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Lepidodendron hickii and Generic Delimitation in Carboniferous Lepidodendrid Lycopods

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ABSTRACT. *Lepidodendron hickii* is the only anatomically preserved Carboniferous lepidodendrid with leaf cushions referable to the compression-based *L. aculeatum*, the type of *Lepidodendron*. Historically *Lepidodendron* has come to encompass several kinds of arborescent lycopods with distinctive vegetative and reproductive morphologies, among which no truly intermediate forms are known. These include totally or in part *Lepidophloios* (and *Sublepidophloios*, a possible congener), *Paralycopodites*, "*Lepidodendron*" sensu *L. vasculare* and others, and a large number of fragmentary specimens of varying affinities. The discrete nature of the character states defining these genera suggests that anatomy is sufficient for delimitation of lepidodendrid genera. Simple leaf-cushion shape is of dubious value in the delimitation of *Lepidodendron* because the "*Lepidodendron*"-shape appears to be plesiomorphic (ancestral). *Lepidodendron hickii* is associated with *Achlamydocarpon takhtajanii* megasporangium-sporophyll units, which suggests close alliance with the herbaceous *L. serratum*, also a producer of *A. takhtajanii*. At the generic level, *Lepidodendron* (sensu *L. hickii* and *L. serratum*) is most similar phenetically to *Lepidophloios*.

The ordering of fossil plants into taxonomic hierarchies reflective of phylogeny, or even of shared morphological characters, has been a problematic part of paleobotany. Difficulties in approximating natural relationships of extinct plants center on frequent lack of organic connection between vegetative and reproductive parts, limits in assessing the developmental significance of morphology from static and non-connected specimens, and the diversity of names applied to different forms of preservation. These difficulties are reflected by the Carboniferous lepidodendrid lycopods. Years of study have yielded a wealth of morphological information but also produced a tangled web of nomenclature, which inhibits recognition of discrete forms and the evolutionary relationships among them. The reasons for this are complex, rooted in the traditional treatment of certain forms and in the truly untested belief that anatomy is not a diagnostic taxonomic tool and does not correlate with distinctive leaf-cushion form, the character upon which most "genera" are based. Central to this problem has been an extreme overextension of the name *Lepidodendron* both to compression and petrification fossils.

The type species of *Lepidodendron* (fide Thomas 1970) is *L. aculeatum* Sternb., a species based on compression specimens with distinctive, vertically elongate leaf cushions that have infrafoliar parichnos. The only species of ana-

tomically-preserved lycopod stems that has leaf cushions with infrafoliar parichnos and general leaf-cushion form of the *L. aculeatum*-type is *L. hickii* Watson (Watson 1907). Other anatomically-preserved forms that historically have been placed in *Lepidodendron* include, totally or in part, *Paralycopodites brevifolius* (DiMichele 1980), *Lepidophloios* (DiMichele 1979a), *Sublepidophloios*, and a group of lepidodendrids including "*Lepidodendron*" *vasculare* (DiMichele 1981). These distinctive vegetative forms, differing from each other in leaf-cushion architecture and anatomy, are correlated with different reproductive structures, further emphasizing their distinctiveness. The application of names to them, although not trivial, is secondary in importance to the recognition that they are distinct, that there are not morphological clines among them, and that not all of them can be *Lepidodendron*, despite historical treatments, if the name is ever to have any biological significance.

Lepidodendron hickii, the focus of this report, is the best representative of *Lepidodendron* anatomy in light of uniquely shared similarities between *L. hickii* leaf cushions and those of the type species, *L. aculeatum*. The distinctiveness of *L. hickii* anatomy when compared to other lepidodendrids with leaf-cushion height: width ratios > 1 suggests that the height: width ratio of cushions is not a sufficient basis for generic circumscription; greater leaf-cushion height

than width appears to be plesiomorphic and thus of limited usefulness. The other major group of lycopods that regularly have *Lepidodendron*-shaped leaf cushions in axes of all sizes regardless of developmental stage are "*Lepidodendron*" *vasculare* and its relatives (DiMichele 1981). Leaf cushions of these plants undergo little change in form with changes in axis diameter, lack infrafoliar parichnos, and are borne on plants distinct from *L. hickii* both in anatomy and reproductive morphology. In this paper they will be referred to as "*Lepidodendron*" because a new generic name has yet to be applied to them. *Sublepidophloios* and *Lepidophloios* may also have vertically elongate or equidimensional cushions at some developmental stages. Recognition of more than one anatomically and reproductively discrete form with leaf cushions that are higher than wide allows use of the infrafoliar parichnos and developmental patterns to segregate compression specimens into groups, even without anatomical data, by extrapolation from the more extensive petrification data base.

METHODS AND MATERIALS

Stems of *Lepidodendron hickii* preserved in 23 coal balls were studied by cellulose acetate peel preparations (Joy et al. 1956). Leaf-cushion architecture was studied by making a series of close tangential peels; stem anatomy was examined in longitudinal and cross section. A single large stem was preserved as a pyrite petrification from roof shales above the Springfield (No. 5) Coal. Carbonized, three-dimensionally preserved leaf cushions were present on the outer surfaces of this petrification. Internal anatomy was studied with cellulose acetate peels following etching in concentrated HNO₃.

The following *Lepidodendron hickii* specimens are preserved in coal balls housed in the Paleobotanical Collections, University of Illinois, Urbana: No. 1125, Lower Westphalian A of England; No. 12858, Minwin Coal Corp. Mine, Sandy Hook Quad. (NW, SE, NE, Sec. 13, T1N, R8W), Pike County, Indiana; Nos. 19274, 22785, Lemmon's and Co., Inc., Kennedy Pit, Boonville Quad. (Sec. 12, T5S, R8W), Warrick County, Indiana, Springfield (No. 5) Coal, Petersburg Formation, Carbondale Group, Middle Pennsylvanian; Nos. 10971, 11006, 11009, 11011, Derringer Corners (Darlington), Lawrence

County, Pennsylvania, unnamed coal between the Middle Kittaning Coal and Washingtonville Marine Shale, Allegheny Formation, Middle Pennsylvanian; Nos. 14284, 14587, 22284, Sahara Coal Co., Mine No. 6, Harrisburg 7½' Quad. (Sec. 30, T9S, R5E), Saline County, Illinois, Herrin (No. 6) Coal, Carbondale Formation, Kewanee Group, Middle Pennsylvanian.

The following specimens are preserved in coal balls housed in the Collections of the Paleobotany Laboratory, Université des Sciences et Techniques du Languedoc, Montpellier, France: Nos. 408, 411, 428, 438, 445, 449, 462, 475, 481, 484, 486, 496, Hapton Valley, England, Union Seam, Lower Westphalian A, Upper Carboniferous.

Specimen No. X1 was preserved as a pyrite petrification in a gray shale above the Springfield (No. 5) Coal, Petersburg Formation, Carbondale Group, Middle Pennsylvanian, in the Lemmon's and Co., Inc., Kennedy Pit, Boonville Quad. (Sec. 12, T5S, R8W), Warrick County, Indiana. Specimen X1 and voucher slides of *L. hickii* (UW 156-192) are housed in the Paleobotanical Collections, University of Washington, Seattle.

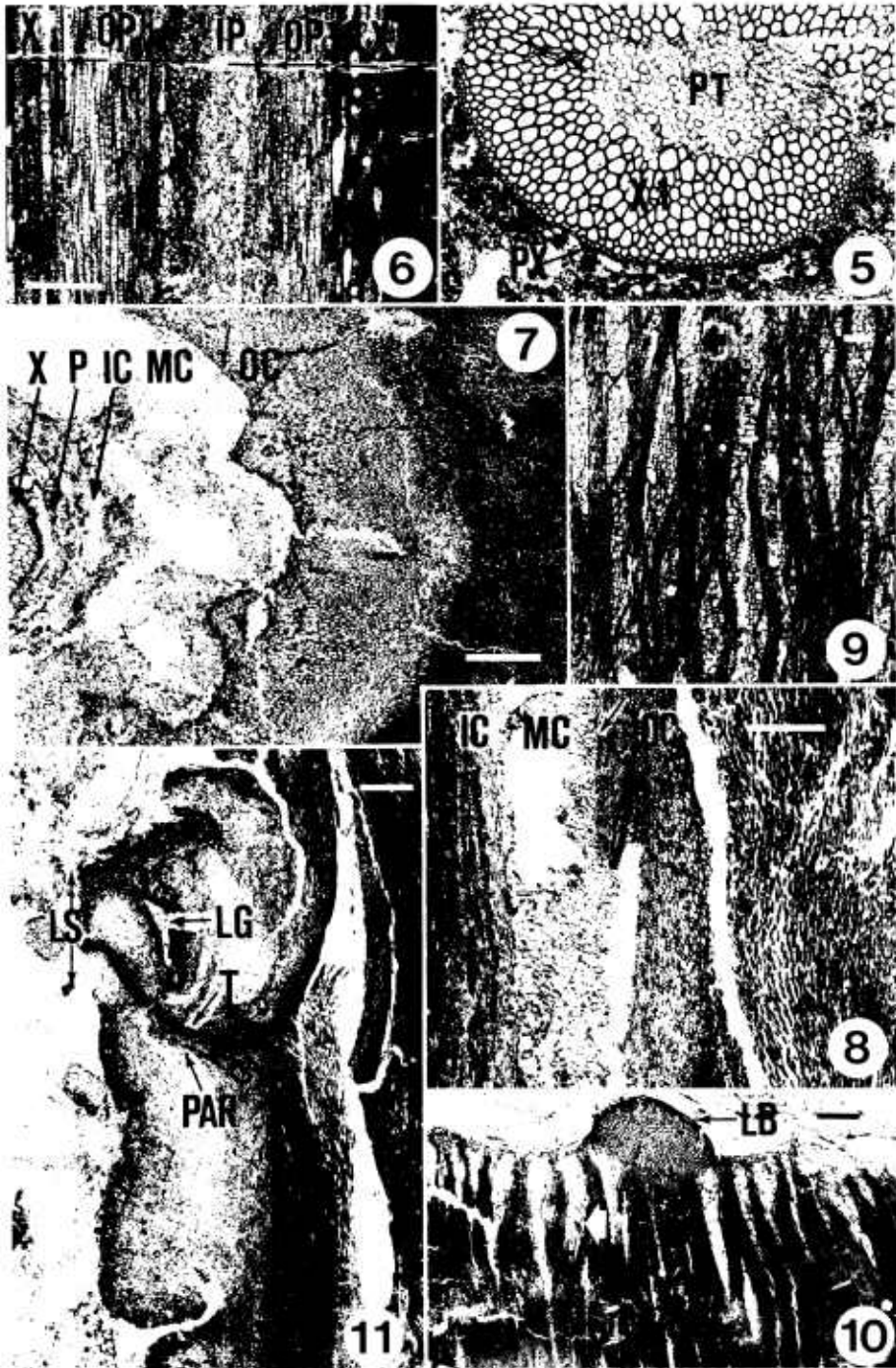
MORPHOLOGY AND ANATOMY OF *LEPIDODENDRON HICKII*

Lepidodendron hickii was described by Watson (1907), who recognized that the descriptions of *L. harcourtii* by Williamson (1893) had included more than one distinctive form. Koopmans (1928) listed publications that illustrate or describe axes referable to *L. hickii*. The list reveals the confusion that has surrounded this morphological form, including specimens described as *L. hickii*, *L. harcourtii*, *L. fuliginosum*, *L. obovatum*, *Lepidophloios fuliginosus*, and *Halonia regularis*. Koopmans (1928) himself described as *Lepidodendron obovatum* and *L. aculeatum* specimens that are in fact segments of *L. hickii* axes from more basal parts of stems.

The purpose of redescribing herein the morphological features of *Lepidodendron hickii* is to provide a single, complete description that takes into account new material, the observations and concepts of previous investigators, and changed perceptions on the distribution and limits of morphological variation in lepidodendrid taxa. The documentation of general determinate growth patterns in lycopod trees (Eggert 1961),



FIGS. 1-4. Cross sections of *Lepidodendron hickii* stems. S = stele, IC = inner cortex, MC = middle cortex, OC = outer cortex, PD = periderm, LB = leaf cushion. Scales = 5 mm. 1. An isotomously dichotomized large axis (slide 156). 2. Westphalian A age specimen from England (slide 157) for comparison with American specimens (all other sections). 3. Axis of size bearing protostelic lateral branches (slide 162). 4. Protostelic halonial, or lateral, branch, probably base of cone peduncle (slide 173).



FIGS. 5-11. Anatomy of *Lepidodendron hickii*. Scales = 1 mm. 5. Cross section of stele with protoxylem (PX) continuously distributed forming small, blunt points (slide 157). PT = pith, X1 = primary xylem. 6. Longitudinal section of stele with two-zoned pith (slide 166). Outer pith (OP) of vertically elongate septate cells adjacent to metaxylem (X). Inner pith (IP) hyphal. 7. Cross-sectional tissue zonation (slide 162). P = phloem zone, small arrow marks contact of middle cortex (MC) and outer cortex (OC). 8. Tangential section

an increasing list of vegetative-reproductive correlations, and interest in reproductive biology and paleoecology provide the framework within which the distinctiveness of the *L. hickii* morphotype can be recognized.

Morphology and anatomy are illustrated in figures 1-24. Figures 1 to 4 are cross sections that illustrate general architecture of different size stems. Figures 5 and 6 illustrate stelar morphology, 7 and 8 cortical tissues, and 9 and 10 anatomy of the periderm. Details of leaf-cushion anatomy and morphology are illustrated in figures 11 to 13; 14 to 17 are from serial sections through the leaf cushions of a small stem; and 18 to 23 are from serial sections through the leaf cushions of a large stem. Figure 24 is a reconstruction of the leaf cushion that shows the relationship between foliar and infrafoliar parichnos.

Stelar tissues. Stelar terminology paralleling that used for ferns has been applied to the arborescent lycopods. Most notable is the term siphonostele, which is used for a distinct cylinder of tracheids with a central parenchymatous area or pith. However, the pith region of lycopod steles with this type of organization consists of cells that have basically the same lengths and cross-sectional diameters as the innermost metaxylem tracheids. These elongate pith cells appear to represent procambial derivatives that have remained unligified, a pattern seen in the steles of several lepidodendrids (Bower 1935; Walton 1935; DiMichele 1979a). In this sense, the lepidodendrid siphonostele is in fact a medullated protostele, in that the entire stelar region is of procambial derivation.

Steles of most *L. hickii* stems are medullated, becoming solid strands of tracheids in the smallest branches of 10 mm diameter or less (figs. 1-4). The outer margin of the primary xylem consists of a nearly continuous one- to two-cell layer of protoxylem that thickens to form blunt ridges. In cross section this appears as a corona of small, blunt protoxylem points (fig. 5). Leaf traces are formed by the divergence of the coronal ridges.

In stems with stelar diameters of 5-6 mm or more the pith is usually two-zoned (fig. 6) with elongate pith parenchyma surrounding an inner core of hyphal parenchyma. The contorted hyphae may be a result of cell proliferation from the margins into an initially hollow central pith. This architecture is similar to that of *Lepidophloios* (Walton 1935; DiMichele 1979a). The entire pith averages 50% of the stelar cross-sectional diameter (range: 25-70%).

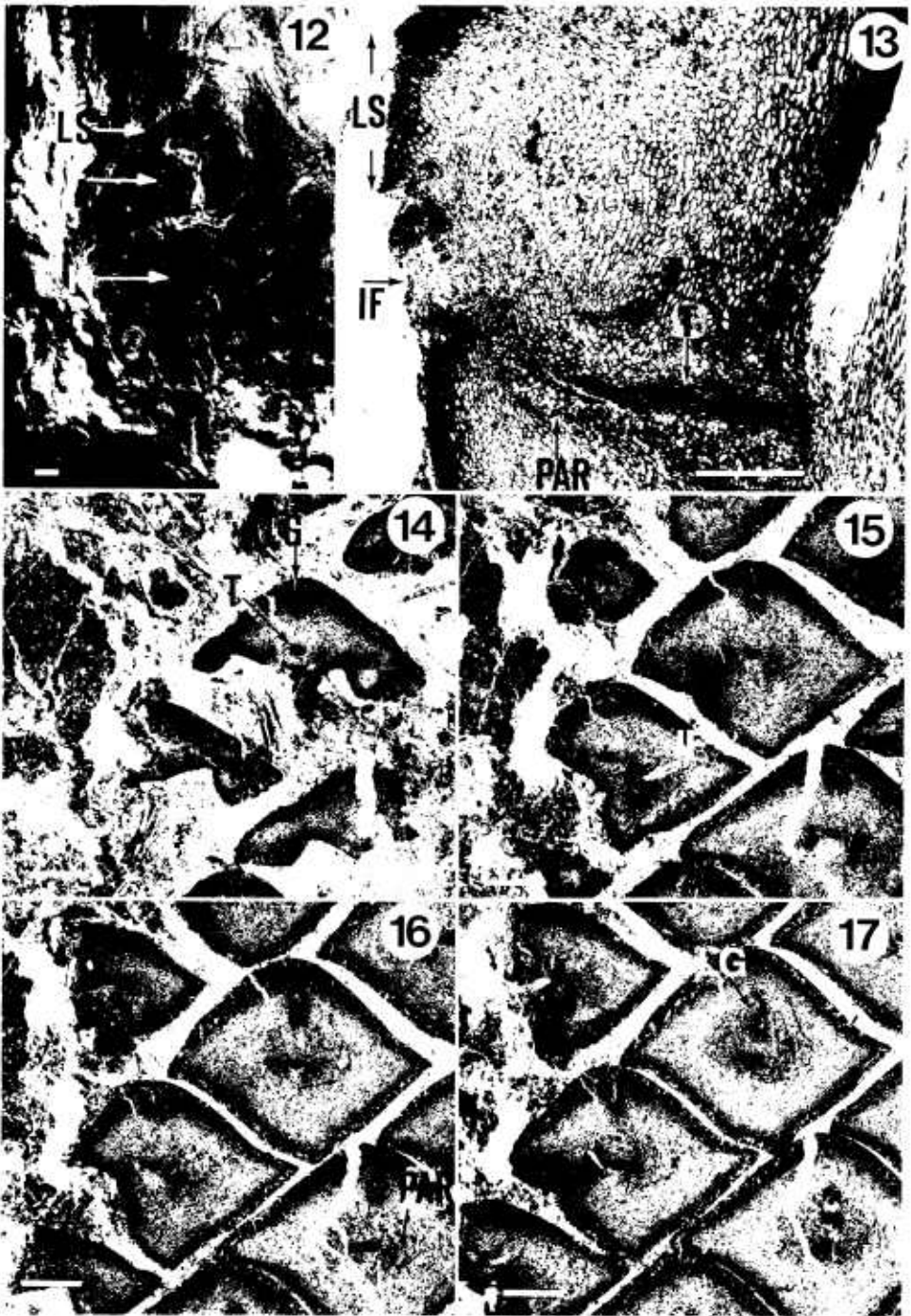
Extraxylary stelar tissues were usually totally or partially degraded in the specimens examined. In a few instances a tissue zone of up to 0.5 mm wide consisting of small-celled parenchyma was preserved between the primary xylem and the inner cortex. A varying percentage of this tissue was degraded into large, elongate cavities that may correspond to patches of sieve cells of the type described by Eggert and Kanemoto (1977) in "*Lepidodendron*" (of the *L. scleroticum* and *L. dicentricum* forms). Secondary parenchyma consisting of cells in short radial files was observed between the primary xylem and primary phloem of some stem specimens. It appears to result from cell divisions of extraxylary stelar parenchyma (Eggert and Kanemoto 1977).

Secondary xylem. Secondary xylem has not been observed in any of the *L. hickii* stems in this study. It is probable that secondary xylem developed in the trunk and lower crown; periderm is known to occur in *L. hickii*, and there are no known lepidodendrids that produced periderm but lacked secondary xylem. Koopmans (1928) illustrated a specimen with a secondary xylem cylinder, as *Diploxylon* 144, that had primary xylary and periderm characteristics of *L. hickii* but lacked leaf cushions and cortex. Pyritized primary and secondary xylem has been collected from the bases of stump casts above the Herrin (No. 6) Coal by Philip J. DeMaris of the Illinois State Geological Survey and myself. The stumps bear leaf-cushion impressions of *L. aculeatum*, a compression relative and possible equivalent of *L. hickii*.

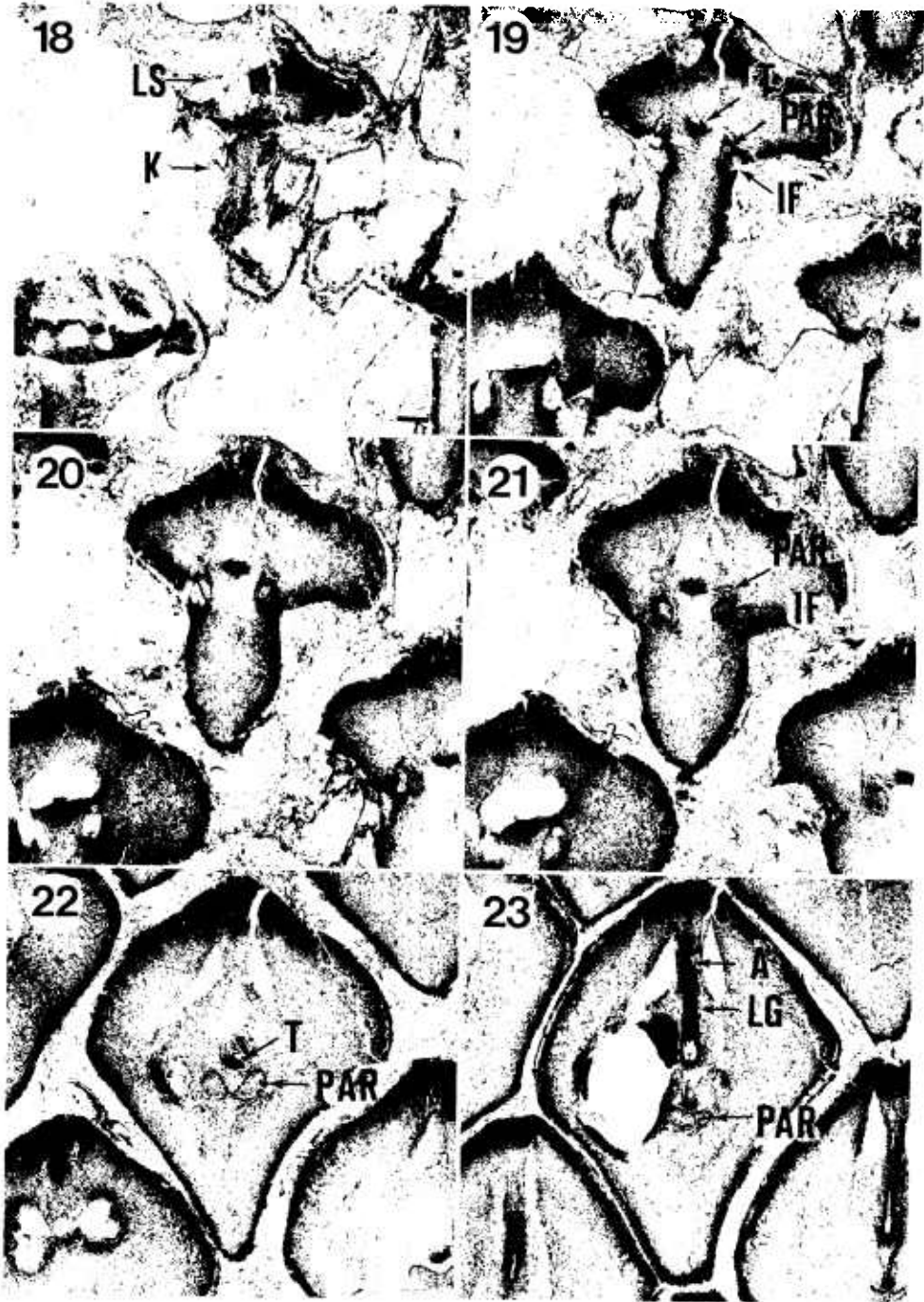
Cortical tissues. The cortex of *Lepidodendron hickii* is three-zoned (figs. 7-8) and similar in

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of periderm below leaf cushions (slide 158). Column of tangentially expanded cells marked by arrow. 9. Cross section of outer periderm with regions of tangential cellular expansion (arrow) (slide 172). LB = leaf cushion. 10. Longitudinal section of cortex (slide 164). Small arrow marks MC-OC contact. 11. Radial section of leaf cushion (slide 169). LS = leaf scar, LG = ligule pit, T = leaf trace, PAR = parichnos.



FIGS. 12-17. *Lepidodendron hickii* leaf cushions. IF = infrafoliar parichnos, PAR = parichnos, LS = leaf scar, T = leaf trace, LG = ligule pit, K = keel. Scales = 1 mm. 12. Three-dimensionally preserved cushion from pyritized axis (specimen X1). 13. Near-radial section through infrafoliar parichnos (slide 168). Parichnos strand forms the base of this area, filled with loosely arranged cells. 14-17. Serial, tangential sections of nearly equidimensional leaf cushions from small axis (slides 176-178, 180). IF appear granular due to filling of stellate parenchyma.



FIGS. 18-23. Serial tangential sections of leaf cushions from large diameter *Lepidodendron hickii* stem (slides 186-188, 190, 193). A = triangular ligule pit aperture, LS = leaf scar, K = keel, T = leaf trace, PAR = parichnos, IF = infrafoliar parichnos, LG = ligule pit.

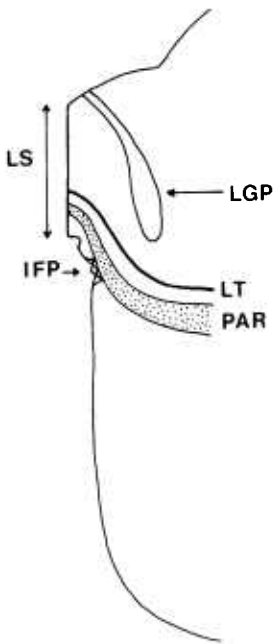


FIG. 24. Schematic radial section of *Lepidodendron hickii* leaf cushion combining median and non-median features. Bifurcation of parichnos strand at base of ligule pit is not shown for simplicity of reconstruction. LS = leaf scar, LGP = ligule pit, IFP = infrafoliar parichnos, LT = leaf trace, PAR = parichnos.

organization to that of other lepidodendrids. The inner cortical zone reaches a maximum thickness of 1 mm in stems >5 cm in diameter and is composed of closely packed cylindrical cells 0.025–0.08 mm in diameter and up to 0.1 mm long. At the inner margin of this zone, where it contacts the phloem region, the cell lumens of one or two layers are occluded by dark, possibly secretory material. As the leaf traces pass through the narrow inner cortex, the inner cortical cells on the abaxial side of the trace also have dark occlusions.

The middle cortex is 2–>10 times as wide as the inner cortex and consists of thin-walled cells 0.025–0.1 mm in diameter that are arranged in filaments. Leaf traces in this cortical zone are enclosed by a 3–4-cells-thick sheath of elongate parenchyma cells. Much of the thin-walled middle cortical parenchyma is degraded in most specimens.

The outer cortical region ranges from slightly thicker than to over twice the thickness of the middle cortex. Most cells of the outer cortex

are thick-walled and 0.025–0.1 mm in diameter. Lengths of these cells increase from isodiametric and of the smallest diameters at the inner margin of the outer cortex to lengths of up to 0.25 mm in the outer parts of the outer cortex, below the leaf cushions (fig. 8). Most stems from the Springfield (No. 5) and Herrin (No. 6) Coals of the Illinois Basin have distinctly bipartite outer cortical regions with an inner half composed of typically elongate, thick-walled cells and an outer half composed of cells with lumens occluded by a dark substance, possibly of secretory origin. There is a smooth transition in the dimensions of the cells across the sharp line delimiting these two areas of the outer cortex. The feature does not seem to be a happenstance of preservation. However, a pyrite petrification of a *L. hickii* stem from shales above the Springfield (No. 5) Coal has a uniformly non-secretory outer cortex.

Periderm. The periderm of *L. hickii* is a fairly uniform tissue of small cells, with cell lumens frequently occluded by a dark substance of probable secretory origin (figs. 9–10). In specimens with periderm 1–2 cm thick, the tissue is often irregularly three-zoned with non-secretory cells forming narrow bands along the inner and outer margins; this is not as uniformly developed as in the periderm of *Lepidophloios hallii* (DiMichele 1979a). None of the specimens examined provided evidence of bifaciality in development, as found in "*Lepidodendron*" sensu *L. vasculare* and closely related species (DiMichele 1981), and in none was there suggestion of multiple phellogens.

Periderm thickness in the *L. hickii* specimens examined was not as great as that found in *Lepidophloios* and "*Lepidodendron*". *Lepidodendron hickii* stems <20 mm in diameter usually have a periderm <1 mm thick; such stems are probably from terminal portions of the crown. The largest intact stem examined, 8 cm in diameter, was composed entirely of primary tissues; in other axes, 20–55 mm in diameter, periderm ranged from 0.5 to 3 mm thick. Maximum observed thicknesses of 2 cm occurred in isolated sheets of bark bearing intact leaf cushions. These observations suggest little allocation to secondary support tissues, at least in the crown branches.

Distinguishing characteristics of leaf cushions. All size classes of *Lepidodendron hickii* leaf cushions are distinguished by deep ligule pits

(fig. 11), infrafoliar parichnos (figs. 12-13), relatively large radial thickness, and an S-shaped arching of the leaf trace and parichnos such that these tissues enter the proximal side of the cushion at a lower level than their point of exposure on the leaf scar (figs. 11 and 13). Stomata are recessed in cavities approximately 0.15 mm deep on the cushion surfaces above and below the leaf scar. Large *L. hickii* leaf cushions have a characteristic low keel with plications or bars and a relatively broad lower cushion surface region. On small leaf cushions the keel is poorly developed and recedes steeply from the leaf scar, which is the most radially projecting part of the cushion. Both small and large cushions are radially thick, relative to the height and width dimensions. Leaf-cushion thickness on stems <2 cm in diameter was up to 3 mm, with height or width rarely exceeding 5 mm. Thicknesses of 1-1.5 cm were found on cushions up to 3 cm high.

Infrafoliar parichnos are oval areas below the leaf scar on either side of the lower median keel (figs. 12-13). They are openings up to 1 mm in diameter and 0.5 mm deep filled with stellate parenchyma. Thomas (1970) suggested that infrafoliar parichnos of *L. aculeatum* lack cuticle; my observations support his suggestions. Weiss (1907) described and illustrated the connection of these infrafoliar parichnos openings with the middle cortical parichnos strands. The floor of the infrafoliar parichnos is formed by the parichnos strand, which is continuous from the middle cortex to the leaf-scar surface. The leaf trace and subtending parichnos strand arch upward steeply immediately after the point of entry into the base of the leaf cushion. The parichnos strand is bifurcated close to the base of the ligule pit after which, on its arched path, each branch passes close to the leaf-cushion epidermis. The infrafoliar parichnos cavities connect through to the parichnos below the leaf scar and create openings in the cushion epidermis. Thus the infrafoliar parichnos are not blind endings for separate parichnos strands but are openings that "tap" the main parichnos bundles where they pass close to the cushion epidermis (figs. 13 and 24).

Ligule pits of *L. hickii* are very deep relative to the dimensions of the leaf cushion (figs. 11 and 24). In small, approximately equidimensional leaf cushions, ligule-pit depth is approximately one-half of total leaf-cushion height

(vertical dimension). In larger, more vertically elongate leaf cushions the ligule pit is about one-third of total cushion height. The only lycopods with comparably deep ligule pits are *Lepidophloios* (DiMichele 1979a), *Sublepidophloios*, and *Lepidodendron serratum*, which are similar to *L. hickii* in many aspects of morphology. The "*Lepidodendron*" *vasculare*-group of lepidodendrids does not have comparably deep ligule pits. The ligule pit in *L. hickii* is connected to the leaf trace by sparse transfusion tracheids. The lining of the ligule pit is not conspicuously multicellular, and the cells are similar to surrounding parenchyma in size and shape.

Ontogenetic variation in leaf cushions. The leaf cushions of *Lepidodendron hickii* show distinct variation in gross morphology that corresponds to the size of the primary body in the parent axis. The variation appears to be a manifestation of determinate growth (Andrews and Murdy 1958; Eggert 1961), not a result of later secondary thickening of the axis. Similar patterns of variation in leaf-cushion form induced by determinate growth have been described in *Lepidophloios halli* (DiMichele 1979a).

Leaf cushions of "typical" *Lepidodendron* form, with cushion height greater than cushion width, occur with regularity on stems >4 cm in diameter. Stems <4 cm in diameter nearly always have leaf cushions with maximum width exceeding maximum height by a small amount. The change in height:width ratio from small stems (figs. 14-17) to large stems (figs. 18-23) is continuous. However, leaf cushions from specimens of small diameter will appear, in isolation, to be quite different than cushions borne on stems of large diameter.

Variation of leaf-cushion form that is dependent upon diameter of stem primary body has been noted also in *Lepidophloios* (DiMichele 1979a), and there are some similarities between leaf cushions of small *Lepidophloios* stems and small *Lepidodendron hickii* stems. Other forms historically attributed to *Lepidodendron*, e.g., "*Lepidodendron*" *vasculare* and "*Lepidodendron*" *scleroticum*, do not exhibit this pattern of variability in leaf-cushion morphology. These forms are clearly distinct from *L. hickii* anatomically and reproductively and have very uniform cushion height:width ratios and cushion morphology throughout the shoot system (DiMichele 1981).

Mechanisms of leaf-cushion retention. Leaf cushions in *Lepidodendron hickii* (and the possibly equivalent compression, *L. aculeatum*) were not readily sloughed off the stem surface. All intact specimens examined in this study, up to a diameter of 8 cm, had attached leaf cushions. In addition, some trunks of *L. aculeatum* 0.5 to 1 m in diameter have large persistent leaf cushions that are not widely separated. Thomas and Watson (1976) reported on the external characters of a 34.5 m long *L. aculeatum* trunk; recognizable, closely spaced leaf-cushion outlines were visible 18 m above the base of the trunk. In the Thomas and Watson (1976) specimen there was gradual obliteration of leaf cushions by secondary stem expansion rather than sloughing of the leaf cushions as axis diameter increased.

Mechanisms for maintenance of leaf cushions on stems as secondary growth occurred varied among the arborescent lycopods. In *Lepidodendron hickii* there was extensive lateral expansion of cells in the base of the leaf cushions and in the outer parts of the periderm (figs. 8 and 10) that allowed leaf cushions to be retained. Thomas (1966) reported interarea development in *L. aculeatum* that is limited in extent but does provide an additional mechanism for the maintenance of intact leaf cushions.

Architectural constraint and leaf-cushion retention. The phenomena associated with leaf-cushion retention appear to be correlated with leaf-cushion shape. Lateral expansion of interareas or general lateral expansion in basal cushion parenchyma and periderm have been demonstrated unequivocally only in lycopod trees with vertically elongate or isodiametric leaf cushions that, with a single exception, do not overlap (non-imbricate). This includes *Sigillaria* (Thomas 1972), *Asolanus*, *Lepidodendron* (*L. aculeatum* or *L. hickii*-type), "*Lepidodendron*" (sensu *L. vasculare*, *L. scleroticum*, *L. dicentricum*, or *L. phillipsii*; DiMichele 1981), and *Sublepidophloios* (Hopping 1956), the only one of these genera with imbricate leaf cushions. Plants such as *Lepidophloios* with large, horizontally elongate leaf cushions, or *Paralycopodites*, with leaves permanently retained on usually horizontally elongate to isodiametric leaf bases (DiMichele 1980), have not been shown to have leaf-cushion retention mechanisms. In *Lepidophloios* very large, imbricate cushions are found on stems with massive primary bodies that usually lack

secondary growth; stems with >1–2 cm of periderm lack leaf cushions in most cases. These observations conflict with the suggestions of Thomas (1977, 1978), based on compression specimens, that *Lepidophloios* leaf cushions enlarged as secondary growth proceeded. Anatomically preserved specimens indicate that *Lepidophloios* specimens with large leaf cushions have otherwise large primary bodies; change in cushion shape is related to determinate growth and is correlated with apical meristem size, not stem girth increase.

The retention of possibly photosynthetically active active leaf cushions on lycopod stems (Thomas 1966) may be better accommodated architecturally by stems with non-imbricate, vertically elongate leaf cushions than by those with horizontally elongate, imbricate cushions. This is a consequence of the shape of resultant leaf-cushion interareas that are more vertical in lepidodendrids with vertically elongate cushions. Vertical interareas are the most effective means of accommodating tangential-horizontal tensions at the stem circumference that result from secondary expansion because they allow preferential longitudinal fissuring or tangential expansion of cells in longitudinal files. A parallel is the ray parenchyma of secondary phloem in some dicotyledons that expands tangentially with continued vascular cambium activity. In *Lepidophloios*, with largely horizontal interareas, tangential-horizontal stress cannot be accommodated easily without cushion disruption. The possible adaptive value of cushion retention may in part explain why the largest primary bodies and most limited secondary growth are found in lepidodendrids such as *Lepidophloios*, which have no mechanisms for cushion retention. Development of massive axes from primary meristems in such plants resulted in less disruption of outer tissues but further constrained frequency and angle of branching and total size (DiMichele 1979a).

Branching-habit. Branching in *Lepidodendron hickii* was anisotomous and of two basic types: the major form resulted in two unequally sized axes (fig. 1), the second produced protostelic lateral branches and left the main axis undeflected. The habit of the tree was apparently like that of *L. aculeatum* (Thomas and Watson 1976), in which a period of monopodial growth produced a massive trunk, topped by an anisotomously branched determinate crown.

There is no evidence of deciduous lateral branches, and it appears that individual trees were determinate. Similar forms of growth are known in *Lepidophloios hallii* (DiMichele 1979a) and *Lepidodendron dicentricum* (DiMichele 1979b).

Protostelic lateral branches probably represent cone branches. Branch diameters are 9–11 mm, with stele diameters 0.35–0.50 mm (fig. 4). Protostelic branches are found arranged in opposite rows, spirally, and sometimes as isolated branches on axes <25 mm in diameter that lack wood and have limited periderm. Binney (1872) described as *Halonnia regularis* axes bearing spirals of such small lateral branches and believed the main axes to be roots bearing lateral roots in a manner similar to *Stigmaria*; anatomically they are clearly *L. hickii* stems. Williamson (1893) also illustrated a number of such stems (as *Lepidodendron harcourtii*), which served as the basis for the description of *L. hickii* by Watson (1907). Although cones have not been found in direct attachment to these lateral branches, uniformity of size, anatomy, and size of parent axes strongly suggest a cone bearing function.

Associated reproductive structures. In this study the association of *Lepidodendron hickii* specimens preserved in coal balls coincides almost totally with occurrences of relatively large, bilaterally flattened, monosporic megasporangial-sporophyll units comparable to *Achlamydocarpon takhtajanii* or *A. belgicum* (Balbach 1966; Schumaker-Lambry 1966). The sporangial wall is complex and more than one cell-layer thick; the lateral alations of the basal lamina are short and stubby.

The size and anatomy of *Achlamydocarpon takhtajanii* axes are comparable to those of the protostelic lateral branches of *Lepidodendron hickii*. Dimensions reported for *A. takhtajanii* cones, summarized by Leisman and Rivers (1974), lend further support to the suggestion that the protostelic lateral branches of *L. hickii* are cone branches.

Discovery of *A. takhtajanii* organically connected to *Lepidodendron serratum* by Leisman and Rivers (1974) could introduce some confusion into correlation of *L. hickii* and *A. takhtajanii* based on co-occurrence. The two stem species occur together in Westphalian A specimens from England and in coal balls from the Springfield (No. 5) Coal of the Illinois Basin, the uppermost occurrence of *L. serratum*. How-

ever, in coal balls from western Pennsylvania (unnamed coal above the Middle Kittanning Coal) and from the Herrin (No. 6) Coal of Illinois *L. hickii* and *A. takhtajanii* co-occur without associated *L. serratum*; both coals are above the known stratigraphic range of *L. serratum* (Phillips 1980). *Lepidodendron hickii* and *L. serratum* have in common many vegetative morphological characteristics. It is plausible to expect similar basic kinds of reproductive structures, particularly because different kinds of anatomy are known to be correlated with different reproductive structures in general among lepidodendrid lycopods.

Too few microsporangiote cones have been found in association with *Lepidodendron hickii* to permit correlations. Similarities of vegetative anatomy and megasporangiote reproductive structures in *L. hickii* and *L. serratum* suggest similarities in microsporangiote reproductive organs. *Lepidodendron serratum* has been found in association with a small, monosporangiote cone, *Lepidostrobus minor* (Leisman and Rivers 1974), that produced *Lycospora* microspores. If *L. hickii* bore *Lycospora*-producing cones it could explain the great abundance of this spore in paleoenvironments where *L. hickii* (or the compression *L. aculeatum*) is abundant but *Lepidophloios* and *Paralycopodites*, also *Lycospora* producers, are absent.

DISCUSSION

Generic delimitation. Structurally preserved arborescent lycopods with leaf cushions similar to those of *Lepidodendron aculeatum* have been found consistently to have internal structure attributable to *L. hickii*. Included are specimens from the Westphalian A of England (Watson 1907), the Donets Basin of the Soviet Union (Zalessky 1909, 1911), the Finefrau-Nebenbank Horizon of the Netherlands (Koopmans 1928), the Aegir Horizon of the Netherlands (Koopmans 1934), the approximate horizon of the Middle Kittanning Coal of the Appalachian Basin in Pennsylvania, and the Springfield (No. 5) and Herrin (No. 6) coals of the Illinois Basin.

The only recorded exceptions to this pattern are three specimens purported to have *L. aculeatum* leaf cushions, with anatomy like that of *Lepidophloios*, particularly a coronate siphonostele. These specimens were described as *Lepidodendron aculeatum* by Seward (1906) and Za-

TABLE 1. Correlations of anatomically preserved forms of lepidodendrid lycopods with compression forms and reproductive structures.

Morphotypes	Traditional treatment (petrifaction)	Compression equivalent	Cones (petrifaction)
<i>Lepidodendron hickii</i>	<i>Lepidodendron hickii</i> , <i>aculeatum</i> , <i>obovatum</i>	<i>Lepidodendron aculeatum</i> and related forms with intrafoliar parichnos	<i>Achlamydocarpon</i> <i>takhtajanii</i>
<i>Lepidodendron serratum</i>	<i>Lepidodendron serratum</i>	None	<i>Achlamydocarpon</i> <i>takhtajanii</i> , <i>Lepidostrobus</i> <i>minor</i>
<i>Lepidophloios harcourtii</i> , <i>fuliginosus</i> , <i>hallii</i>	<i>Lepidodendron</i> in part (<i>L. harcourtii</i>), <i>Lepidophloios</i>	<i>Lepidophloios</i> , mostly of the <i>L. laricinus</i> type	<i>Lepidocarpon</i> , <i>Lepidostrobus</i> <i>oldhamius</i>
" <i>Lepidodendron</i> " <i>vasculare</i> , <i>phillipsii</i> , <i>scleroticum</i> , <i>dicentricum</i>	<i>Lepidodendron</i> spp.	<i>Lepidodendron</i> of the type lacking intrafoliar parichnos	<i>Achlamydocarpon varius</i>
<i>Paralycopodites</i> <i>brevifolius</i>	<i>Lepidodendron</i> <i>brevifolium</i>	<i>Ulodendron</i> spp.	<i>Lepidostrobus diversus</i> , <i>scottii</i> , <i>schopfi</i>
<i>Sigillaria</i> spp.	<i>Sigillaria</i> spp.	<i>Sigillaria</i> spp.	<i>Mazocarpon</i>
<i>Sublepidophloios</i>	<i>Lepidodendron aculeatum</i> , <i>obovatum</i> ; <i>Lepidophloios</i> <i>macrolepidotus</i>	<i>Sublepidophloios</i>	?
<i>Bothrodendron</i>	None	<i>Bothrodendron</i>	<i>Bothrodendrostrobus</i>
<i>Asolanus</i>	None	<i>Asolanus</i>	?

lessky (1909) and as *L. obovatum* by Scott (1906). Thomas (1970) suggested that *L. obovatum* be considered a synonym of *L. aculeatum*. The specimen of Scott (1906) has never been illustrated. That of Seward (1906) has been pivotal in confirming the belief that anatomy is insufficient to separate *Lepidodendron* and *Lepidophloios* and, as an extension of that thinking, that the two genera intergrade morphologically. A logical outcome of this reasoning is that intermediate forms will exist. However, the leaf cushions of Seward's (1906) specimen are so poorly preserved that only their gross outlines are visible; they are not well-enough preserved to attribute to any compression-based lepidodendrid. The specimen of Zalesky (1909) has leaf cushions that in gross outline are of *Lepidodendron* form but bulge outward and partially imbricate like leaf cushions of *Sublepidophloios* Sterzel (Hopping 1956).

Sublepidophloios, as defined from compressions, has imbricate leaf cushions with the leaf scar at the end of a bulging overhang, similar to *Lepidophloios*. Unlike *Lepidophloios*, *Sublepidophloios* cushions have a *Lepidodendron* outline at their bases. Therefore, partially destroyed or highly compressed *Sublepidophloios* leaf cushions would have a *Lepidodendron* aspect. Probably attributable to this genus are specimens described as *Lepidophloios macrolepidotus* by Koopmans (1928), who believed that the Seward (1906) and Zalesky (1909) specimens were not *Lepidodendron aculeatum* but were *Lepidophloios macrolepidotus*. I agree that the specimens are all of the same kind and suggest that the entire suite is attributable to *Sublepidophloios*.

The distinctiveness of *Lepidophloios* and *Sublepidophloios* is a question of considerably different magnitude than that of the distinctiveness of *Lepidophloios* and *Lepidodendron*. It is possible that *Lepidophloios* and *Sublepidophloios* are congeneric, representing two subgroups within *Lepidophloios*. Evidence from newly discovered specimens indicates many similarities in vegetative anatomy; basic leaf-cushion outline is the only major difference. Leaf cushions with a greater vertical than horizontal dimension appear to be plesiomorphic. Thus, *Lepidophloios* can be distinguished from *Sublepidophloios* by the apomorphic condition of horizontally elongate leaf cushions. The plesiomorphic state in *Sublepidophloios* does not in-

dicate an integral link to other forms with vertically elongate cushions that also have retained the ancestral state.

The problems inherent in the use of a shared ancestral character as an indicator of evolutionary relationship are the root cause of confusion in arborescent lycopod taxonomy. Polarity determinations of arborescent lycopod characteristics as part of a cladistic analysis (DiMichele and Young, in preparation) indicate, through a two-taxon outgroup comparison, that the gross *Lepidodendron* leaf-cushion shape (greater vertical than horizontal dimension) is the ancestral (plesiomorphic) character state in the arborescent lycopods. Thus leaf cushions with a greater vertical than horizontal dimension are not useful indicators of phylogenetic relatedness. *Lepidodendron* has been circumscribed almost solely on leaf-cushion shape and, as a result, many otherwise distinct forms have been included in the genus (table 1). In fact, *Lepidodendron* can be characterized only by the further derived aspects of cushion morphology, which evolved as part of the separation of this lineage from other evolutionary lineages (some of which have also retained the basic, ancestral leaf-cushion shape). Correlations of anatomically preserved lepidodendrid stems with compressions and reproductive organs are presented in table 1.

Affinities of Lepidodendron. The morphology of the *Lepidodendron aculeatum*-group of lepidodendrids, which includes the anatomically preserved forms *L. hickii* and *L. serratum*, is characteristic and distinct from other lycopod morphotypes. The greatest phenetic similarity of *Lepidodendron* is with *Lepidophloios*; shared features include a large primary body with large diameter medullated stele, development of a hyphal pith core, massive outer cortex, homogeneous to tri-zoned periderm composed largely of cells with "resinous" coloration and contents, relatively fleshy leaf cushions that change size and shape in conjunction with changes in the diameter of the primary body (a determinate-growth phenomenon), deep ligule pit in which the pit aperture may be distant from the leaf scar, and laterally borne cones on "halonial" branches. There are also several characters shared by the *Achlamydocarpon takhtajanii*-type megasporangium of *Lepidodendron* and *Lepidocarpon* produced by *Lepidophloios* (Phillips 1979; Leisman and Rivers

1974). These include the general features of a single functional megaspore and expanded basal sporophyll laminae plus the uniquely shared features of distal dehiscence of sporangial and megaspore walls to expose the archeogonia and bilateral flattening of the megasporangium, which has a dorsal ridge and contains a *Cystosporites giganteus*-type megaspore. In addition, *Lycospora* microspores are found in *Lepidostrobus minor*, the microsporangiate cone associated with *A. takhtajanii* (Leisman and Rivers 1974), and in *Lepidostrobus oldhamius*, the microsporangiate cone of *Lepidophloios* (Phillips 1979; DiMichele 1979a).

Lepidodendron can be differentiated from *Lepidophloios* as follows: Leaf cushions of *Lepidodendron* are not imbricate, which is the most common state in *Lepidophloios*. Leaf cushions of *Lepidodendron* have infrafoliar parichnos, which have not been demonstrated in any other group of lepidodendrids. The stele of *Lepidodendron* lacks the clearly defined protoxylem corona that is characteristic of *Lepidophloios*. Branching is predominantly anisotomous in *Lepidodendron* and isotomous in *Lepidophloios*. Leaf cushions of *Lepidodendron* are retained, even on larger diameter axes (Thomas and Watson 1976), by tangential expansion of cell files in the periderm, resulting in interarea expansion and gradual cushion obliteration; *Lepidophloios* has no evidence of interarea expansion, and cushions appear to have been sloughed off as girth increased. In addition, although they share several features that indicate close affinity, *Achlamydocarpon takhtajanii* and *Lepidocarpon* differ in a number of characters related to sporangial wall thickness, basal sporophyll lamina proliferation, and distal lamina construction (Phillips 1979). *Sublepidophloios*, as far as it is known, is so similar to *Lepidophloios* that it has the same relationship to *Lepidodendron* as does *Lepidophloios*, with the exception of leaf-cushion outline.

Lepidodendron hickii has much greater phenetic similarity to *Lepidophloios* and *Sublepidophloios* than it does to the other major group of lycopods with *Lepidodendron*-type leaf cushions, represented by "*Lepidodendron*" *vasculare*, *L. scleroticum*, *L. phillipsii*, and *L. dicentricum*. I recently reviewed these species as representative of the coal-swamp forms of *Lepidodendron* (DiMichele 1979b, 1981). However, they clearly must be segregated as a new genus if tax-

onomy is to be an accurate reflection of evolutionary relationship. These lepidodendrids differ from *Lepidodendron hickii* in a large number of characters including the following character states: mixed protosteles or longitudinally dissected siphonosteles, dictyoxylon outer cortex, clearly bifacial periderm with thinner phellem, development of tangential bands of thin-walled cells in the phelloderm, lack of infrafoliar parichnos in leaf cushions, uniform leaf-cushion morphology throughout the plant, fundamentally excurrent habit with deciduous lateral branches, and terminal cones of the *Achlamydocarpon varius*-type producing *Capposporites* microspores (Courvoisier and Phillips 1975).

The inclusion in *Achlamydocarpon* of both *A. takhtajanii* (the cone of *Lepidodendron hickii* and *L. serratum*) and *A. varius* (the cone of "*Lepidodendron*" *vasculare* and its relatives) is a further nomenclatural complication not reflective of evolutionary relationships. The type species of *Achlamydocarpon* is *A. belgicum* Schumaker-Lambry, which is probably identical to *A. takhtajanii* (Phillips 1979; Leisman and Rivers 1974). The inclusion of *A. varius* (Taylor and Brack-Hanes 1976; Leisman and Phillips 1979) in this genus is based on the occurrence of a single functional megaspore in a non-integumented megasporangium; treated in this way, *Achlamydocarpon* is strictly a form genus. *Achlamydocarpon takhtajanii* and *A. belgicum* have complex, multi-layered sporangial walls, distally opening sporangia that are bilaterally flattened with a dorsal ridge, *Cystosporites giganteus*-type megaspores, a well-developed basal keel, and small, fleshy alations of the basal lamina. In contrast, *A. varius* has a complex but single-layered sporangial wall that opens proximally, the sporangium is dorsiventrally flattened and has intrasporangial parenchyma, a *Cystosporites varius*-type megaspore with complex proximal massa, a poorly developed keel, and broad lateral alations of the lamina. The microsporangiate counterparts of these cones produce different kinds of microspores, *Capposporites* in the case of *A. varius* and *Lycospora* in the case of *A. takhtajanii*. The two species have no substantive morphological features in common; *A. takhtajanii*, in contrast, has several major similarities to *Lepidocarpon*. This suggests that *Achlamydocarpon takhtajanii* and *A. varius* may represent similar "grades" of evolution—unintegumented megasporangia with single functional

megaspores, shed as a unit from the cone axis with the sporophylls. However, the details of their morphology suggest independent derivation and no close phylogenetic relationship.

Relationships of Lepidodendron serratum. Felix (1952) suggested that *L. serratum* was herbaceous. Other investigators (Baxter 1965; Leisman and Rivers 1974; DiMichele 1981) similarly have found no secondary tissues in stems up to 10 by 4 cm in cross section (Baxter 1965). *Lepidodendron serratum* is allied most closely with *L. hickii* on the basis of shared features, which include a stele of relatively large diameter with a well-defined pith but lacking a distinct corona, non-ensheathed leaf traces in the middle cortex, massive outer cortex, and predominantly anisotomous branching. Intrafoliar parichnos have not been observed. *Lepidodendron serratum* further shares with *L. hickii* the reproductive features of *Achlamydocarpon takhtajanii* cones, which Leisman and Rivers (1974) found attached to *L. serratum* stems. The association of *L. hickii* and *A. takhtajanii* is one of repeated co-occurrence, and not one of attachment. However, *A. takhtajanii* and *L. hickii* occur together in several coals from which *L. serratum* is unknown despite intensive sampling, e.g., the Herrin Coal of Illinois.

Morphological differences between *Lepidodendron serratum* and *L. hickii* are probably attributable to the herbaceous habit of *L. serratum* and include the permanently retained leaves, lack of periderm and secondary xylem, and highly branched, scrambling habit of *L. serratum* stems. *Lepidodendron serratum* is not part of the "*Lepidodendron*" *vasculare*-group of lycopods as I suggested previously (DiMichele 1981). In *L. serratum* the broad-diameter stele with a uniform, well-delimited, homogeneous pith and a weakly developed protoxylem corona is similar to *L. hickii*; *L. vasculare* and relatives have steles with mixed piths or longitudinally dissected xylem cylinders. The massive outer cortex of *L. serratum* and *L. hickii* contrasts with dictyoxylon cortex of the *L. vasculare*-group. *Achlamydocarpon takhtajanii* and *A. varius* are morphologically distinct.

Paleoecological considerations. *Lepidodendron hickii* and *L. serratum* illustrate the great differences in form that evolved in *Lepidodendron* during the Carboniferous. Most of the taxonomic diversity in this genus was confined to clastic swamp and mesic-lowland environ-

ments rather than to coal swamps, i.e., few species of *Lepidodendron* evolved the capacity to exploit peat-substrate swamp habitats. *Lepidodendron hickii* probably was not a coal-swamp-centered species; its rarity in coal balls and the unusual fern- and pteridosperm-dominated assemblages in which it occurs suggest that it was a clastic-swamp-centered species that occurred occasionally in certain specialized kinds of coal-swamp habitats. In this sense it is probably a preservational state of a species such as *L. aculeatum*, or a closely related form with infrafoliar parichnos, that was common in clastic-swamp and mesic-lowland habitats. A more exact correlation is not yet possible because the taxonomy of compression-impression lepidodendroids still needs to be reassessed in light of findings from petrifications. *Lepidodendron serratum* is known only from coal balls and may have been coal-swamp-centered.

Other kinds of lycopods including "*Lepidodendron*" *vasculare* and related species, *Lepidophloios* and possibly *Paralycopodites*, were largely centered in coal swamps and occur rarely in compression floras. The largely different types of preservation representing coal-swamp and clastic-substrate vegetation is in itself a complicating factor for taxonomists. However, recognition of largely different evolutionary lineages in coal swamps and surrounding lowlands magnifies the preservational problem because it diminishes the possibility of meaningful cross-preservational correlations. The general anatomy and external morphology of *Lepidophloios*, *Lepidodendron* (sensu *L. hickii*-*L. aculeatum*), *Paralycopodites* (*Ulodendron*?), "*Lepidodendron*" (sensu *L. vasculare*), and *Sigillaria* are known and can be identified in both petrification and compression. *Asolanus* and *Bothrodendron* are still inadequately known anatomically. The identification of an anatomical form with leaf cushions attributable to the *Lepidodendron aculeatum* complex (i.e., *L. hickii*) is a key to sorting out most of the taxonomic problems that have characterized this group because it allows a rigorous application of the name *Lepidodendron* to both petrifications and compressions.

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