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Diaphorodendron, gen. nov., a Segregate from *Lepidodendron* (Pennsylvanian Age)

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ABSTRACT. *Diaphorodendron* is described as a new genus on the basis of anatomically preserved specimens previously included in *Lepidodendron*. Species include *D. vasculare* (type species), *D. scleroticum*, *D. dicentricum*, and *D. phillipsii*. Circumscription of this new genus leaves *Lepidodendron* as a monophyletic, morphologically cohesive taxon. Traditionally *Lepidodendron* has been recognized by its higher-than-wide leaf cushions, a character that appears to be the ancestral (plesiomorphic) state in the Lepidodendrales. The consequence of relying on this single trait has been inclusion of forms distinct in most aspects of basic morphology within *Lepidodendron*, masking rather extensive diversification in the Lepidodendrales. While sharing basic leaf-cushion shape, *Diaphorodendron* and *Lepidodendron* differ in many anatomical features and details of leaf-cushion morphology (especially relative "thickness" of leaf cushions and presence or absence of infrafoliar parichnos). By correlating anatomy and leaf-cushion morphology, characteristics can be recognized by which *Diaphorodendron* and *Lepidodendron* can be distinguished in compression preservation.

The purpose of this report is to establish a new generic name for a distinctive, structurally-preserved group of Pennsylvanian-age lepidodendrid lycopods previously included in the genus *Lepidodendron* Sternberg. The species that form the nucleus of this segregate genus are *Lepidodendron vasculare* Binney, *L. scleroticum* Pannell, *L. phillipsii* DiMichele, and *L. dicentricum* Felix (= *L. schizostelicum* Arnold) (see DiMichele 1979b, 1981, 1983a).

Historical factors have confused and complicated the taxonomy of lepidodendrids. This is most apparent in the application of taxonomic concepts based on compression-impression specimens to anatomically-preserved specimens. Compression specimens display only external morphology; many such characters potentially have a high degree of covariation and probable correlation (leaf cushion traits such as height, width, etc.). Anatomically-preserved specimens offer a much larger suite of characters for comparison, and include most of those that can be observed in compressions. Generic concepts in lycopods, in almost all cases, were first established on the basis of compression specimens. Thus, the application of names between preservational-types has been largely unidirectional. Names used for compression-impression specimens have been used to encompass anatomically preserved forms. One of the best examples of this is provided by *Lepidodendron*. Scott (1906) and Seward (1906) noted that more than one distinct kind of anatomy

was associated with leaf cushions having height to width ratios greater than one (the principal character by which *Lepidodendron* was recognized). They concluded that anatomy varied greatly within a genus and therefore was not useful in distinguishing genera of lepidodendrids. This view has prevailed in the literature until recently even though it would appear more reasonable to conclude that the character of having higher-than-wide leaf cushions is inappropriate for delimiting *Lepidodendron*.

The extensive anatomical data base can be used to resolve questions of lycopod taxonomy if anatomically preserved leaf-cushion morphologies are characterized in such a way that they can be compared to the compression record. This, in turn, would allow correlation of compression taxa with more broadly-circumscribed anatomical taxa, and improve our understanding of the taxonomic significance of variability in leaf-cushion form. For example, the type species of *Lepidodendron*, *L. aculeatum* Sternberg (Thomas 1970), is based on compression specimens. While several distinctive anatomically-based taxa have leaf cushions that are higher than wide, only one, *Lepidodendron hickii* Watson, has leaf cushions with the characteristics found only in *L. aculeatum* and similar compression forms: radially raised or protruding leaf cushions that bear infrafoliar parichnos, and that change shape from slightly elongate on small branches to relatively more elongate on larger stems (Watson 1907; Di-

Michele 1983a). Height to width ratio alone will not permit correlation of the type species of *Lepidodendron* with one of the several distinct kinds of stem anatomies that have vertically elongate leaf cushions. Certain "minor" attributes of cushion morphology allow the *L. aculeatum*-*L. hickii* correlation. As a consequence, it is now possible to segregate other taxa from *Lepidodendron* that have anatomy and aspects of leaf-cushion morphology different from those of *L. aculeatum*-*L. hickii*. This paper concerns one of these segregates.

ANATOMICALLY-PRESERVED MORPHOTYPES
(GENERA) OF PENNSYLVANIAN AGE

The anatomically-preserved Pennsylvanian-age lepidodendrids represent six distinct organizational plans. Stem organ-taxa can be correlated with cone organ-taxa by two means, in the absence of attachment. First, co-occurrence in coal balls (concretions of structural peat from coal seams) is particularly compelling if only one species of lycopod stem and one kind of lycopod reproductive organ are known from the coal deposit. Second, comparison of cone-axis anatomy with various metric and anatomical aspects of stem anatomy and morphology may indicate that the organs are parts of the same natural taxon. The following architectural groups have been recognized—(stem names are given first, followed by reproductive structures): 1) *Lepidophloios*-*Lepidostrobus oldhamius*-*Lepidocarpon*, 2) *Sigillaria*-*Mazocarpon*, 3) *Paralycopodites*-*Flemingites* (*Flemingites* is a recent segregate from *Lepidostrobus*, see Brack-Hanes and Thomas 1983), 4) *Sublepidophloios* (no cone correlation yet possible), 5) *Lepidodendron*-*Achlamydocarpon takhtajanii*, 6) "*Lepidodendron*" (*Diaphorodendron*)-*Achlamydocarpon varius*. The two species of cones included in the genus *Achlamydocarpon*, *A. takhtajanii* and *A. varius*, have no substantive anatomical similarities (DiMichele 1983a), so their placement in this genus does not reflect close phylogenetic relationship. The congeneric status of *A. takhtajanii* and *A. varius* reflects certain organizational similarities that appear to have been attained independently; they represent similar "grades" of cone evolution in different lineages.

Species from all of these genera, except *Sigillaria*, have been included at some historical point, often only by tradition, in *Lepidodendron*.

In a series of earlier articles I have attempted to re-circumscribe these forms and illustrate that no intermediates have yet been found (DiMichele 1979a, b, 1980, 1981, 1983a). The recognition of an additional genus, segregated from *Lepidodendron*, will largely complete the process of defining architecturally distinct, monophyletic genera of Pennsylvanian-age lepidodendrid lycopods. Two genera described from compressions have yet to be described convincingly from petrifications, *Bothrodendron* and *Asolanus*. Both of these may be subsumed by already recognized forms, or may be found to have distinctive structural organization.

Diaphorodendron DiMichele, gen. nov.—TYPE: *Diaphorodendron vasculare* (Binney) DiMichele, comb. nov. BASIONYM: *Lepidodendron vasculare* Binney, Quart. J. Geol. Soc. Lond. 18:106-112, pl. IV, figs. 1-5, 1862. Binney described and illustrated only one specimen.—TYPE: Slides prepared from Binney specimen No. 3—SM M. 4318 a-e; Sedgwick Museum, University of Cambridge, Cambridge, England. Collection locality: Bullion Mine, Spa Clough, Burnley, Lancashire, England. Stratigraphy: Westphalian A (Lower Pennsylvanian), Lower Coal Measures, Lancashire. [Illustrations in Binney (1862) include SM M. 4318 a = pl. IV, figs. 2 and 3; SM M. 4318 b = pl. IV, fig. 4; SM M. 4318 c = pl. IV, fig. 5.]

Description of genus. *Diaphorodendron* includes lycopods with arborescent habit. Growth form is either an excurrent trunk bearing deciduous lateral branches, or a columnar trunk, which at maturity terminated growth with a dendritic, synchronously determinate crown. Branching is anisotomous. Leaf cushions are vertically elongate on stems of all sizes; their ornamentation is simple and may include shallow plications above or below the leaf scar. Parichnos are strictly foliar (confined to the leaf scar, not present below the scar as infrafoliar prints). The leaf scar is at or above the middle of the cushion. The keel is relatively prominent, but the cushions are not "fleshy" (strongly protruding). Interareas are present between leaf cushions, as fissures or tangentially expanded zones on stems with developed periderm. The periderm is bizonate, with a thick phelloderm and thinner phellem. Phelloderm

is composed usually of tangentially alternating layers of thicker- and thinner-walled cells, especially well developed in the larger specimens; the thinner-walled cells are often degraded. Phellem is homogeneous and usually resinous in appearance. As in most other lepidodendrid lycopods, the primary cortex is three-zoned. The outer cortex is composed of radially aligned areas of thicker- and thinner-walled cells (dictyoxyton), the thinner-walled cells clustered around the leaf traces; the middle and inner cortical zones are variable in character, but usually contain cells with dark contents, and the inner zone is thin. The stele is usually a mixed protosteles; however it may be a distinctly medullated protosteles with primary xylem longitudinally dissected. Cones are borne on protostelic lateral branches, produced on axes usually <2 cm in diameter (cones therefore terminal or subterminal). Leaf abscission and secondary xylem occur.

Stems of the type described here co-occur with cones of the *Achlamydocarpon varius*-type (Taylor and Brack-Hanes 1976; Leisman and Phillips 1979), which bear *Cappasporites* microspores (Courvoisier and Phillips 1975) and *Cystosporites varius* megaspores. *Diaphorodendron* stems probably were attached to root systems of *Stigmara*. This is inferred from *Stigmara* with the distinctive periderm architecture characteristic of *Diaphorodendron* stems; such *Stigmara* may occur in coals containing one or more species of *Diaphorodendron*.

Etymology. The name *Diaphorodendron* is derived from the Greek words *diaphoros* (different) and *dendron* (tree). It is neuter.

Additional new combinations.

Diaphorodendron scleroticum (Pannell) DiMichele, comb. nov. **BASIONYM:** *Lepidodendron scleroticum* Pannell, Ann. Missouri Bot. Gard. 29:245-273, 1942.—**TYPE:** LECTOTYPE, designated herein, Specimen No. WCB 56, and slides and peels thereof. **PARATYPE,** Specimen No. WCB 55, and slides and peels thereof. Both specimens housed in Paleobotanical Collections, University of Connecticut, Storrs, Connecticut.

Diaphorodendron dicentricum (Felix) DiMichele, comb. nov. **BASIONYM:** *Lepidodendron dicentricum* Felix, Ann. Missouri Bot.

Gard. 39:263-288, 1952.—**TYPE:** Specimen No. WCB 781, and slides and peels thereof; peels in Paleobotanical Collections, Department of Plant Biology, University of Illinois-Urbana. Emended description and further synonymy in DiMichele (1979b).

Diaphorodendron phillipsii DiMichele, comb. nov. **BASIONYM:** *Lepidodendron phillipsii* DiMichele, Palaeontographica, Abt. B 171: 122-136, 1981.—**TYPE:** Specimen No. 9876, and slides and peels thereof; Paleobotanical Collections, Department of Plant Biology, University of Illinois-Urbana.

DISCUSSION

Segregation of *Diaphorodendron* from *Lepidodendron* permits formal recognition that these two groups have distinctive morphologies. This also results in a more narrow morphological circumscription of *Lepidodendron*, which may now constitute a monophyletic ("natural") group. The anatomical characteristics of true *Lepidodendron* are described and illustrated by Watson (1907) and DiMichele (1983a) in descriptions of *Lepidodendron hickii*, the only described species of petrification lepidodendrid with leaf cushions like those found on *Lepidodendron aculeatum* and similar forms. The major characteristics of *Lepidodendron* and *Diaphorodendron* are contrasted in table 1. In final consideration, the anatomy of true *Lepidodendron* is much more like that of *Lepidophloios* (DiMichele 1979a) than it is like that of *Diaphorodendron*, accentuating the inadequacy of leaf-cushion shape as the basis for recognizing true *Lepidodendron*.

Lepidodendron historically has included many morphologically distinctive forms on the basis of higher-than-wide leaf cushions in which the leaf scar is above the vertical midpoint of the cushion. This leaf-cushion construction appears to be the ancestral (plesiomorphic) state in the Lepidodendrales on the basis of comparison with a number of different lycopod outgroups (DiMichele 1983b; DiMichele and Young in prep.). Thus, the level of applicability, or universality, of this character state lies at or somewhere above the Lepidodendrales in the taxonomic hierarchy, so far as can now be determined. The major lepidodendrid genera (architecturally distinct organizational plans) appeared during the Lower Carboniferous

TABLE 1. Comparative morphology of selected features of *Diaphorodendron* and *Lepidodendron*.

	DIAPHORODENDRON	LEPIDODENDRON
Pith	Mixed parenchyma and tracheids or uniformly parenchymatous	Uniformly parenchymatous to bizonate with an inner core of hypha-like parenchyma
Primary xylem	Protosteles or ring of tracheidal tissue with longitudinal parenchymatous partings	Continuous ring of tracheidal tissue
Protoxylem	Exarch, distributed uniformly around margin of primary xylem	Exarch, clustered into blunt points at margin of primary xylem
Cortex	Three zoned	Three zoned
Inner	Narrow, may contain cells with dark contents, may partially ensheath leaf trace into middle cortex	Narrow, may contain cells with dark contents
Middle	Composed of thin-walled parenchyma, usually degraded	Composed of thin-walled parenchyma, usually degraded
Outer	Broad; composed of alternating radial bands of thicker- and thinner-walled cells that anastomose vertically; each thin-walled band encloses a leaf trace	Broad; composed uniformly of thick-walled parenchyma, or bizonate, with parenchyma of outer zone containing dark contents
Periderm	Bizonate; inner zone (phellogen) thick-walled, composed of tangentially alternating thick-walled and thin-walled cells; outer zone (phellem) homogeneous, the cells often have resinous appearance	Massive, homogeneous to bizonate, without a clear phellem-phellogen distinction; cell-files tangentially expanded in the outer part of larger stems
Leaf-cushion anatomy	Relatively shallow ligule pits; leaf trace straight, with nearly horizontal path	Relatively deep ligule pits; leaf trace 'S'-shaped
Cones	<i>Achlamydocarpon varius</i>	<i>Achlamydocarpon takhtajanii</i>
Microspores	<i>Capposporites</i>	? <i>Lycospora</i>

(Meyer-Berthaud 1984). In some cases these lycopods retained the ancestral leaf-cushion shape at some stage in their development, as in the genera considered in this report; in other cases leaf-cushion shape was among the divergent characters, as in *Lepidophloios*. Wider-than-high leaf cushions are an apomorphic (derived) state that distinguishes *Lepidophloios* from those forms that retained the ancestral state of this one character. Those taxa retaining the ancestral state are not necessarily allied more closely to each other than any one may be to *Lepidophloios*, since they diverge from each other in other morphological aspects. Because the nature of the evolutionary process is one of divergence from ancestral form, creation of taxonomic groups based only on ancestral characters does not recognize that evolutionary divergence in other traits has occurred and new architectures arisen. Such characters cannot delimit "natural" taxa.

Lepidodendron, as it is presently applied to

compression specimens, encompasses both true *Lepidodendron* and *Diaphorodendron*. Differentiating these genera in compression-impression preservation is likely to be more difficult than in anatomical preservation. Considerable progress has been made by Thomas (1970) in attaining a clearer delimitation of compression species of *Lepidodendron* sensu lato. However, findings from anatomy only recently have been applied to compressions (DiMichele 1983a; Wnuk 1985), and the acceptability and utility of conclusions drawn from these studies has yet to be evaluated. As mentioned above, compression fossils of lycopods display a very limited range of morphological characters, especially in fragmentary specimens. Because of this, *Diaphorodendron* may be recognizable more by its lack of those leaf-cushion characters that distinguish *Lepidodendron* than by unique features of its cushion architecture (this is not to say that *Diaphorodendron* lacks other derived traits).

As I now understand the problem, true *Lepidodendron* may be recognized in compression-impression preservation by the combination of the following characters: leaf-cushion height to width ratios greater than, equal to, and occasionally less than one (ratios close to one apparently occur on small stems of all species, and are the rule in other species on stems of all diameters); leaf cushions raised or radially-thick, sometimes with barred (deeply plicate) lower keels; ontogeny of individual cushions possibly isometric, at least in early stages (DiMichele, Pfefferkorn, and Gillespie in prep.); infrafoliar parichnos present below leaf scar; leaf cushions maintained on large-diameter stems by expansion of sub-epidermal cells and limited development of interareas, thus large diameter stems have closely spaced, large leaf cushions; branching largely isotomous, except for the production of cones, which are borne on small lateral branches (halonial branches) produced by anisotomy. In contrast, *Diaphorodendron* leaf cushions are generally simple. The limited capacity of stem interarea expansion caused the cushions, ultimately, to be sloughed from the stem surface. The following criteria, however unorthodox in light of traditional usage, may allow this genus to be recognized in compression: leaf cushions generally small; cushion height greater than width on stems of all diameters; cushions relatively flat, protruding little from the stem surface; ontogeny of individual cushions probably allometric; infrafoliar parichnos lacking; interareas develop but cushions ultimately sloughed from surfaces of larger stems; branching mostly anisotomous.

Compressions with higher-than-wide leaf cushions must be recognized as encompassing more than *Lepidodendron*; otherwise the genus becomes a polyphyletic group, and will, consequently, be of limited use in phylogenetic and evolutionary analyses. Recognition of this problem is the first step toward its solution, which will be determined in final analysis by the names that are used in floristic and taxonomic studies.

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