

Diaphorodendraceae, fam. nov. (Lycopsida: Carboniferous): Systematics and Evolutionary Relationships of Diaphorodendron and Synchysidendron, gen. nov



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American Journal of Botany, Vol. 79, No. 6 (Jun., 1992), 605-617.

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DIAPHORODENDRACEAE, FAM. NOV.
(LYCOPSIDA: CARBONIFEROUS): SYSTEMATICS AND
EVOLUTIONARY RELATIONSHIPS OF DIAPHORODENDRON
AND SYNCHYSIDENDRON, GEN. NOV.¹

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Synchysidendron, gen. nov., is segregated from *Diaphorodendron* DiMichele emend. Both genera are determinate, rhizomorphic, arborescent lycopsids that share identical reproductive organs but differ radically in growth architecture and consequently in the timing of reproduction. Cones in *Synchysidendron* (two species) are borne on late-formed crown branches; in *Diaphorodendron* (three species) cones are borne on deciduous lateral branches, produced over much of the life of the tree. The two genera also differ in several characteristics of the stele and periderm. We hypothesize that *Diaphorodendron* gave rise to *Synchysidendron* within their shared Late Carboniferous coal-swamp habitat, by heterochronic suppression of lateral branching during ontogeny. Together, these genera form a highly apomorphic clade, here recognized as the new family Diaphorodendraceae, that is distinguished primarily by siphonostelic axes, a bifacial periderm, distinctive megasporangia, and gulate megasporangia.

Arborescent lycopsids dominated peat-swamp forests during most of the Pennsylvanian (Late Carboniferous). These bizarre plants represent the culmination of lycopsid morphological complexity, and demonstrate many unusual developmental, physiological, and ecological features that have no close parallels in the modern flora. Their solutions to the common ecological problems faced by land plants have attracted renewed interest since the lycopsids were recognized as the sister group to the rest of the vascular plants (Banks, 1968; Crane, 1990; Bateman and DiMichele, 1991). Thus, the attributes of these most complex and highly derived lycopsids probably evolved independently of superficially similar features in the sphenopsids, ferns, and seed plants: examples include central root systems, the tree habit (arborescence), siphonosteles, vascular cambium (arborescence), phellogen, leaves, and seedlike reproductive organs. In addition, their unique shootlike stigmarian root systems (e.g., Eggert, 1972; Rothwell and Erwin, 1985) may have been photosynthetic, dictating ecological dynamics in the extensive wetland ecosystems that they dominated (Phillips and DiMichele, in press).

Recently, far greater taxonomic diversity has been recognized in this group than previous studies suggested. Most of this diversity has been described at the generic level, largely as a consequence of studies of anatomically preserved specimens. These studies were designed to reconstruct conceptual "whole plants" and thereby determine their growth forms and life histories (DiMichele, 1979a, b, 1980, 1983; Bateman and Rothwell, 1990; Bateman and DiMichele, 1991; Bateman, in press).

Two additional factors have prompted the proliferation of genera; both are related to the increasing rigor with which phylogenies are being constructed by systematists. First, classifications using only the compressed remains of arborescent lycopsid axes were constrained to external characteristics of the vegetative axes. Thus, the epitome of arborescent lycopsids, *Lepidodendron*, traditionally had been delimited solely by the greater vertical than horizontal dimension of its diamond-shaped leaf bases (leaf cushions). Studies of anatomically preserved specimens revealed extensive diversification in reproductive and vegetative morphology, concomitant with conservation of the leaf-base shape. In other words, vertically elongate leaf cushions represent the primitive morphological state in this group of plants. The tradition of lumping diversity based on this shared primitive characteristic obscured the true evolutionary diversity and the pattern of evolutionary diversification within this group.

Second, segregation of new genera from *Lepidodendron sensu lato* left a residual group of species that still contained several disparate lineages. The breakup of this paraphyletic group into monophyletic genera led to an increasingly narrowly delimited and more meaningful concept of the genus *Lepidodendron*. The recent segregation of *Hizemodendron* (Bateman and DiMichele, 1991) further disaggregated the paraphyletic *Lepidodendron* complex.

THE NEW FAMILY DIAPHORODENDRACEAE
AND NEW GENUS SYNCHYSIDENDRON

Rationale for recognition of new taxa—The recognition of a new family and genus of arborescent lycopsid was prompted by a detailed phylogenetic analysis of this group (Bateman, DiMichele, and Willard, in press). The genus *Diaphorodendron sensu* DiMichele (1985) proved to be supported by more synapomorphies than the widely recognized families Lepidodendraceae and Sigillariaceae, justifying its elevation to family status. However, the genus as originally conceived was shown to encompass two

¹ Received for publication 8 July 1991; revision accepted 19 February 1992.

The authors thank Tom L. Phillips (University of Illinois) for access to collections and for providing peels of the type specimen of *Synchysidendron*; and Mary Parrish (Smithsonian Institution) for preparation of the final versions of the figures. This research was supported by a Smithsonian postdoctoral research fellowship to RMB.

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TABLE 1. *Synapomorphies delimiting the Diaphorodendraceae. Homoplastic synapomorphies are reversals (-) or parallel acquisitions (=); nonhomoplastic characters are considered more reliable (data and character numbers from Bateman, DiMichele, and Willard, in press; see also Fig. 16)*

Character	Apomorphic state
Vegetative axes	
14	Siphonostele
15-	Stelar medullation <i>lost</i>
35=	Thin-walled parenchyma surrounds trace in outer cortex
38	Phellem and phelloderm histologically differentiable
41	Periderm bifacial
Leaf bases	
56=	Upper field plicate
58=	Lateral line separates upper and lower fields
Cones	
79	Sporangium wall heterocellular
82=	Megasporophyll alations short and horizontal
86	Megasporangium strongly dorsiventrally flattened
88	Megasporangium dehiscence proximal
Spores	
94	Megaspore gulate
107=	Microspore with crassitude equatorial thickening
110	Microspore contact face granulo-foveolate
114	Microspore distally papillate

morphologically distinct lineages that needed to be distinguished repeatedly in discussions of vegetative characters and overall growth habit. Thus, the circumscription of the new genus reflects our philosophy of segregating, at this taxonomic level, groups with distinctive architectures and anatomies (Bateman and DiMichele, 1991; Bateman, in press). The decision to segregate the new genus *Synchysidendron* from *Diaphorodendron* within the Diaphorodendraceae was made more difficult by the apparently identical reproductive organs borne by all species of both genera. Nonetheless, we do not expect evolution to proceed in such a stereotyped fashion that reproductive morphology should, a priori, be weighted more heavily than profound divergence in vegetative features, including

growth habit and life history attributes. As is demonstrated below, *Synchysidendron* and *Diaphorodendron* are separated by a large suite of morphological differences. Each genus contains a few well-known species that have been shown to differ in details of their characteristic morphological attributes (DiMichele, 1985; Bateman, DiMichele, and Willard, in press).

Materials—The following descriptions are based on anatomically preserved specimens from coal balls. All come from coals of the United States and Europe, which are listed for each genus (in ascending stratigraphic order):

Synchysidendron: Rock Springs Coal of Tennessee, Mineral and Fleming Coals of Kansas, Springfield Coal of Indiana, Herrin Coal of Illinois, Baker (No. 13) Coal of western Kentucky. All are of Middle Pennsylvanian age. In European terminology, the Rock Springs Coal is of Westphalian C age, whereas all other coals are from the Westphalian D (Phillips, Peppers, and DiMichele, 1985).

Diaphorodendron: Union Seam of England, Buxhamont Seam of Belgium, Katharina Seam of Germany, Hamlin Coal of Kentucky, several unnamed coals of Iowa, Buffaloville Coal of Indiana, unnamed Indiana coal equivalent to the Murphysboro Coal of Illinois, Secor Coal of Oklahoma, Bevier Coal of Kansas, Colchester Coal of Illinois, Summum Coal of Illinois, Iron Post Coal of Oklahoma, Springfield Coal of Illinois and Indiana, Middle Kittaning Coal of Ohio, Upper Freeport Coal of Ohio, Herrin Coal of Illinois, Baker (No. 13) Coal of Kentucky, Danville Coal of Indiana. These coals are of Lower and Middle Pennsylvanian age equivalent to the Westphalian A through Westphalian D of Europe (DiMichele, 1981; Phillips, Peppers, and DiMichele, 1985).

Taxonomy—In this section we describe formally the new family and new genus, and emend the description of *Diaphorodendron*. More rigidly cladistic descriptions of taxa are presented in Tables 1–3.

Diaphorodendraceae, *fam. nov.*

Familial description: Arborescent lycopsids. Protostelic

TABLE 2. *Character states separating Synchysidendron and Diaphorodendron. States apomorphic in the broader context of the analysis of the arborescent lycopsids performed by Bateman, DiMichele, and Willard (in press; see also Fig. 15 of this paper) are asterisked, and placed in parentheses where homoplastic. Alternative states for characters 42–43 and 44–45 were treated as alternative apomorphies relative to other plesiomorphic states found in more primitive arborescent lycopsids but not in the Diaphorodendraceae; thus, they have not been polarized in this more restricted context (data and character numbers from Bateman, DiMichele, and Willard, in press, Fig. 6; see also Fig. 16 of this paper)*

Character	<i>Diaphorodendron</i>	<i>Synchysidendron</i>
Overall habit		
3 Dichotomy of trunk apex:	Infrequent or absent (*)	Frequent
6 Lateral branches and/or cone peduncles borne on:	Excurrent trunk (*)	Dichotomous crown
7 Number of cones borne on lateral branches:	More than one (*)	One
Vegetative axes		
17 Pith:	Not solidly parenchymatous	Solidly parenchymatous*
20 Deep parenchymatous invaginations or radial partings:	Absent	Present*
31 Rays:	Homogeneous	Heterogeneous*
42–43 Phelloderm:	Uniform	Alternating bands of thin- and thick-walled cells
44–45 Leaf cushion retention mechanism:	Interarea fissuring	Tangential interarea expansion
Cones		
74 Pith in trace of peduncle or lateral branch:	Present (*)	Absent

to siphonostelic. Primary xylem maturation centripetal (exarch). Cortex three-zoned; outer cortex composed of weakly to strongly radially alternating areas of thick- and thin-walled cells. Periderm bifacial, phellem and phelloderm histologically differentiable; phelloderm composed of tangential arcs of alternating thicker- and thinner-walled cells. Leaf bases with distinct leaf scar in upper half, keeled, parichnos confined to foliar scar, ligule pit present above scar, overall tangential height greater than width. Separate megasporangiate and microsporangiate cones, assignable to *Achlamydocarpon varius*: sporangium wall heterocellular, megasporangium strongly dorsiventrally flattened with proximal dehiscence. Megaspore assignable to *Cystosporites*: gulate. Microspore assignable to *Gransporites*: circular to rounded triangular amb, scabrate proximal surface, minutely granulate to granulo-foveolate distal surface, variable number of large, round grana distributed sparsely across distal surface and equatorial region.

Type species: *Diaphorodendron vasculare* (Binney) DiMichele (DiMichele, 1985).

Synchysidendron DiMichele and Bateman, gen. nov.

Generic description: Arborescent lycopsids. Stellar pith present in all but stem base and ultimate branches, composed of compact cylindrical parenchyma cells. Protoxylem exarch (centripetal maturation), distributed in continuous layer at margin of tracheary cylinder without noticeable clustering or projection. Longitudinal parenchyma areas, multiple cells wide and high, present in primary xylem cylinder, areas appear to dissect the outer primary xylem margin in cross-sectional view, and in large axes dissect primary xylem into discrete wedges.

Cortex three-zoned. Inner cortex of compact, barrel-shaped parenchyma. Middle cortex of thin-walled parenchyma. Outer cortex largely of homogeneous, elongate, thick-walled parenchyma cells; areas of thinner-walled cells around leaf traces impart weak radial alternation of thick- and thin-walled cell areas in outer cortex.

Leaf traces originate by direct angular departure from xylary margin. Traces are ensheathed adaxially and laterally within middle cortex by cells with inner cortical characteristics. Cells like those of the middle cortex persist abaxial to trace through outer cortex and into leaf base.

Leaf bases developed as leaf cushions with distinct leaf scar. Parichnos confined to foliar scar. Cushions somewhat protuberant, generally with greater vertical than horizontal dimension when measured tangentially but approaching equidimensionality in smaller branches. Lower keel generally with several distinct plications; weaker upper keel without plications. Below leaf scar, at upper end of keel, depression or groove is formed by folding of the cushion surface; depression is particularly distinct in tangential section or surface view. Ligule pit deep, bulbous, opens immediately above leaf scar and extends back at slight angle into leaf cushion. Ligule is ovoid in shape, lacking distinct differentiation between stalk and apex.

Secondary xylem present, attenuating into terminal branches. Large rays, multiple cells wide and high, present in larger axis segments. Large rays connect directly with multicellular parenchymatous partings in primary xylem. Periderm present, bipartite, with greatest development centripetally (phelloderm). Phelloderm composed of

TABLE 3. Apomorphies delimiting the species of *Diaphorodendron* and *Synchysidendron*. Homoplastic apomorphies are reversals (–) or parallel acquisitions (=); true (nonhomoplastic) autapomorphies are asterisked (data and character numbers from Bateman, DiMichele, and Willard, in press; see also Fig. 15 of this paper)

Character	Apomorphic state
<i>Diaphorodendron vasculare</i> - <i>D. scleroticum</i>	
30	Lateral branches with secondary xylem
<i>D. vasculare</i>	
(None)	
<i>D. phillipsii</i>	
36*	Outer cortex-periderm transition marked by cavities
<i>D. scleroticum</i>	
4*	Lateral branches persistent
68=	Foliar vascular strand dorsiventrally flattened
70=	Foliar vascular strand with lateral abaxial grooves
<i>Synchysidendron dicentricum</i>	
19*	Pith parenchyma with secondary wall thickenings
33–	Intracortical leaf-trace sheath secretory cells lost
<i>S. resinsum</i>	
18*	Pith parenchyma with secretory cells
34*	Intracortical leaf-trace sheaths adaxial

weakly alternating tangential bands of thicker- and thinner-walled cells. Thinner-walled cells tend to compress or degrade, forming tangential arcs to rings of small cavities in phelloderm. Phellem relatively homogeneous, somewhat resinous. Distinct areas of tangential cellular expansion develop between leaf bases, expressed superficially as flat, ribbonlike interareas.

Growth determinate. Extensive crown present only in terminal phases of development, formed by near-isotomous apical branching. Cones borne on minor branches of strong anisotomies with protostelic architecture. Cone branches produced on portions of crown lacking wood, and thus presumed near ends of crown branches. Overall reproductive habit is monocarpic, with high late-stage reproductive allocation.

Rooting organs of stigmarian rhizomorph-type. Rhizomorph periderm similar to that of stem. Lateral appendages (rootlets) lack connectives.

Cones assignable to *Achlamydocarpon varius*, megaspores to *Cystosporites varius*, and microspores to *Gransporites medius*.

Etymology: 'Synchysis' is a Greek word of neuter gender meaning comixture or confusion, reflecting the confusion of this genus with *Diaphorodendron*, and of both genera with *Lepidodendron*. 'Dendron' is a Greek word of neuter gender meaning tree.

Illustrations: The anatomy of *Synchysidendron* is illustrated in Figs. 1–13. Figure 14b illustrates generalized habit.

Synchysidendron resinsum, sp. nov.

Species diagnosis: Vegetative and reproductive characters as described for genus. Cells containing dark contents, which appear amorphous and fill cell lumens, present in pith, inner cortex, on adaxial side and flanks of leaf traces within middle cortex, and outer cortex particularly at inner margin. Dark cells may be present in any com-

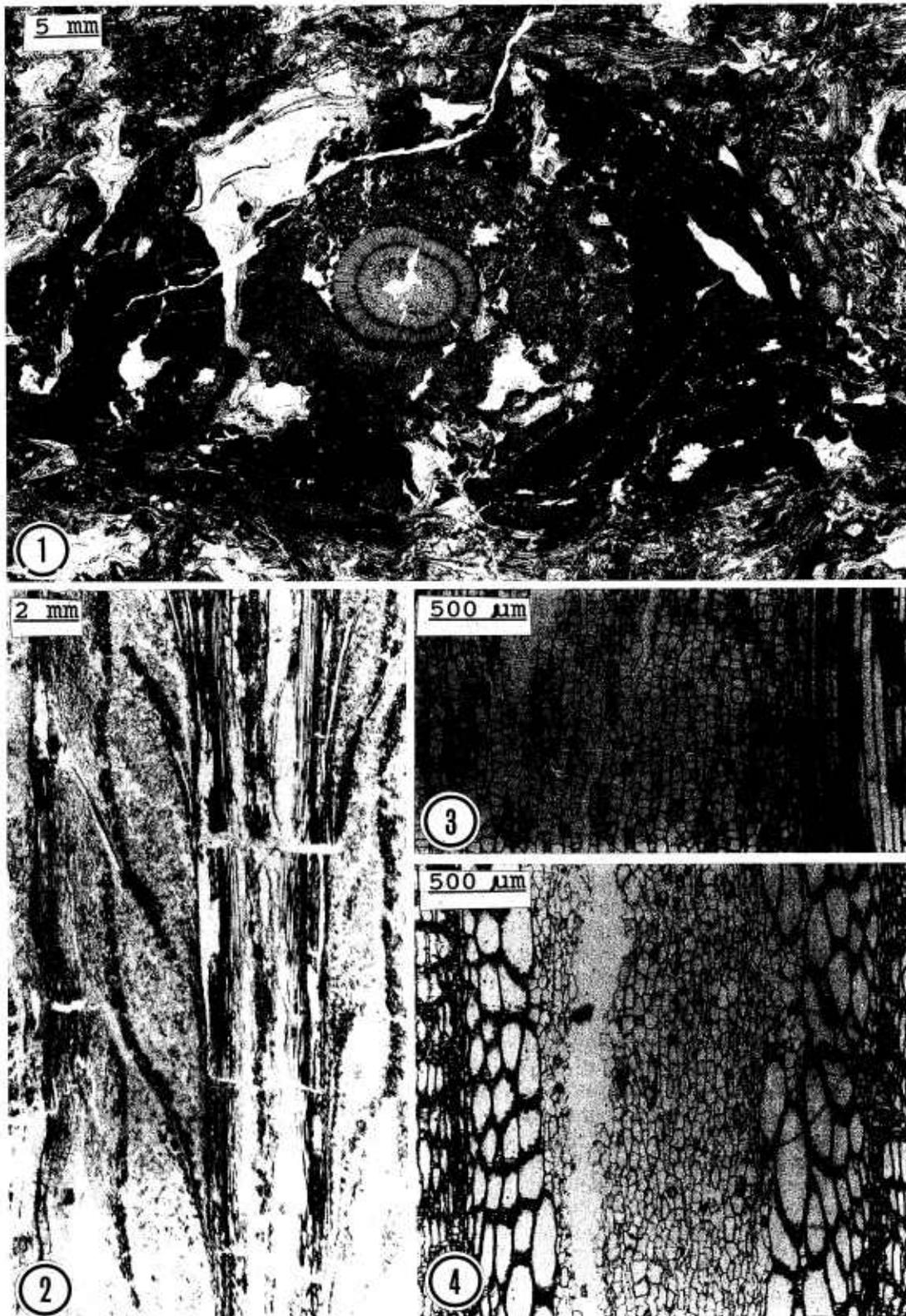


Figure Abbreviations (Figs. 1–13): All are mounted acetate peels photographed in transmitted light, except Fig. 1, which was photographed unmounted with reflected light. Sections: TS, transverse section; MLS, median longitudinal section; TLS, tangential longitudinal section; OS, oblique section.

Figs. 1–4. *Synchysidendron resinosum* unless otherwise stated. 1. TS of axis (holotype); characteristic features include division of stele and secondary xylem into wedge-shaped sections, resinous cells in pith, lunate sheaths of resinous cells surrounding leaf traces adaxially, weakly

bination of these tissue layers, in varying densities or absent in rare cases.

Holotype: Specimen Number 29138, Department of Plant Biology, Paleobotanical Collections, University of Illinois, Urbana, IL.

Four duplicate cellulose acetate peels of holotype (slice C-top) are housed in the Paleobotanical Collections, National Museum of Natural History, Smithsonian Institution, Washington, DC. USNM Number 455481 (455481-1 is illustrated in Fig. 1).

Holotype is from the Sahara Mine No. 6, 8 km southwest of Harrisburg, Saline County, IL (see Phillips and DiMichele, 1981, Fig. 7.2, for locality details). Specimen is from the Herrin (No. 6) Coal, Carbondale Formation; it is of Desmoinesian age (Westphalian D) of the late Middle Pennsylvanian (Phillips, Peppers, and DiMichele, 1985). This is "*Synchysidendron* sp. nov." of Bateman, DiMichele, and Willard (in press).

Etymology: The species name *resinosum* refers to the diagnostic dark cells in tissues of the pith and cortical regions.

Illustrations: The characteristics of *Synchysidendron resinosum* are illustrated in Fig. 1 (cross section of holotype), Figs. 2 and 6 (longitudinal sections of stems), Fig. 3 (longitudinal section of stele), Fig. 5 (cross section of stele and wood), Figs. 8–10 (tangential longitudinal sections of leaf cushions), and Figs. 11 and 13 (cross sections of representative stems).

Synchysidendron dicentricum (C. Felix) DiMichele and Bateman.

Basionym: *Lepidodendron dicentricum* C. Felix. 1952. *Annals of the Missouri Botanical Garden*, 38: 275, Figs. 8, 10–16, 18–22.

Lectotype: Specimen number WCB 781, designated in W. A. DiMichele. 1979b. *Palaeontographica*, Abt. B, 171: 133. Peels of type specimen also are housed in the Paleobotanical Collections, Department of Plant Biology, University of Illinois, Urbana, IL.

Synonymy: *Diaphorodendron dicentricum* (C. Felix) DiMichele. 1985. *Systematic Botany*, 10: 455. *Lepidodendron schizostelicum* Arnold. 1960. *Contributions from the Museum of Paleontology, University of Michigan*, 15: 255, Plates 1–4 (ten figures). Holotype, Number 36880, University of Michigan, Museum of Paleontology.

Emended species diagnosis: Vegetative and reproductive characters as described for genus. Cells of pith bear helical to scalariform thickenings on cell walls. Thickenings may occur on all cells, or cells with wall thickenings may be scattered throughout the pith without apparent order.

Illustrations: Selected anatomical characteristics of *Synchysidendron dicentricum* are illustrated for comparison with *S. resinosum*: Fig. 4 (longitudinal section of

stele), Fig. 7 (cross section of stele), and Fig. 12 (cross section of representative stem).

Although not appropriate for the diagnosis, it is noteworthy that *S. dicentricum* has not been observed to have secretory cells in any of its tissues. Only the derived histological traits borne by each of the *Synchysidendron* species allow their separation; they do not differ in fundamental aspects of tissue zonation or organization. The occasional lack of resinous cells in the parenchymatous tissues of *S. resinosum* appears to be an ecophenotypic response to brackish-water conditions (DiMichele, 1979b).

The segregation of *Synchysidendron* from *Diaphorodendron* necessitates emendation of the latter genus.

Diaphorodendron DiMichele, emend. DiMichele and Bateman.

Emended generic description: Arborescent lycopsids. Mixed protosteles with ratio of parenchyma to tracheids increasing toward core. Stellar parenchyma of smaller diameter and shorter length than tracheary cells. Protoxylem exarch (centripetal maturation), distributed continuously at the margin of the tracheary cylinder, without noticeable clustering or projection.

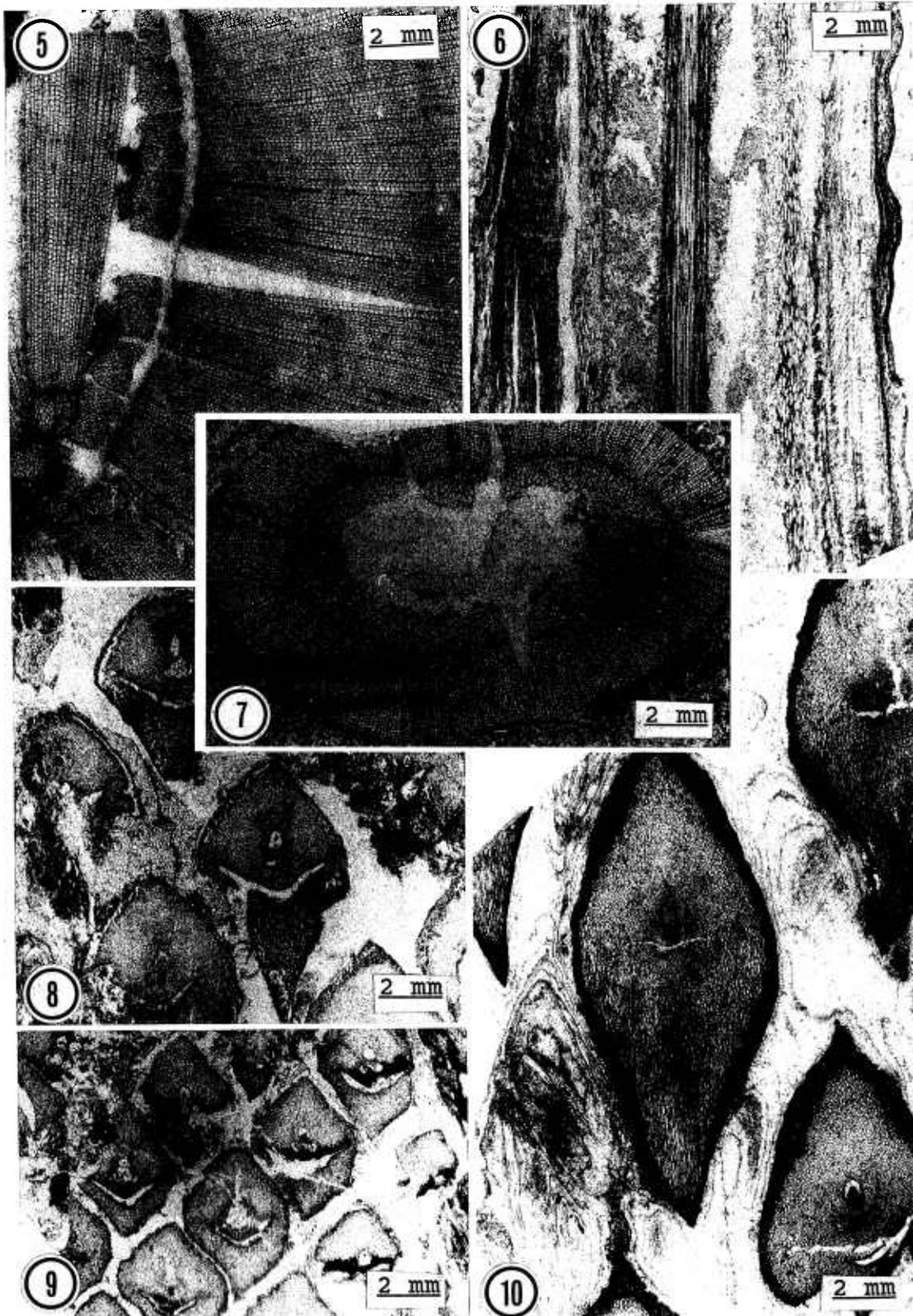
Cortex three-zoned. Inner cortex of compact, barrel-shaped parenchyma. Middle cortex of thin-walled parenchyma. Outer cortical parenchyma composed of thick-walled, vertically elongate cells surrounding areas of thinner-walled cells associated with leaf traces, which imparts strongly developed alternation of thick- and thin-walled cell areas to outer cortex.

Leaf traces originate by direct angular departure from xylary margin. Ensheathment of leaf traces in middle cortex by cells with inner cortical characteristics poorly developed. Cells with middle cortical characteristics persist abaxial to trace through outer cortex and into leaf base.

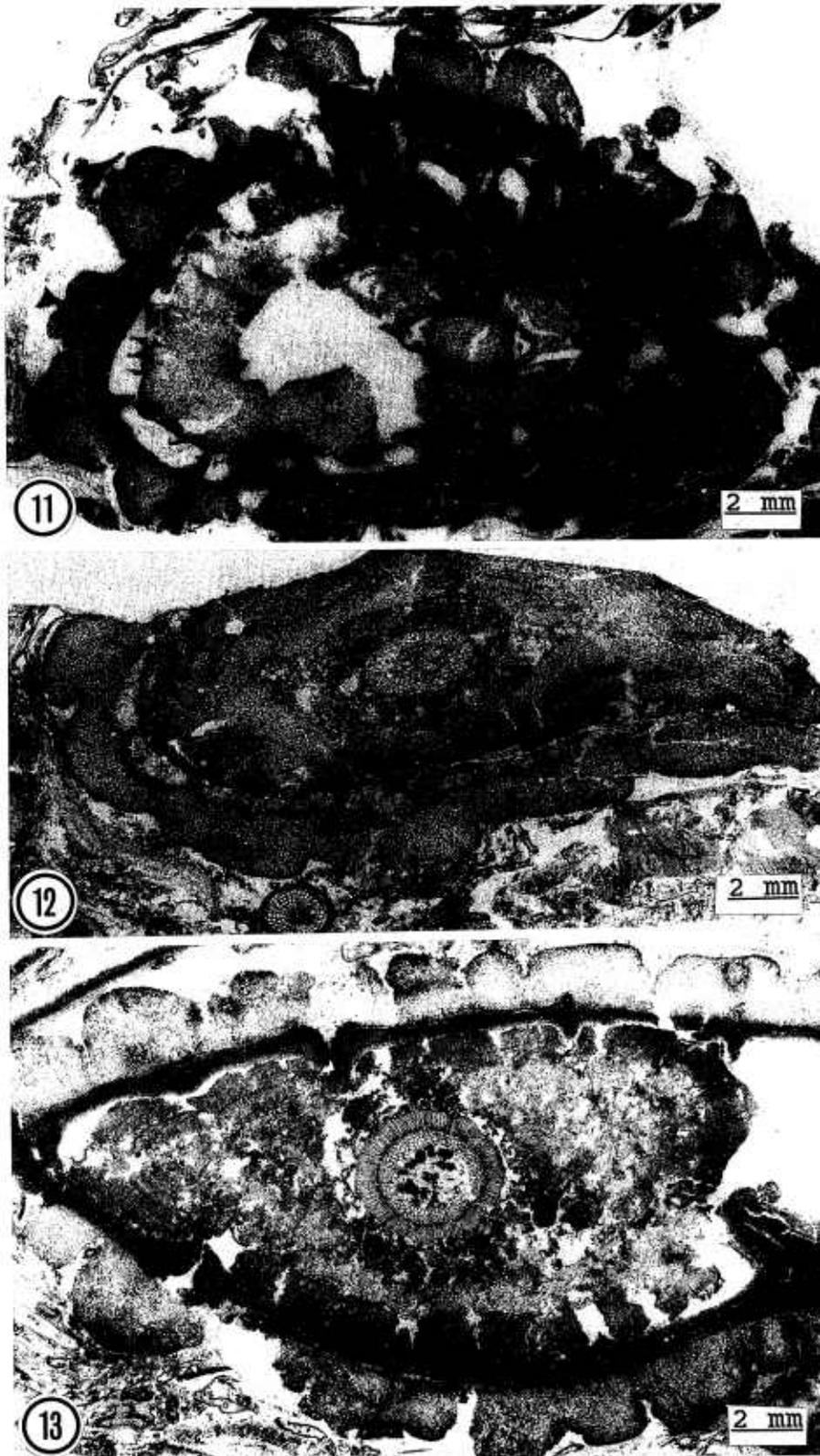
Leaf bases developed as leaf cushions with distinct leaf scar. Parichnos confined to foliar scar. Cushions only slightly protruding from stem surface, higher than wide in tangential view on axes of all diameters. Lower keel generally with several distinct plications; upper keel may have one to several plications. Ligule pit shallow, narrow, and tends to be vertically oriented, opening just above the leaf scar. Ligule small, ovoid, often filling ligule pit.

Secondary xylem present, attenuating into or absent from lateral, cone-bearing branches. Periderm present; bipartite, with greatest development centripetally (phellogen). Phellogen composed of distinctly alternating arcs or rings of thicker- and thinner-walled cells. Thinner-walled cells degrade or collapse, forming distinct zones of cavities alternating tangentially with areas of thick-walled cells, best developed in larger axis segments. Homogeneous phellem of densely packed cells, generally yellowish and resinous in character; phellem quite thick in

←
dictyoxylon outer cortex, and periderm with alternating tangential bands of thicker- and thinner-walled cells. University of Illinois Coal-ball 29138; duplicate peels: USNM 455481-1, ×2. 2. RLS of axis illustrating resinous cells adaxial to leaf traces in middle cortex, and scattered in pith. University of Illinois slide I 14647, ×5. 3. RLS of stele illustrating distinct size difference between pith parenchyma cells and innermost metaxylem tracheids (at right in photograph). University of Illinois slide I 14785, ×30. 4. *S. dicentricum*, OS of stele illustrating size disparity between pith parenchyma and innermost metaxylem tracheids, as in *S. resinosum*, and presence of parenchyma with secondary wall thickenings, the diagnostic character for this species. University of Illinois slide I 14645, ×30.



Figs. 5-10. *Synchysidendron resinosum* unless otherwise stated. 5. TS of stele. Primary xylem is divided into wedges by radial-longitudinal parenchymatous partings; these partings pass into the secondary xylem, permitting primary xylem and wood to fracture as a unit (note fragment on left displaced from the main xylem cylinder). University of Illinois coal ball 4800 B1, $\times 5$. 6. RLS of axis with little resinous parenchyma. University of Illinois slide I 14780, $\times 5$. 7. *S. dicentricum*, TS of stele; primary and secondary xylem divided into distinct wedges by radial-longitudinal parenchymatous partings (cf. Fig. 5). University of Illinois slide I 14673, $\times 5$. 8. TLS of medium-sized leaf bases; note groove below leaf trace. University of Illinois slide I 14675, $\times 5$. 9. TLS of small leaf bases; leaf trace, flanking foliar parichnos, and ligule pit above trace, are well marked. University of Illinois Coal-ball 7740C, slide 14 of series, $\times 5$. 10. TLS of large leaf bases. University of Illinois Coal-ball 16785, $\times 5$.



Figs. 11–13. *Synchysidendron resinosum* unless otherwise stated. **11.** TS of axis with only minor development of resinous cells at inner margin of outer cortex. University of Illinois Coal-ball 9681, $\times 5$. **12.** *S. dicentricum*, OS of axis entirely lacking resinous cells. University of Illinois slide I 14637, $\times 5$. **13.** TS of axis with typically developed resinous cells in pith and cortex. University of Illinois Coal-ball 15513, $\times 5$.

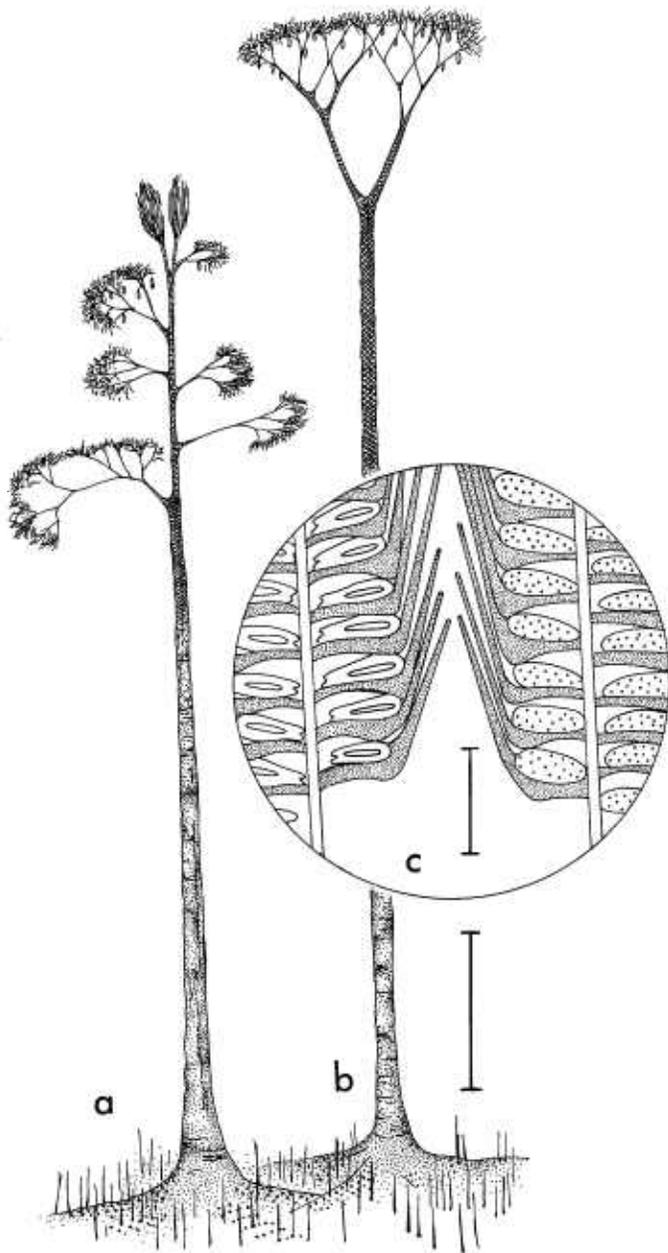


Fig. 14. Reconstructions of (a) *Diaphorodendron scleroticum* and (b) *Synchysidendron dicentricum*, together with (c) the megasporangiate (left) and microsporangiate (right) *Achlamydocarpon varius* cones shared by both whole-plant genera. Bars = 5 m (a, b), 1 cm (c). Sources: Bateman, DiMichele, and Willard, in press, Fig. 1 (a, b); Phillips and DiMichele, in press, Fig. 5 (c).

larger axes, but may be thin and difficult to recognize in smaller axes, especially those lacking secondary xylem. Increase in periderm thickness accommodated by fissuring of phellem in areas between leaf cushions; no tangential cellular expansion in intercushion areas.

Mature trees exhibit determinate growth, with trunk dichotomizing isotomously only in final phases of development. Gross habit consists of a central trunk bearing rows of deciduous lateral branches, produced by strongly anisotomous branching of the trunk apex. Lateral branch traces associated with gap in stem primary xylem. Lateral

branch systems dichotomize anisotomously. Cones borne on minor branches resulting from strong anisotomies; cone branches generally protostelic (although core of parenchyma cells may be present), rare. Overall habit suggests polycarpic reproduction, with low reproductive allocation at any one period of time.

Rooting organs of stigmarian rhizomorph-type. Rhizomorph periderm similar to that of stem. Lateral appendages (rootlets) lack connectives.

Cones assignable to *Achlamydocarpon varius*, megaspores assignable to *Cystosporites varius*, microspores assignable to *Granisporites medius*.

Type species: *Diaphorodendron vasculare* (Binney) DiMichele. 1985. *Systematic Botany*, 10: 454.

Lateral branch systems of *Diaphorodendron vasculare* have moderate amounts of wood and periderm and slightly anisotomous to isotomous branching. Secretorylike cells are common at the inner edge of the outer cortex. Cell walls of stelar parenchyma frequently are secondarily thickened. Phelloderm has weakly to moderately developed tangential alternation of thick-walled and thin-walled arcs of cells. Leaf cushions have little ornamentation and a strongly angular diamond shape.

Additional species:

Diaphorodendron scleroticum (Pannell) DiMichele. 1985. *Systematic Botany*, 10: 455.

Lateral branches of *Diaphorodendron scleroticum* are strongly anisotomous, rarely deciduous, and possibly were retained for extended periods on the main trunk. Stems generally have extensive development of sclerotic or secretory tissue in all cortical zones. Phelloderm shows a strongly developed alternation of thick-walled and thin-walled tangential arcs of dark-colored cells. Phellem is distinctly yellowish in color and appears secretory or resinous. Leaf cushions are relatively flat, with complex external morphology, including a well-defined, plicate lower keel, an upper keel plication that partially overhangs the ligule pit aperture, and a small ligule pit.

Diaphorodendron phillipsii DiMichele. 1985. *Systematic Botany*, 10: 455.

The shoot system of *Diaphorodendron phillipsii* is haplostelic throughout, although the central part of the stele is highly parenchymatous in larger axes. Lateral branch systems branch in a nearly isotomous manner, lack wood, and have little or no periderm. Small cavities are present at the outer edge of the outer cortex. Little or no secretory tissue is present in the cortex. Periderm in the stem is characterized by very thick phellem, equal to or greater than the thickness of the phelloderm. Leaf cushions are oval in shape with a poorly developed keel that is flat and highly plicate, particularly below the leaf scar.

TAXONOMIC DELIMITATION AND CHARACTER ANALYSIS

Families—A recent cladistic analysis encompassing 16 species of ten arborescent lycopsid genera showed that there are several well-supported groups of species that warrant recognition as families (Bateman, DiMichele, and Willard, in press). Some of these species groups conform

well to already recognized families, whereas others do not. Families of arborescent lycopsids traditionally have served mainly as categories in the management of form- and organ-taxa, with reproductive and vegetative parts of the same species placed in different families (e.g., Chaloner, 1967; Meyen, 1987); such families have not been based on reconstructed whole plants, nor have they been delimited using the criterion of monophyly.

Diaphorodendron and *Synchysidendron* are united in the new family Diaphorodendraceae by a large number of derived traits. Although extensive, the character state list (Table 1) does not convey the full degree of morphological distinctiveness these traits confer on the *Diaphorodendron-Synchysidendron* clade, the best supported higher-level group of species in the arborescent lycopsids.

Other distinct monophyletic groups among the arborescent lycopsids analyzed by Bateman, DiMichele, and Willard (in press) include *Anabathra* (formerly *Paralycopodites*), *Sigillaria*, and the derived *Hizemodendron-Lepidodendron* s.s.-*Lepidophloios* clade. These are comparable with the families Flemingitaceae, Sigillariostroboaceae, and Lepidocarpaceae of Thomas and Brackhanes (1984), although there are important differences that render this existing classification incompatible with our phylogenetic analysis (we are currently preparing a high level taxonomic revision of the rhizomorphic lycopsids).

Genera—*Synchysidendron* is distinctive in numerous attributes, which include features of all stem tissue regions (Table 2). Particularly characteristic are the parenchymatous partings in the stele (Figs. 5, 7, 13) that led Arnold (1960) to name the new species *Lepidodendron schizostelicum* (a synonym of *Synchysidendron dicentricum*). The connection of these partings to broad wood rays, which are much larger than the rays found in any other arborescent lycopsid, is highly diagnostic. These large areas of vascular parenchyma limit the energetic investment of the plant in lignified tissues, which is consistent with its monocarpic habit and probable rapid growth (DiMichele and Phillips, 1985; Phillips and DiMichele, in press).

Lunate leaf-trace sheaths in the middle cortex also are diagnostic of the genus. These are very conspicuous in *S. resinotum*, where they usually are filled with dark secretorylike substances (Figs. 1, 3, 6). These cells were unusually resistant to decay, and frequently persisted longer than the other parenchyma cells of the middle cortex. Such leaf-trace sheaths characterize even the smallest twigs, permitting them to be distinguished from comparably sized branches of *Diaphorodendron*.

Synchysidendron leaf cushions (Figs. 1, 8–13) are more like those of *Lepidodendron* s.s. (i.e., *L. hickii*) than those of *Diaphorodendron*. The relatively fleshy character, the tendency of the cushions on smaller branches to be of nearly equal height and width, the distinct adaxial slope of the ligule pit, and the large size of the ligule are quite distinct from *Diaphorodendron*, but similar in morphology and pattern of shape change to *Lepidodendron* (DiMichele, 1983; DiMichele, Pfefferkorn, and Gillespie, 1984). The lack of infrafoliar parichnos, the subscar transverse groove (which is not connected to the parichnos system as illustrated by Felix, 1952), and the smaller maximum size of cushions permit *Synchysidendron* leaf

cushions to be differentiated from those of *Lepidodendron*.

Growth habit clearly distinguishes *Synchysidendron* from *Diaphorodendron* (Fig. 14). Much of what has been inferred about their growth architectures (DiMichele, 1979b, 1981) has been corroborated by discoveries of entire fallen trees; although compressed, they can be correlated with petrifications using leaf-cushion morphology (Wnuk, 1985). Most of the life of a *Synchysidendron* tree was spent as an unbranched pole shrouded in leaves. A crown was produced only in the final phases of growth and associated reproduction, rendering the tree functionally monocarpic (DiMichele and Phillips, 1985). The remains of such trees are consistently associated with large numbers of the disseminule *Achlamydocarpon varius*, suggesting high reproductive output over a short period of time (DiMichele and Phillips, 1985; Phillips and DiMichele, in press).

In contrast, *Diaphorodendron* generated small cone-bearing branches lateral to the main trunk (DiMichele, 1981). As a consequence of this habit, *Diaphorodendron* trees were polycarpic (DiMichele and Phillips, 1985), but devoted comparatively little energetic effort to reproduction at any one time, suggested by their repeated association with relatively small numbers of *Achlamydocarpon varius* disseminules (Phillips and DiMichele, in press).

Despite the numerous differences of vegetative morphology and habit, all species of *Synchysidendron* and *Diaphorodendron*, as presently understood, appear to possess identical reproductive organs (Leisman and Phillips, 1979; Phillips, 1979; DiMichele, 1981; DiMichele and Phillips, 1985). Although evidence for this is associational, species of each genus have been found in deposits where they are either the only arboreous lycopsid present or the only one other than *Lepidophloios* (which has markedly different reproductive organs); in either circumstance, *Achlamydocarpon varius* is consistently the only lycopsid reproductive structure present. In cases such as *Diaphorodendron vasculare* in the Murphysboro-equivalent coal of Indiana, *Diaphorodendron phillipsii* in the Summum Coal of Illinois, or *Synchysidendron dicentricum* in the Fleming Coal of Kansas, thousands of coal balls have been examined from each site without encountering evidence contradicting this interpretation.

The large suite of vegetative differences allows unambiguous assignment of species to the two genera, which define two ecological groups with distinct life history strategies, each closely linked to the timing of reproduction.

Species—Two species of *Synchysidendron* are known sufficiently well to allow formal recognition. *Synchysidendron dicentricum* is restricted to the Mineral and Fleming Coals of Kansas and northern Oklahoma, and *S. resinotum* occurs widely throughout the later Middle Pennsylvanian (Westphalian C and D). Other species undoubtedly exist. The most likely possibility is represented by some of the leaf cushions described by Hovelacque (1892) as "*Lepidodendron selaginoides*" (= *Diaphorodendron vasculare*). Probably from the Westphalian B-age Katharina Horizon in the Ruhr area of Germany, these have the distinctive characteristics of *Synchysidendron* (although the stems to which they were attached were not illustrated). *Synchysidendron*-type leaf cushions also occur in attachment to distinctive fragmentary axes in early

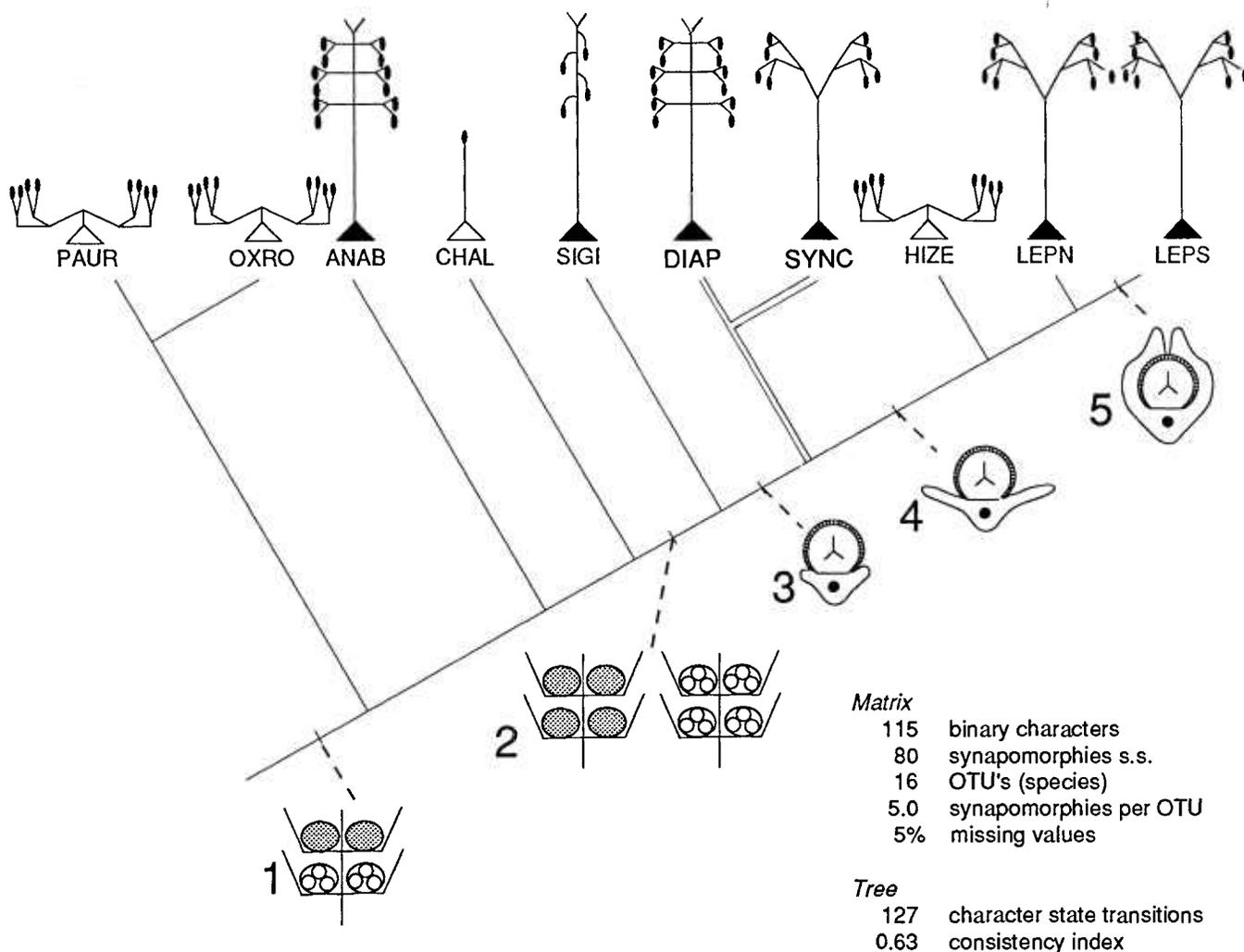


Fig. 15. Phylogeny of ten arborescent rhizomorphic lycopsid genera. Key reproductive innovations are shown on the major axis: 1) bisexual cone, 2) segregation of megasporophylls and microsporophylls into separate unisexual cones, 3) reduction to a single functional megaspore, 4) lateral expansion of megasporophyll alations, 5) enclosure of megasporophyll by alations. Growth habits (not to scale) are mapped onto the cladogram: pseudoherbs (*Paurodendron*, *Oxroadia*, *Hizemodendron*), terminal cone/fertile zones (*Chaloneria*), lateral cauline peduncles (*Sigillaria*), lateral branches (*Anabathra*, *Diaphorodendron*), terminal crown branches (*Synchysidendron*, *Lepidodendron*, *Lepidophloios*). Trees are indicated by solid triangles, small-bodied genera by open triangles. Cladogram topology reduced from Fig. 6 of Bateman, DiMichele, and Willard (in press). Double lines denote the Diaphorodendraceae; full details of the part of the cladogram encompassing the Diaphorodendraceae are given in Fig. 16 and Tables 1–3 (see also Bateman, in press).

Middle Pennsylvanian (Westphalian B) coals of the Appalachian Basin in the United States.

Synchysidendron dicentricum and *S. resinosum* are identical in most aspects of their vegetative and reproductive morphologies (Figs. 1–13). This led to their treatment as a single species in an earlier morphological study (DiMichele, 1979b). However, the two species are diagnosable (*sensu* Nixon and Wheeler, 1990); they have fixed autapomorphic traits that permit unambiguous recognition (Table 3; cf. Figs. 3, 4), provided that the relevant tissues have persisted. This morphological species concept is widely (if implicitly) used in paleontology, where we have access only to the structural attributes of extinct organisms.

Diaphorodendron species, like those of *Synchysidendron*, differ in relatively minor traits (Table 3); nonetheless, these have a marked effect on the overall appearance of isolated, fragmentary axes. *Diaphorodendron phillipsii*

is characterized by cavities at the interface of the outer cortex and periderm. The more robust *D. scleroticum* possessed persistent lateral branches and larger leaves, the latter reflected in abaxial grooves of the leaf and dorsiventral flattening of the leaf trace (these character states also typify leaves of *Lepidodendron* and *Lepidophloios*).

EVOLUTIONARY RELATIONSHIPS

Species—The close similarities of species within *Synchysidendron*, and within *Diaphorodendron*, are reflected in the small numbers (zero to three; Fig. 16) of character state transitions on the terminal branches of the cladogram; the number of characters supporting these branches would increase if the exclusively bistate characters used here were supplemented with meristic and metric attributes. Determining the relationship between the two species of *Synchysidendron* presents the same difficulty as

that between the two genera; three-taxon statements cannot be made. The small degree of divergence may reflect adaptation to subtly different environments of growth, possibly salinity tolerance in the case of *S. dicentricum* (DiMichele, 1979b).

The cladogram does present a three-taxon statement for the species of *Diaphorodendron*, but we believe that the most parsimonious solution (Fig. 16) is incorrect! *Diaphorodendron phillipsii* (Westphalian D) is shown as primitive relative to the appreciably older *D. vasculare* (Westphalian A), which is depicted as sister group to *D. scleroticum* (also Westphalian D) on the basis of a single synapomorphy, specifically the presence of secondary xylem in lateral branches. In this instance, we favor evidence of first occurrences in the well-documented Pennsylvanian coal-swamp stratigraphy over strict adherence to morphological parsimony. Hence, we would prefer to add one step to the tree length by depicting woody lateral branches as a synapomorphy of *Diaphorodendron* per se that was subsequently lost in *D. phillipsii*. This would allow interpretation of *D. vasculare*, which lacks autapomorphies in our bistate character matrix, as ancestral to *D. phillipsii* and *D. scleroticum*; together, these three species form a cline of increasing complexity in leaf-cushion morphology. *Diaphorodendron scleroticum* is the most distinctive species of the genus (Table 3, Fig. 16; see also DiMichele, 1981, 1985); its persistent woody branches, dense cortical sclerenchyma, and stem with thick wood and periderm suggest that it was more robust and possibly longer-lived than its progenitors.

Genera—Although the evolutionary divergence of *Diaphorodendron* and *Synchysidendron* involved a profound change in reproductive biology, the morphology of the reproductive organs apparently was unaffected. Rather, a radical change in the timing of, and short-term allocation to, reproduction resulted from a change in growth habit. Although the cladogram (Figs. 15, 16) by definition cannot resolve the ancestor-descendant relationship between these two sister genera, such evidence as we have suggests that *Diaphorodendron* is the more primitive of the pair. *Diaphorodendron* pre-dates *Synchysidendron* in the geological record (Fig. 16); first appearances of the two genera differ by approximately 2 million years, if Hovelacque's (1892) material is accepted as bona fide *Synchysidendron*, or approximately 6 million years if the unequivocal Westphalian D reconstructions are used as a baseline (time-scale of Hess and Lippolt, 1986). *Diaphorodendron* also has a growth habit that is arguably plesiomorphic among the arborescent lycopsid clade (Bateman, DiMichele, and Willard, in press).

The environmental factors mediating this evolutionary change are open to speculation. There are, however, consistent differences in the kinds of plant associations in which *Diaphorodendron* and *Synchysidendron* occur. *Diaphorodendron* species, as polycarpic trees, appear to have tolerated a wide range of swamp habitats subject to disturbances of minor effect, including floods but not fires (DiMichele and Phillips, 1985, 1988; Lesnikowska, 1989). They occur in coal zones characterized by taxonomically and structurally heterogeneous vegetation, where they typically are quantitatively abundant to dominant. This suggests a *K*-selected, site-occupying strategy. In contrast,

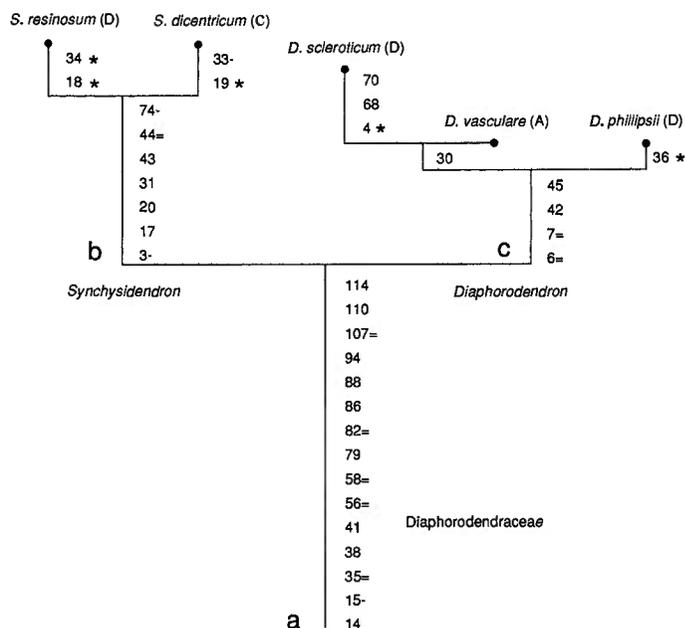


Fig. 16. Phylogeny of the Diaphorodendraceae, abstracted from the preferred most parsimonious cladogram of Bateman, DiMichele, and Willard (in press, Fig. 6; see also Fig. 15 of this paper). Branch lengths are proportional to the number of character state transitions occurring on branches following MINF optimization (e.g., Swofford, 1990). Categories include reversals (-), parallel acquisitions (=), and species-level autapomorphies (*); the latter are absent from *D. vasculare*. Character state transitions on branch "a" are listed in Table 1, those on branches "b" and "c" are listed in Table 2, and those occurring on terminal branches are listed in Table 3. Earliest recorded occurrences of species are also shown, by citing one of stages A–D of the Westphalian in parentheses (cf. Leeder, 1988).

Synchysidendron species are rarely dominant elements, occurring in low abundance (5%–10% of the biomass) in many kinds of assemblages. They reach greatest abundances in assemblages that are among the most taxonomically and structurally diverse of the coal-swamp forests (DiMichele and Phillips, 1988), hence possibly from areas of recent disturbance. *Synchysidendron* species appear more opportunistic and *r*-selected than those of *Diaphorodendron*. Wnuk (1985) determined that mature late Westphalian D-age *Synchysidendron* trees (named '*Lepidodendron*' *rimosum* in the compressed preservation state) were substantially larger than contemporaneous *Diaphorodendron* trees (named '*Lepidodendron*' *brettonense*), which appears to contradict the *r*-*K* (i.e., opportunist vs. site-occupier) distinction. However, height in arboreous lycopsids was probably related more strongly to propagule dispersal than to light capture. Consequently, greater stature would increase the likelihood of success of a monocarpic opportunist that exploited localized disturbance.

If *Diaphorodendron* were ancestral to *Synchysidendron*, the many morphological changes that reflect these radical changes in habit and reproductive biology could have been caused by simple modifications to the relative timing of branching and reproduction. Our model of arborescent lycopsid construction emphasizes four basic structural modules: root, stem (trunk), terminally dichotomous "crown," and cone-bearing lateral branches (Bateman and DiMichele, 1991; Bateman, DiMichele, and Willard, in

press, Fig. 14; Bateman, in press). The transition from *Diaphorodendron* to *Synchysidendron* requires only a delay in the onset of production of cone-bearing lateral branches until terminal crown branching has begun. Associated changes include reduction of the number of cones per lateral branch to one, increase in the number of orders of crown dichotomy, and increase in trunk height. These are secondary, however, and only modify in detail the fundamental change in reproductive timing, which confers on the derived growth form of *Synchysidendron* a short reproductive interval at the end of the life span, and thereby heavily concentrates reproductive output. Similar changes in habit apparently generated the Lepidodendraceae, sister family of the Diaphorodendraceae (Fig. 15). The growth changes in these two phylogenetically distinct clades represent a parallelism in the sense of Kellogg (1990): transformationally homologous, but historically independent, events.

On the admittedly equivocal evidence of the distinctive leaf cushions illustrated by Hovelacque (1892), *Synchysidendron* appears in the fossil record of coal swamps soon after a period of minor extinctions and accompanying change in coal-swamp community structure near the Westphalian A-B boundary (Phillips and Peppers, 1984; Phillips, Peppers, and DiMichele, 1985), though whole-plant reconstructions have not been achieved for assemblages of *Synchysidendron* older than the Westphalian C (Fig. 16). Westphalian A swamps of Euramerica generally were dominated by a diversity of arboreal lycopoid species, though the pteridosperm *Lyginopteris* was locally dominant. In the Westphalian B, the lycopoid diversity of any one swamp was markedly lower than that of earlier times, lyginopterids and numerous small ferns had become extinct, and cordaitalean gymnosperms had become prominent components of many plant communities. Several lines of evidence suggest that these vegetational changes reflect a change in climate and possibly greater intraswamp disturbance (Phillips and Peppers, 1984; Phillips and DiMichele, 1990; Winston, 1990).

These paleoecological, morphological, and stratigraphic patterns, and the inferences made from them, can be integrated into a credible scenario of constrained speculation. We suspect that the stem-species of *Synchysidendron* evolved from a species of *Diaphorodendron* in the coal swamps during a time of increasing intraswamp disturbance. The morphological transition may have been rapid, involving changes in habit and associated timing of reproduction of the kind outlined above. Trees with greater height and massive, short-term reproduction may have been capable of establishing and maintaining populations in swamps with a patchy pattern of disturbance, such as locally severe flooding or fire. *Synchysidendron* species were interstitial opportunists, present in low abundances across a swamp landscape; this strategy would have offered a low likelihood of establishment within more stable coal swamps. Thus, we envision the evolution of an *r*-selected opportunistic species from a more *K*-selected site-occupier during a narrow window of evolutionary opportunity. Once interbreeding populations were established, the probability of survival of the new life history would have been much higher than that of establishment as a new species under stable swamp conditions. In this case, the period of instability appears to be a time in which

the equilibrium (or near-equilibrium) dynamics of the swamp community were upset, permitting the invasion or establishment of new species. Following this geologically short interval, a new set of equilibrium dynamics was established; in effect, swamp community composition and the nature of interspecies interactions were reset (Knoll, 1985; DiMichele, Phillips, and Olmstead, 1987).

Although arboreal lycopoids are regarded as especially characteristic of coal swamps, most generic divergences may have occurred in clastic wetlands surrounding peat swamps or in more distant extrabasinal habitats, with subsequent migration into the coal swamps (DiMichele and Phillips, 1985; Scheckler, 1986a, b). This renders the probable intracoal-swamp divergence of *Synchysidendron* from *Diaphorodendron* unusual (possibly unique). Regardless of habitat, this was one of the last generic divergences within the arboreal lycopoid clade prior to major extinctions at the Westphalian-Stephanian boundary (Phillips et al., 1974). If our phylogeny (Fig. 15) is correct, the occurrence of probable *Lepidophloios* (the most derived genus of the Lepidodendraceae) in upper Tournaisian strata (Long, 1968) of the Lower Carboniferous (Long, 1968) means that the Lepidodendraceae and Diaphorodendraceae must have diverged by the mid-Lower Carboniferous (Bateman, DiMichele, and Willard, in press, Fig. 16). We would not be surprised to find evidence of *Diaphorodendron* in strata as old as the Upper Devonian.

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