mm thick) is divisible into two relatively distinct zones (Fig. 7). The inner of the two is composed of radially aligned cells that are square-rectangular in cross section. The cells are relatively thin-walled like those of the outer cortex and exhibit a mean tangential width of 66 μm (SD = 16 μm, N = 75). These cells grade almost imperceptively into the thick-walled cells of the outer periderm (Fig. 7). In this region the cells are ca. 10 times longer than wide (mean length = 308 μm, SD = 82 μm, N = 57; mean tangential width = 31 μm, SD = 7 μm, N = 75) and have tapering ends (Fig. 8–10). Near the periphery of the periderm, the files of thick-walled cells are divided into radially arranged groups by wedge-shaped zones of cells that are substantially broader than the fiber-like cells (Fig. 8), resulting in the formation of "fissures" (Eggert, 1961; DiMichele, 1983) or "meshes" (Kisch, 1913). Cells that compose the wedges are aligned in somewhat irregular radial files; the cells increase in tangential width near the periphery of the axis (Fig. 8–10) and some become longitudinally subdivided (Fig. 10). The broad cells occur in the same files as the narrow cells, indicating that the former were derived ontogenetically from the latter. In this respect, the narrow, fiber-like cells appear to have dedifferentiated to form the broad cells and thus must have been alive at maturity.

DISCUSSION—*Taxonomy*—Based on our current understanding of fossil Lycopsida, the axes described in this report are most similar to those presently included in the order Lepidodendrales. In the absence of information pertaining to leaf bases, this assignment is made in accordance with the appearance of the stele, the presence of significant amounts of periderm and secondary xylem, and the distinctive scalariform thickening of the primary xylem and secondary xylem tracheid walls. Assuming that this assignment is accurate, and in view of the proposed early Tournaisian age of the deposits from which the material was collected (Scott et al., 1984), the axes represent the oldest permineralized lepidodendralean vegetative remains currently known.

Anatomically preserved stems of nonlepidodendralean lycopsids, where known, are typically rather slender, and rarely exhibit evidence of extensive secondary growth. A notable exception is the isoetalean genus *Chaloneria* Pigg and Rothwell, in which parts of the stems are characterized by a parenchymatized protostele and moderate amounts of periderm and secondary xylem (Pigg and Rothwell, 1983). The primary xylem cylinder in *Chaloneria,* however, is dissected by parenchymatous plates and, thus, is distinct from that in the New Albany Shale material. In protolepidodendralean lycopsids, some of which are presumed to have been arborescent, the stems, where known, are characterized either by lobate protosteles (*Colpodexylon*-Banks [1944]) or by protosteles that are triangular or terete in cross section, with prominent longitudinal ridges (*Protolepidodendron*-Banks [1944]; Grierson and Banks [1963]). As such, the anatomy of the lycopsid axes described herein is unlike that of any protolepidodendralean stems reported to date. It is important to note, however, that a large number of protolepidodendralean species are currently known only from compression and impression remains, and that the New Albany Shale lycopsid may actually be an anatomically preserved form of one of these taxa. In this regard, Cai and Qin (1986) describes a partially permineralized lycopsid axis from the Upper Devonian of China that he interprets as *Leptophloeum rhombicum* with secondary xylem. One of us (CBB) has had the opportunity to examine this material and agrees that secondary xylem is present.

Anatomically preserved lycopsid stems from the Lower Carboniferous that can confidently be assigned to the Lepidodendrales are rare. Early studies of the New Albany Shale flora (Read, 1936; Read and Campbell, 1939) resulted in the description of several permineralized axes that were classified as lepidodendralean, including *Lepidodendron boylensis* Read, *Lepidodendron novalbaniense* Read and Campbell, and *Lycopogenia callicyrta* Read.

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Fig. 1–6. **1.** Cross section of primary xylem (left) and secondary xylem (right). Pith is at arrow. P1789b no. 1, ×41. **2.** Cross section of secondary xylem. Inner xylem is at top. Note files of tracheids and rays. P1789b no. 1, ×104. **3.** Tangential section of secondary xylem showing uniseriate rays (arrows) and tracheids with scalariform wall thickenings. P1789c side no. 2, ×104. **4.** Tangential section of secondary xylem. Note three leaf traces (arrows). P1789c side no. 8, ×41. **5.** Radial section of secondary xylem showing two rays and tracheids with scalariform wall thickenings. P1789c side no. 5, ×104. **6.** Cross section of parenchymatous middle cortex. P1788a no. 1, ×104.

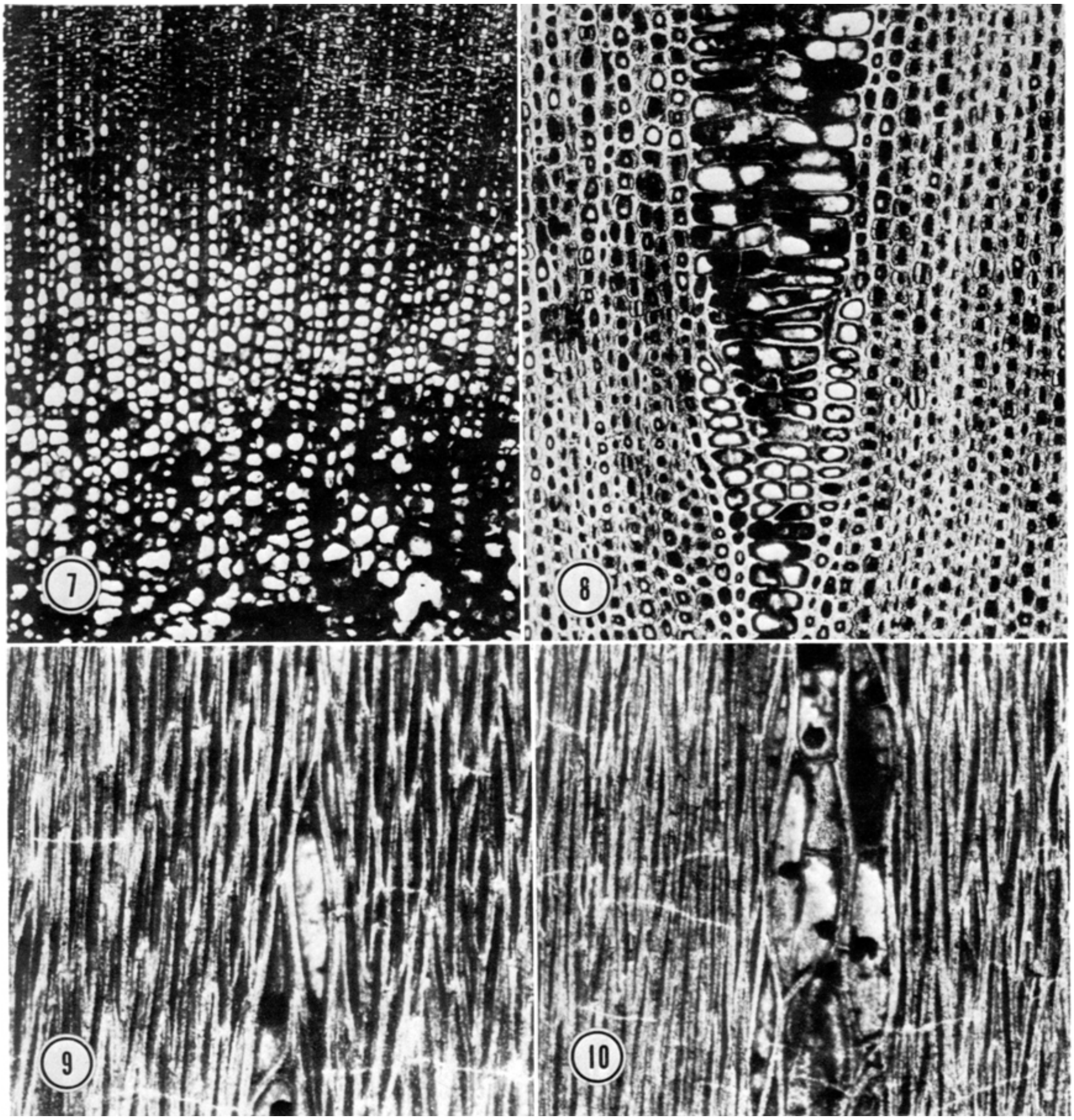

Fig. 7–10. **7.** Cross section of outer cortex (bottom) and inner periderm (top). Note gradual transition from large, thin-walled cells to relatively small, thick-walled cells arranged in radial files. P1784a no. 4, ×41. **8.** Cross section of outer periderm (outer periphery at top) showing radial files of large-diameter parenchyma cells continuous with those of thick-walled periderm cells. P1784a no. 4, ×104. **9.** Tangential section of periderm. Note that tissue is composed of elongate, thick-walled cells. P1784a side no. 3, ×95. **10.** Tangential section of outer periderm showing large-diameter parenchyma cells (center). P1784a side no. 3, ×95.

These stems are all rather small (ca. <2 cm in diameter), with a slender protostele (ca. 1–2 mm in diameter), a thick parenchymatous cortex, and little or no evidence of secondary growth. External features of the stems (i.e., leaf cushions) are not preserved. *Phytokneme rhodona* (Andrews, Read, and Mamay, 1971), a lycopsid axis also from the New Albany Shale, is likewise characterized by a terete protostele and a broad tripartite cortex. The middle portion of the cortex is composed of irregularly shaped parenchyma cells traversed by strands of radially elongate cells. Thin zones of parenchyma cells in radial files are present near the inner and outer margins of the outer cortex, and a narrow (2–4 cells thick) band of tissue interpreted as secondary xylem surrounds the primary xylem cylinder. Vascular rays, however, have not been demonstrated in this tissue.

At present, there is no anatomical evidence indicating that the specimens reported in this study correspond to the proximal parts of any of the previously described New Albany Shale lycopsids. The stems lack both the "scalloped" outline of the stele in *Lycopogenia callicyrta* and *Lepidodendron novalbaniense* and the distinctive histology of the cortex in *Lepidodendron boylensis* and *P. rhodona.* It is important to note, however, that the figures and abbreviated text that accompany the descriptions of *L. novalbaniense,* and *L. callicyrta,* are insufficient to permit precise comparison of cortical features. In this respect, a critical reevaluation of the "herbaceous," New Albany Shale lycopsids is in order, particularly with regard to the results of recent work by Meyer-Berthaud (1984) on the nonlepidodendralean lycopsids from the Tournaisian of Europe.

The woody stems described in the present work correspond most closely to a suite of lepidodendralean axes from the Lower Carboniferous of Europe, including *Lepidophloios wünchianus* (Seward and Hill, 1900; Walton, 1935), *Lepidophloios scottii* (Gordon, 1908), and *Lepidophloios kilpatrickensis* (Smith, 1962) and also *Lepidodendron johnsonii* from the Lower Pennsylvanian of Colorado (Arnold, 1940). These protostelic axes are all characterized by a broad, parenchymatous cortex and a periderm composed of elongate, radially arranged, thick-walled cells. Unlike the New Albany Shale specimens, however, "secretory cells" typically occur in the European axes at the boundary of the cortex and periderm. Moreover, leaf bases are preserved in the European stems, allowing for a reasonably confident assignment of the material to established genera. Because information pertaining to the occurrence and morphology of leaf bases in the New Albany Shale axes is presently lacking, we hesitate to assign the stems to a particular lepidodendralean genus. Although the importance of leaf base morphology in generic delimitation within the Lepidodendrales has recently been downplayed (DiMichele, 1983), and thus such reluctance may seem unwarranted, we cannot be certain that the stems were characterized by persistent leaf cushions since the surface has been completely abraded. This cautious approach is further justified in view of the fact that the specimens, as possibly the oldest anatomically preserved lepidodendralean stems currently known, may not correspond to generalizations based on analysis of more derived, Upper Carboniferous taxa. Definitive statements regarding the taxonomic placement of the specimens must await the discovery of better-preserved material.

Ecology—The results of recent work on functional aspects of wood anatomy in Carboniferous plants (Cichan, 1986) indicate that the general correlation between xylem anatomy and ecology in extant seed plants (e.g., Carlquist, 1977) may also apply to fossil gymnosperms and woody pteridophytes. Within a given lineage, secondary xylem tracheid diameter may be a general indicator of edaphic conditions, with broad tracheids occurring in plants from mesic habitats and narrow elements occurring in plants from more xeric regions. In lepidodendraleans from the Middle Carboniferous coal swamps, secondary xylem tracheids typically exhibit mean widths in excess of 100 μm (Williamson, 1872; Pannell, 1942; Felix, 1952; Cichan, 1985), and in some specimens of *Lepidodendron kansanum,* tracheids are more than 200 μm wide (Felix, 1952). In contrast, secondary xylem tracheids in the New Albany Shale axes average less than 40 μm wide. Thus, if the proposed relationship between tracheid width and environmental conditions can be extended to include fossil groups, it is likely that the New Albany Shale axes grew in a locality that was substantially drier than the Upper Carboniferous coal swamps. Critical to this hypothesis, however, are assumptions concerning positional variability in wood anatomy and potential irregularities in the relationship between wood anatomy and edaphic conditions.

Valid comparison of secondary xylem features between plants can be made only if the respective axis fragments are from equivalent parts of the plant (e.g., base of stem, distal twig, etc.) (Bailey and Faull, 1934). Recognizing positional equivalency in fossil lepidodendralean stems is not a significant problem, at least in theory, because of the documented relationship that exists between axis morphology and position (Walton, 1935; Eggert, 1961; Meyer-Berthaud, 1984). Stems with small, nonparenchymatous protosteles and large quantities of secondary xylem (i.e., total xylem radius/primary xylem radius $\gg 1.0$) represent basal parts of the trunk. The secondary xylem cylinder decreases in thickness acropetally, and the primary xylem becomes parenchymatized and increases in width (i.e., total xylem radius/primary xylem radius decreases). At still higher levels in the axis, the primary xylem and secondary xylem cylinders become narrower, and the pith tapers. Specimens with nonparenchymatous protosteles, small amounts of primary xylem, and no secondary xylem (i.e., total xylem radius/primary xylem radius = 1.0) correspond to distal branches. The New Albany Shale specimens described in this study exhibit a relatively thick cylinder of secondary xylem (radius = 3.6 mm) and a narrow (radius = 0.6 mm) protostele and therefore probably represent near-basal portions of the stem. If the width of secondary xylem tracheids in lepidodendralean axes decreases acropetally within the plant, as assumed by Cichan (1986), then the elements in the axis fragments described in this study are likely to be among the broadest for the entire plant. Thus, secondary xylem tracheids in the New Albany Shale axes are likely to have been substantially narrower than those in coal swamp lepidodendraleans regardless of the position of the sampled coal swamp stem fragments within their respective axis systems.

Analysis of living groups has shown that the relationship between wood anatomy and edaphic conditions is not universally consistent in that plants with wood exhibiting mesomorphic features may occur in xeric habitats (Rury and Dickison, 1984; Rury, 1985). It has been noted, however, that the leaves in these plants are typically characterized by a set of xeromorphic features and, thus, probably act to buffer the wood from the effects of water stress. The secondary xylem in the Mississippian lycopsid stem described herein appears to be characterized by features that are xeromorphic relative to those in other woody lycopsids. As far as is currently known, wood with xeromorphic features (as judged by comparison between plants within the same lineage) does not occur in plants growing in mesic conditions. Thus, the suggestion that the woody lycopsid from the New Albany Shale grew in a relatively dry environment appears to be valid insofar as the relationship between wood anatomy and environment is currently understood.

At present, virtually nothing is known about the environment of the source region of the New Albany Shale flora. Based on the evidence from wood anatomy, it is proposed that the woody lycopsid described herein grew in an environment that was substantially drier than that of the Carboniferous coal swamps and may have been subjected to occasional periods of water stress. It should be noted that the absence of growth rings in the wood is of little significance in this interpretation. The pattern of cambial activity in lepidodendralean axes appears to have been fundamentally different from that in seed plants (Cichan, 1985), and it is unlikely that members of these two divergent groups responded to environmental variations in a similar manner. Clearly, the suggestion of a relatively dry environment, being based solely on the analysis of a single element of the flora, is preliminary, and continued study of New Albany Shale plants is needed to refine (or negate) the hypothesis. Nevertheless, the work illustrates the potential value of ecophyletic analysis of wood anatomy in evaluating the environmental characteristics of source regions in the study of fossil floras.

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