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COMPARATIVE ECOLOGY AND LIFE-HISTORY BIOLOGY OF ARBORESCENT LYCOPSIDS IN LATE CARBONIFEROUS SWAMPS OF EURAMERICA¹ Tom L. Phillips² and William A. DiMichele³

ABSTRACT

The comparative ecologies of *Diaphorodendron*, *Lepidodendron*, *Lepidophloios*, *Paralycopodites* (= *Anabathra*), and *Sigillaria* in Late Carboniferous coal swamps serve as a context for assessing life cycles and exploring possible structure-function relations. The distinctive aspects of the "lycopoid tree habit" in lepidodendrids are emphasized as part of the arborescent reproductive architecture of relatively short-lived (10–15 years) plants. These include: determinate apical growth of the aerial shoot system and the anchoring stigmarian system, which have marked homologies; limited amount of secondary xylem, lack of secondary phloem, and periderm as the major support tissue; differentiated gas-diffusion system associated with appendages, including lacunae and parichnos; abscission of appendages and lateral branches; retention of leaf cushions; and close relationships between mode and timing of branching, to cone-bearing and heterosporous reproductive biologies. Vegetative structure-functions explored include the possibility that lacunae and parichnos were involved in internal mediation of gas diffusion as opposed to aeration functions. The possibility exists that parts of the stigmarian system were involved in CO₂ acquisition from substrates; some may have been photosynthetic. These functions are considered in the context of the light sharing and diffuse photosynthesis evident in the pole architecture. The combination of such possibilities is related, in part, to the xeromorphic characteristics of the arborescent habit, raising the question about a modified kind of C₃ photosynthesis such as CAM (Crassulacean Acid Metabolism). Stigmarian lycopsids dominated tropical Westphalian coal swamps as an array of genera with relative distributional abundances reflecting habitat partitioning according to edaphic conditions, including temporal disturbance patterns. Species appear to exhibit different levels of tolerance to disturbances and range from colonizers to site occupiers. *Paralycopodites*, with prolific, free sporing, bisporangiate cones, was most abundant in frequently disturbed, partially exposed, peat- to mineral-rich habitats (ecotonal). Monosporangiate *Lepidophloios* and *Lepidodendron* were associated typically with deeper, standing-water habitats, and, in association with terminal branching, monocarpically produced specialized monosporic megasporangium-sporophyll units, termed aquacarpus. *Diaphorodendron* species were monosporangiate with aquacarpus and range from a typically persistent, low level reproductive output on deciduous lateral branches, to monocarpy (*D. dicentricum*) with terminal branching. *Sigillaria* was less closely associated with peat swamps, as a sporadic occupant associated with major disturbances, such as flood/dry down cycles. Whorls of monosporangiate cones were produced intermittently, perhaps in seasonally wet-dry conditions, with megaspore-sporangial dispersal units derived from cone fragmentation. In North America *Sigillaria* was the principal lepidodendrid survivor of the swamp extinctions near the Middle-Upper Pennsylvania boundary. The ecological roles of stigmarian lycopsids in Westphalian coal swamps are distinctive as an array of heterosporous reproductive architectures that were collectively dominant. Plants were characteristically much taller than other trees, yet did not shade out lower vegetation. They also were a major stabilizing influence on substrates with their extensive, baffling and anchoring systems in the high disturbance and abiotically stressed environments of peat swamps. The environmental circumstances of the first major coal age appear to have selected against long-lived or slow-growing trees in most coal swamps. Lepidodendrids constituted the most important of the arborescent genera both because of their unusual array of reproductive biology in such large structural and yet short-lived growth habits, as well as many physiological attributes that are only partially known or conjectured.

Trees referred to as lepidodendrids or stigmarian lycopsids encompass lycopoid zeniths in size, structural complexity, and heterosporous diversification as well as ecological dominance in Late Carboniferous tropical swamps. Lepidodendrid trees were so different anatomically, functionally, and ecolog-

ically from arborescent forms of other non-lycopoid lineages as to merit distinction of a "lycopoid tree habit." The principal lepidodendrid genera of the Late Carboniferous coal swamps, known from anatomical preservation, include *Diaphorodendron*, *Lepidodendron*, *Lepidophloios*, *Paralycopodites*

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(= *Anabathra*), and *Sigillaria*. Anatomical and developmental studies drawn from these genera provide a composite picture of the lycopsid tree habit that emphasizes some of the differences from conventional trees.

Lepidodendrids were apically determinate in both the aerial shoot system (Andrews & Murdy, 1958; Eggert, 1961; Lemoigne, 1966; Chaloner & Meyer-Berthaud, 1983) and apparently also in the anchoring stigmarian system (Frankenberg & Eggert, 1969); the anatomical transition from stem to rhizomorph occurred in the unbranched base of the trunk. Marked homologies between stem and rhizomorph systems, both in axial organization and in appendage anatomy and arrangement, indicate that the stigmarian rhizomorph was, in part, functionally but not morphologically a "root system." Its anchorage and support of the pole-type trunk was provided by dichotomous branchings and the extensive appendages they bore. There were no root caps or root hairs. The apex of the growing stigmarian axes tapered abruptly to a rimlike apical groove associated with appendage origins; this was terminated with a protective plug of apparently parenchymatous tissue (Rothwell, 1984). The cylindrical appendages were largely air filled, apparently buoyant, with a large external surface to biomass ratio. They radiated for lengths of 0.5 m or more; some are known to have been once dichotomous in the sigillarian stigmarias (Lemoigne, 1963).

The aerial shoot system exhibited structural support mainly by nonwoody tissues, especially periderm, formed beneath the leaf cushions or bases in larger stem parts. The relatively modest amount of secondary xylem in the trunk was high in conductance (Cichan, 1986). Both aerial and stigmarian systems had wood and periderm, but neither had secondary phloem (Eggert, 1972; Eggert & Kanemoto, 1977). In the *Lepidodendron* and *Lepidophloios*-type trees with dichotomous terminal branching, the primary body showed progressive diminution of all tissue zones in the branching system. There were progressively fewer and smaller leaf cushions and lamina, and finally maturation of apices. Secondary tissues diminished upward from the trunk base with periderm extending further up than wood. For trees with divided lateral branches (*Paralycopodites*, most *Diaphorodendron* species) the same determinate changes occurred in the lateral branches, and presumably in the main trunks. Genera that ultimately terminated their pole architecture with at most a fork or two (*Para-*

lycopodites, *Sigillaria*) also are thought to have had primary body diminution with apical dichotomy.

Pole branching was coordinated apparently with reproduction (DiMichele & Phillips, 1985). Lateral branches were either ramified, bearing multiple cones, or pedunculate with a terminal cone. Terminal "crown type" branching was simply an expanded scaffolding for cone production and dispersal. Deciduous lateral or terminal branching represented minimal interference with light penetration and wind dispersal. In short, the lepidodendrids represent arborescent reproductive architecture with determinate growth and fairly short life spans (Stewart, 1983: 104; DiMichele & Phillips, 1985) despite their large statures.

Lepidodendrids were indeed tree sized with a pole design; however, their morphology suggests a short life span, perhaps up to 10-15 years as a conservatively high estimate. Their developmental design indicates a different way to be a big pole tree, rapidly and temporarily. Some were also small trees, especially in the coal swamps. Most reconstructions show lepidodendrids in late to terminal reproductive or "death" stages. As unconventional as these trees were structurally, and, by inferences, functionally, we have good reason to query what else is known or likely about their biology, their earlier history, and the origin of genera. In turn, what do these aspects suggest about the wetland environments where they dominated?

Lepidodendrids were confined to the tropical wetlands of the late Paleozoic, apparently associated with soft substrates (peat as well as mostly inorganic). Such habitats are accordingly referred to as coal (peat-forming) or clastic (inorganic substrates) swamps. There were additional lacustrine and fluvial environments associated with the better-drained parts of the wet lowlands. Because the habitats of lepidodendrids were also depositional environments, there is an unparalleled fossil record of compressions, casts/molds (see Gastaldo, 1986), permineralized anatomy, and spore floras. Recognition and interpretation of this record is particularly enhanced by the unusually distinctive structures of tree-sized lepidodendrids.

Stigmarian lycopsids represented in our study were the principal genera of the Westphalian (mid-Late Carboniferous) coal swamps. The five genera coexisted in Westphalian (mid-Pennsylvanian) coal swamps for about nine million years (Hess & Lippolt, 1986) in an area from Europe to mid-continental United States. Additional occurrences in

clastic deposits provide a means of tracking their broader geologic distribution, despite taxonomic limitations of cross-preservational comparison (see Gastaldo, 1987).

One of the most important perspectives to emerge from lepidodendrid ecology is that the biological differences among genera seem to reflect habitat partitioning according to edaphic conditions, including temporal disturbance patterns. Lepidodendrid life cycles apparently constrained the plants to relatively short-term occupation of variously disturbed or certain temporarily stable wetland habitats. The lycopsid tree habit clearly reflects elevation of reproductive organs, permitting dispersal from a high point. This was very important in the face of repeated expansions and contractions of habitable environments, including the necessity of recolonization from scattered refugia. Lepidodendrids had no known means of vegetative propagation. Consequently, the life cycles provide perspectives on ecological resource partitioning, gradient distributions, repetitive occupation of sites, or patterns of replacement by another lepidodendrid ("succession"). The unusual life cycles contributed to the collective dominance of swamps by lycopsids. The heterogeneity of swamp environments, as well as geologic changes in environments, also can be inferred from the mix or combination, and relative abundances of lepidodendrid genera (DiMichele et al., 1985).

The principal lepidodendrid genera of the Westphalian coal swamps had very long geologic ranges, some extending for more than 100 million years. All have anatomically known occurrences in the very early Carboniferous. The lepidodendrid radiation occurred in the earliest Carboniferous, and perhaps latest Devonian (Scheckler, 1986), and it is likely that the development of the stigmarioid system constituted the major adaptive breakthrough. *Paralycopodites* is known from the Tournaisian (Meyer-Berthaud, 1981) and *Lepidodendron*, *Lepidophloios*, *Diaphorodendron*, and *Sigillaria* were present during the Viséan (Long, 1968; Scott et al., 1984). There are several reported, older occurrences of *Lepidodendron*-like plants. Lepidodendrids subsequently attained pantropical distribution as wetlands underwent a net expansion and, as a group, reached their zeniths in Euramerican coal swamps by the onset of the Westphalian. With the exception of *Sigillaria*, these genera became extinct in coal and clastic swamps in North America, rather abruptly, near the Middle-Upper Pennsylvanian boundary (Winslow, 1959; Phillips et al., 1974; Kosanke & Cecil, 1989). A drastic decline occurred in Europe also

near the Westphalian-Stephanian boundary with several genera surviving in the Stephanian of the Donets Basin of Ukraine, Massif Central of France, and Spain (see Phillips et al., 1985; Wagner, 1989). The Westphalian-Stephanian transition and ensuing Permian distribution of lepidodendrids in the Cathaysian paleofloristic province is quite different from that of Euramerica (Li & Yao, 1982; Wang, 1985). Some of the same genera continued as major components of Cathaysian coal swamps to the end of the Paleozoic (Tian & Zhang, 1980; Tian & Guo, 1987).

PERSPECTIVES AND BASES FOR INTERPRETATION

The most important aspect of our inquiry into structure-function relationships is relationship between the peculiar morphology of the lepidodendrids and their physiology and how this best relates to their ecology and reproductive biology. It is known that lycopsids probably represent an evolutionary lineage distinct from other vascular plants. The many distinctive aspects of morphology often are interpreted, however, based on the structure-function relationships of other vascular plants, especially seed plants. In retrospect, most of us have followed such analogies. Lepidodendrids are so quaintly familiar to paleobotanists that such exceptional morphological features as the stigmarioids are reduced to "root system" status without asking what these shootlike systems might be doing that is of importance to lepidodendrids, or to our understanding of other rhizomorphic lycopsids. Similarly, we have relegated structures with seed-like morphology (*Lepidocarpon*, *Achlamydocarpon*) to the status of almost seeds, extrapolated even to the pollination syndrome (Thomas, 1981). In short, our comparative morphological treatments of the lepidodendrids have been too strongly influenced by seed-plant morphology with analogy to its implications of function.

Also misleading have been evolutionary scenarios wherein lepidodendrids are the starting point for a reductional series from arboreal to herbaceous rhizomorphic (centrally "rooted") forms. Quite to the contrary, we believe that the arborescent lycopsids represent an extreme specialization which evolved from diminutive predecessors whose near relatives survive to the present day. In short, the "reduction series" of classic literature treats the true ancestors as the descendants. This places exceptional importance on the study of the surviving members of the isoetalean line. These may provide insights into the lepidodendrids and their relatives, which dominated the swamps and marshlands of

the tropical Carboniferous, and a diversity of environments from wetlands to more xeric habitats of other paleofloristic areas and geologic times (Meyen, 1982, 1987).

The success of rhizomorphic lycopoids in such harsh environments takes on special importance in light of their distinctive morphology and probably unique physiology. Why were rhizomorphic lycopoids so successful in conspicuous contrast to other plant types that also had basic laminate and arborescent characteristics by the late Devonian-earliest Carboniferous? As a consequence of their distinctiveness, lycopoids provide an "outgroup" by which we can assess the constraints form and physiology place on ecology. Despite our own reservations about multiple speculations of form-function relationships, the intent is to utilize lepidodendrids as a model system that has high resolution because of anatomical preservation, size of structures, dominance of vegetation, and long geologic ranges and broad paleogeographic distribution. The rhizomorphic lycopoids are acknowledged to have been generally xeromorphic despite the seemingly contrary ecological associations with wetlands and xeric habitats—both harsh extremes. These extremes in the environments of the late Paleozoic, and even the Triassic, mark capabilities of lycopoids that were not mediated just by differences in reproductive biology, but by particular physiological capabilities.

AVAILABLE DATA

Most data and results drawn upon in this study are derived from anatomically preserved plant assemblages in coal-ball deposits. Coal balls are concretions, principally of carbonate permineralization, entombing peat stages of coal swamps. The greatest abundances of coal balls occur in the Westphalian (middle Upper Carboniferous) of Europe and the United States (Phillips, 1980). More than 60 coals are represented and localities number in the hundreds. These extend from the lowermost Westphalian A to near the top of the Westphalian D, stratigraphically including part of the Lower Pennsylvanian and the entire Middle Pennsylvanian in the United States. At least 10 coals are represented by occurrences in the Upper Pennsylvanian, from the Illinois Basin to the Appalachians. There are significant permineralized deposits also in the Stephanian of France (Galtier & Phillips, 1985).

There is more anatomically based information on the swamp plants of the Late Carboniferous tropics than for any other comparable interval in

the geologic record because of the occurrences of coal balls. This continues to improve resolution of the systematic, ecological, and evolutionary understanding of lepidodendrids and their relatives based, in part, on anatomy, development, and reproductive biology. While the relevant sources are too extensive to cite comprehensively, key publications are given here for major reviews or compilations, revised systematics, developmental studies, and the vegetational data and analyses, with other citations accompanying the pertinent text.

The lepidodendrids are reviewed by Chaloner & Boureau (1967) and Thomas (1978). Reproductive biology of some lepidodendrids has been summarized by Phillips (1979) and DiMichele & Phillips (1985). Extensive reviews of general ecological studies are found in Scott (1977) and Collinson & Scott (1987).

SYSTEMATICS AND DEVELOPMENT

Revisions in the systematics of coal-swamp taxa have resulted in the delineation of *Paralycopodites* (= *Anabathra*) as an arborescent lycopoid (DiMichele, 1980; Pearson, 1986) corresponding to *Lepidodendron brevifolium* in the older literature (see Williamson, 1893). *Diaphorodendron*, the "coal-swamp *Lepidodendron*," has been segregated (DiMichele, 1985) from true *Lepidodendron* (DiMichele, 1983) with additional revision and description of a new species (DiMichele, 1979b, 1981). The megasporangiate and microsporangiate cones of *Diaphorodendron*, known as *Achlamydocarpon varius*, were described in detail by Leisman & Phillips (1979). *Lepidophloios* has been revised (DiMichele, 1979a), including major systematic changes for the fructifications (Balbach, 1965, 1967). The principal *Sigillaria* studies include those by Schopf (1941) on *Mazocarpon* cones, by Delevoryas (1957) on stems, and by Eggert (1972) on stigmarias from the same American deposits. The principal work on European sigillarias is that of Lemoigne (1960). Additional species of *Mazocarpon* have been described from the Appalachians by Pigg (1983) and by Feng & Rothwell (1989). A detailed updated account of *Stigmaria ficoides* is given by Frankenberg & Eggert (1969). The phylogeny of the lepidodendrids is reviewed by Bateman et al. (1992).

While the above and other studies include many developmental aspects of the lepidodendrids, the seminal papers on aspects of arborescent growth include those by Walton (1935), Andrews & Murdy (1958), and Eggert (1961), with excellent summaries by Delevoryas (1964) and Stewart (1983).

Stigmarian biology has received a special emphasis as the result of the studies of Frankenberg & Eggert (1969), Eggert (1972), Paolillo (1982), Jennings et al. (1983), Rothwell (1984), and Rothwell & Erwin (1985).

VEGETATIONAL ANALYSES

Vegetational analyses of Late Carboniferous peat swamps are based on quantified identification of tissues, taxa, and preservational states (fusain). Sampling methods are described by Phillips et al. (1977); modifications of this sampling method have been described by Raymond (1988), Pryor (1988), and Feng (1989). These studies provide an outline of vegetational changes in the Westphalian and Stephanian that are paralleled by more extensive sampling in spore floras of the coals (see Peppers, 1984; Phillips & Peppers, 1984).

Summaries of vegetational data in relation to palynology are given in Phillips & Peppers (1984) and Phillips et al. (1985) with specific site or coal studies appearing in Phillips & DiMichele (1981), DiMichele & Phillips (1985, 1988), Eggert & Phillips (1982), Eggert et al. (1983), Willard (1985, in press), and Winston (1988). The techniques of analyses are found in Phillips & DiMichele (1981), DiMichele et al. (1986), and Raymond (1988).

THE LYCOPSID TREE HABIT

Lycopsids are so different evolutionarily from other vascular plants that even the concept of the "lycopsid tree habit" tends to be misleading because the primary frame of reference for "trees" tends to be non-lycopsids. The lycopsid tree habit has become epitomized by lepidodendrids or "stigmarian trees," which include the largest known lycopsids. However, it is well to emphasize that basic pole architecture was shared by a wide size range of lycopsids from robust "herbs," such as *Chaloneria*, to terminally, determinately branched *Lepidodendron* "trees." The general distinctions of relative pole sizes and even branching do not consistently or meaningfully separate "trees" from robust "herbs" or stigmarian lycopsids from other arborescent forms.

PRIMARY THICKENING

The large primary body and the early addition of secondary xylem necessitate a large primary meristem, a feature also reflected in the large appendages of both axial systems (Andrews & Murdy, 1958; Eggert, 1961; Rothwell, 1984). Such a

large apex may have been supplemented by some kind of primary thickening meristem, particularly important in the establishment growth phase. The common diamond design of most leaf bases may have permitted structural accommodations of growth vectors generated by combinations of vertical and transverse expansion during primary thickening. While distinctions are recognized here-in between primary and secondary thickening meristems, it seems quite possible that the relationships between them were not so clearcut. This may be a matter of shift to more localized meristematic activity and eventually a lack of thickening meristem activity.

XYLARY SYSTEM

The protostele in the shoot-stigmarian transition region is minute, composed of only a few tracheids. Primary xylary expansion in both directions led to progressively larger diametered "siphonosteles" (or medullate protosteles) corresponding to an increase in the entire primary body size. The protostelic transition region is quite long, encompassing both the trunk and the basal stigmarian axis, including the region where appendage traces first occur.

At some indeterminate distance from the transition zone within the dichotomously forked part of the stigmaria axis, the stelar structure significantly changed. The stigmarian primary xylem apparently expanded into essentially a spiral array of appendage traces, indicated by perimedullary protoxylem groups, closely associated with a mostly hollow parenchymatous pith. There is continuity of the parenchyma with each xylary trace across the secondary xylem. The radial xylary maturation has been described as centrifugal because of associated tracheids thought to be endarch metaxylem. However, it is not possible to distinguish objectively between secondary xylem tracheids and those of the primary appendage trace. Considering the centripetal maturation of stem xylem, it is likely that maturation of stigmarian protoxylem was also centripetal; if so, the perimedullary pith sleeve represents a nontracheidal frame in which the procambial strands, differentiated as appendage traces, were the only stelar xylem. Given the sparse vascular construction of this modified "siphonostele" of the primary xylem or appendage-trace network, conduction requires a continuity of xylem afforded only by the concomitant development of secondary xylem. It is presumed that secondary xylem was rapidly added in the stem at the same time.

The diameter expansion (forking stages) of the

stigmarian primary body may have been more rapid and perhaps less costly to achieve than that of the aerial pole. Each of the four main stigmarian axes were produced apparently almost simultaneously by a pair of successive dichotomies. The pith cavity of most *Stigmaria ficoides* axes has long been considered a taphonomic artifact, but the best preservation available (Williamson, 1887; Frankenberg & Eggert, 1969) argues that there was only a perimedullary pith rim surrounding a hollow central cavity (except at each end). This pith rim had clear continuity with the parenchyma accompanying each xylary trace across the wood. Two aspects of aeration seem important in this regard. First, there was an air cavity in the center of the *Stigmaria ficoides* axes, and secondly, parenchymatous connections extend from perimedullary pith rim not only across the wood but to the base of each appendage where a transverse septum (diffuser) separates the appendage lacuna from the axis. The parenchyma associated with the xylary trace in the wood has been termed a primary medullary ray by Williamson (1871), and a lateral appendage gap and largely secondary ray by Frankenberg & Eggert (1969). The key point here is that these lenticular shaped lacunae, as seen in tangential wood sections, are completely lined with parenchyma, at least 4-5 cells thick, and apparently frame slightly larger-sized cells that are more subject to degradation. The lacuna is slightly wider toward the outer periphery of the wood. In many cases it has been assumed that lack of preservation accounts for the lacunae and that the "ray" or "lateral appendage gaps" were fully filled by parenchyma. This seems likely; however, like the large cells of the middle cortical tissues of the appendages, observed basally in some cases, these may degrade early. The lacunae associated with the appendage xylary traces and surrounded by parenchyma are likely key parts of the aeration system.

The addition of the secondary xylem to the primary body likely occurred very near the apex in both pole and stigmarian axes. This seems reasonable, given the necessity to conduct water to the developing aerial shoot, which otherwise would have a protostelic bottleneck in the transition region. If secondary xylem were added rapidly at a growth level where primary tissues were still radially expanding, radial expansion of both systems in concert may have facilitated incorporation of the traces in the secondary xylem without disrupting them. The continuity of appendage trace systems was maintained during the addition of periderm tissues as well. In stigmaria, the secondary xylem may have provided the functional link be-

tween otherwise isolated traces, as well as providing a structural frame for the incorporated aeration passages. In young forked *Lepidophloios* sporophytes just emergent from the megasporangium, secondary xylem has been observed in both axial systems in what should constitute part of the transition zone (Phillips, 1979).

PHLOEM AND LONG-DISTANCE TRANSLOCATION

Given the developing suite of conducting and support tissues, it is natural to wonder about the long-distance photosynthate translocation system of a tree-sized plant that had no recognizable equivalent of secondary phloem (Arnold, 1960; Lemoigne, 1966; Eggert & Kanemoto, 1977). In lepidodendrid stems (*Diaphorodendron*) the primary phloem occurs as a discontinuous ring of strands separated by regions of parenchyma that accompany departing leaf traces (Eggert & Kanemoto, 1977). A discontinuous ring of primary phloem also occurs in the *Stigmaria ficoides* system where the interruptions in the ring mark locations where lateral appendage traces pass outward (Eggert, 1972).

The primary phloem "bottleneck" in the transition region, in particular, poses the problem of how food from the aerial pole reached the stigmarian system, especially as lepidodendrids became larger. Primary phloem bands were displaced outward, presumably by basal secondary xylem development, and never augmented. Another way to look at the anatomy is that the bands of primary phloem constitute all that were formed. This supposed constraint in long-distance translocation draws general attention to a broader problem: how could lepidodendrids attain such large sizes, even as short-lived plants, if they had limited capabilities to translocate photosynthate between aerial and subterranean systems, as well as within the shoot?

It is suggested that lepidodendrids relied on somewhat different functional uses of pole and stigmarian systems. These may be described generally as diffuse photosynthesis with limited translocation and with tissue growth and maintenance derived from local sites of photosynthesis. This may have occurred independently in both axial systems and was possibly critical in their respective developments. The next topics explore ideas about this in order to frame the constraints broadly; then we attempt to assess the early establishment of growth stages. In assessing these, it is well to keep in mind that lepidodendrids did not develop into large long-lived trees with progressively enlarging crowns, trunks, and anchorage systems. They had arbo-

rescent architectures, but were determinate in all respects.

SECONDARY THICKENING—PERIDERM

The principal secondary structural support of lepidodendrids was the periderm, added in such a way as to retain external tissue integrity for a prolonged growth interval. The circumferential position of the periderm constitutes the maximum support with the least allocation of resources. Also, as Cichan (1986) pointed out, the shift of prime support function to the periderm and other non-vascular tissue circumvented the trade-off between support and conduction roles and permitted more modest development of wood specialized for high conductance. Both pole and stigmarian axes developed a bifacial phellogen with the bulk of the periderm formed toward the inside. In stigmaria, secondary cortex was extensive but less radially aligned and more parenchymatous than in the stems. In *Stigmaria ficoides* (*Lepidodendron*, *Lepidophloios*) there was apparently a continuous meristematic region near the outer edge of the cortex; in sigillarian stigmaria the meristematic zones consisted of concentric rings in the outer cortex (Eggert, 1972). In both cases the accompanying cell division of derivatives was extensive and varied. It should be emphasized that the exact nature of this periderm is uncertain, but it was likely composed of persistently living cells, potentially meristematic, and might have been photosynthetic if exposed to light (Frankenberg & Eggert, 1969).

Secondary thickening in the pole stages resulted in more discretely patterned tissues than in stigmaria, derived from a circumferential meristematic zone beneath the leaf cushions or bases (Kisch, 1913). In some of the studied lepidodendrids (e.g., *Diaphorodendron*), the bifacial meristematic activity resulted in a sharp distinction between the inner and outer periderm. Whereas the inner periderm is usually more abundant and transitional to primary cortical parenchyma, the outer is characteristically dense and somewhat woodlike in cross section and became quite thick in some trees. The outer is the principal support tissue, and judging from its preservation under different circumstances, it was extremely decay resistant, probably quite rigid, and relatively impervious when externally exposed. In other taxa (e.g., *Lepidophloios*, *Lepidodendron*, *Paralycopodites*, and *Sigillaria*) a clear distinction between inner and outer periderm is lacking, the entire tissue is of the decay-resistant, dense, "woody" type. In general, the periderm tissues appear to have been living and could have

been so for most of the plant's life. However, circumferential expansion of the periderm required special mechanisms to retain the external leaf cushions and associated tissues.

The leaf cushion or base of typical diamond outline is also a good structural support design (commonly used in reinforcing mesh for concrete). In lepidodendrids it imposes constraints to stem expansion. As far as we know, leaf cushions had very limited capacity to expand in basal width or height after maturation. Cells beneath lepidodendron-type leaf cushions could divide and accommodate some girth enlargement; in some species intercushion proliferation resulted in separation bands, which interestingly enough, exhibit cuticle and stomata like the leaf cushions (Thomas, 1970). In others, there were simply splits formed between leaf cushions (e.g., *D. scleroticum*). In the *Lepidophloios* leaf-cushion design, with the wide dimension being transverse to the stem, there was little means for such expansion without compromising the leaf-cushion cover. In *Lepidophloios* the primary body seems to have been relatively large. The crown branches had little periderm, which may have permitted leaf cushion retention and photosynthetic input, during the time and in the locus of cone formation.

With circumferential expansion, leaf cushions typically became obliterated or were sloughed off in older, lower trunk portions in most large plants. Some of these observations may be questioned because dead trees may have stood for some time with accompanying loss of cushions before entering depositional environments. However, some trunks as much as a meter in diameter were found buried in situ with leaf cushions still intact at the base. In some cases, the cushions on these stems appear to have "faded" through stretching and weathering, supporting patterns of subcushion expansion seen in petrifications. The persistence of prominent leaf cushions on stems over 0.5 m in diameter is problematic and an explanation for this is lacking.

The key difference in the addition of periderm in lepidodendrids, compared to dicot trees, is that most of the living tissues were formed to the *inside*; the outermost, which were the principal support elements in some taxa, were not actually externally exposed until leaf cushions or bases were sloughed off. The most common concern in speaking about periderm or bark in lycopsids is that such terms tend to convey seed-plant equivalences. The periderm tissues are quite different from traditional bark. The chemical composition of the walls of the tissues is not known (see Logan & Thomas, 1987). The activity of the periderm-producing meristem

in the pole apparently continued longer than secondary xylem formation and eventually extended further up, as well as out into some branches. Secondary xylem was probably fully formed for a given level of the plant early, compared to extended cortical cambial activity. At least one species of *Diaphorodendron* exhibits wood and thick periderm development out into some branches (DiMichele, 1981).

"LIGHT SHARING" AND DIFFUSE PHOTOSYNTHESIS

POLE HABIT

Among the most unusual ecological aspects of lepidodendrid architecture in tropical swamps are the "light sharing" consequences of determinate growth in relation to the lycopsid tree habit. A corollary of this architecture is limited light capture because of the pole design. Needless to say, in comparison to tropical angiosperms it is anomalous for the largest and dominant forest trees to be "light sharing" as opposed to preempting such resources and shading the understories. This is perhaps understandable in the context of intense tropical sunlight and suggested physiological functions mentioned later. In the case of lepidodendrids, this light sharing needs to be assessed, first from the perspective of its implications for lepidodendrid physiology and the peculiar morphological structure of the plants, and second its impact on community structure.

Lepidodendrid trees are commonly pictured as determinately branched with "crown"-like tops, as in the terminal reproductive phase of *Lepidophloios* or *Lepidodendron*. As did the pole habit that constituted most of the plant's life span, these final stages permitted high light penetration. Those genera with lateral branches typically dropped them (deciduous), reflective of the determinate growth of laterals. Such branches were usually not maintained as sources of photosynthesis after local cessation of cone production. Considering that sizes and numbers of leaf cushions and leaves in the lateral and terminal branch systems diminish acropetally (Chaloner & Meyer-Berthaud, 1983), concern about photosynthetic capacity was expressed early in the recognition of determinate growth (Andrews & Murdy, 1958). However, with the progressive loss of the larger, more basal leaf laminae, the leaf cushions were in a position to receive sunlight and continue photosynthesis, even on the mature trunk. Evidence of cuticle and stomata is consistent with continuation of photosynthesis by leaf cushions after leaf abscission (Thomas, 1977).

Leaf cushions also contained parichnos (Weiss, 1907).

High levels of light penetrance through crowns, and through stands of trees, may have been crucial to the success of plants with a limited capacity to translocate photosynthates, as well as dissipate heat with evapotranspiration. Photosynthesis was by necessity a dispersed function in the pole-development phase. Small amounts of phloem placed limits on long-distance source to sink translocation. Yet, cortical cambia evidently continued to function beneath the leaf cushions in lower parts of the plants for some time, suggesting that leaf cushions were a likely local source of photosynthate. Even more intriguing is the implication of limited phloem for massive, in some cases monocarpic, cone production on determinate, terminal branches. The largest of all cones among lower vascular plants were produced on short lateral branches borne within the crown in plants such as *Lepidophloios*. The extremely large distal laminae of the sporophylls, especially of the *Lepidocarpon* type, may have been a major photosynthetic source contributing to cone development and to the massive megaspore reserves (DiMichele & Phillips, 1985). The lepidodendrids produced the largest endosporic megagametophytes among lower vascular plants.

In the above circumstances, high light penetrance permitted by the pole architecture, and the reduced sizes of crown leaves, would allow an appreciable level of photosynthetic capacity in the lower portions of the trees. Loss of leaf laminae and lateral branches would have further minimized obstacles to light penetration allowing sunlight to reach the forest floor and permitting establishment of the propagules of lepidodendrids or other plants. As a consequence, lycopsids were likely not climax species, except where abiotic conditions selected strongly against other kinds of plants. It is likely that many lepidodendrids were seral, and required high-light levels for germination and growth.

STIGMARIAN SYSTEM

The high light penetrance permitted by the pole architecture of lepidodendrid trees is particularly important for interpretation of the functions of the stigmarian system. The stigmarian system represents a special problem for food supply, in that sustained growth of the two axial systems simply exacerbates the puzzle of the lack of a recognizable long-distance, photosynthate translocation mechanism. The primary phloem connection in the transition zone is miniscule and secondary phloem is lacking. The appendages of the main stigmarian

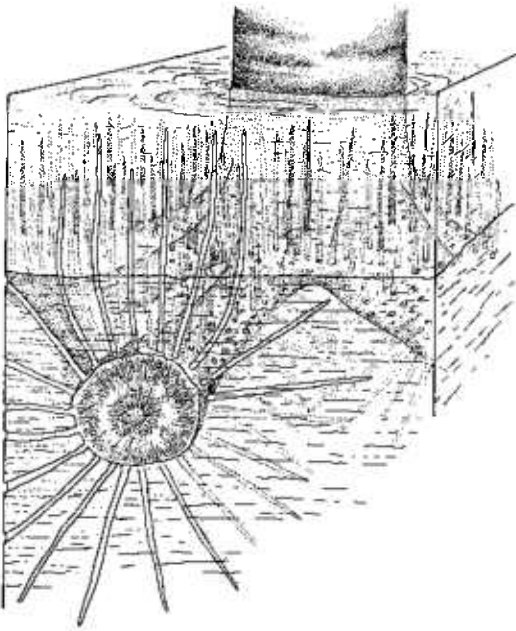


FIGURE 1. Reconstruction of the transition zone between trunk and stigmarian rhizomorph in a lepidodendrid tree. Shallow burial of the dichotomously branched rhizomorph axis and flooding of the swamp surface permit exposure of the stigmarian appendages to light in the water column. The "star-burst" pattern of appendages surrounding the rhizomorph axis can be observed in clastic sediments, where substrates were homogeneous in consistency. Studies of coal balls suggest a less regular pattern in peats, which have a heterogeneous fabric.

axes were helically dispersed and radiated in all directions. Attached to each of the four multiply dichotomized main axes, appendages penetrated and trapped sediment providing shallow anchorage and nutrient supply, along with water conduction. In addition, appendages provided the pathway for diffusion of gases throughout the stigmarian system and into the basal trunk; the aerial system had its own aeration system. Many of the stigmarian appendages were directed upward from the main axis and would have entered the water column after penetrating the substrate surface (Fig. 1). In depths of up to 0.5 m or somewhat more, the appendages could have been buoyant and floated to near the water surface. We do not suggest that they were emergent pneumatophores in *Stigmara ficoides*. Their structural constraints do not seem to have permitted that. In such a water-bathed environment, gas exchange or a higher oxygen content was likely, though probably quite varied according to circumstances.

Several possibilities exist regarding gas exchange, photosynthesis, and the uncertainties about

food supply in the stigmarian system. If the near surface appendages were capable of photosynthesis and light penetration of the water surface were adequate, the stigmarian systems may have been self-reliant, producing their own photosynthate. In this case, the paucity of phloem between the photosynthetic shoot and stigmarian axes would not limit stigmarian growth. One especially critical environmental aspect is that light penetration of the water was adequate. The organic matter in such circumstances could have limited that severely. While there is no anatomical support for the stigmarian appendages being, in part, photosynthetic, this line of reasoning is worth pursuing to some of its theoretical and logical ends.

PARICHNOS AND LACUNAE: INTERNAL DIFFUSION VERSUS EXTERNAL GAS EXCHANGE

PHOTOSYNTHETIC IMPLICATIONS

Aerial shoot-system morphology provides more clues to the internal diffusion of O_2/CO_2 in lepidodendrids than does even the stigmarian system. However, there are some analogies between well-differentiated air exchange passages recognizable in each. Appendicular structures have parichnos or lacunae closely associated with but clearly separated from the vascular strands by parenchymatous tissues in leaf bases, lamina (including sporophylls), and stigmarian appendages.

Whereas the structure and distribution of parichnos differ among the lepidodendrid genera, all have a pair that are present in *primary* tissues of the leaf base and extend, in most genera, into the lamina. The most distinctly traceable, as a pair, are in sporophyll leaves of *Lepidocarpon* from the pedicel to near the tip of the distal lamina. The distinctive cellular construction in the sporophyll lamina is identical to that in the leaf cushion. In the vegetative leaves, such as those of *Lepidophloios*, only a single parichnos or "lacuna" passage occurs abaxial to the vein (Graham, 1935).

Were it not for the presence of both parichnos and stomata in both leaf base (cushion) and lamina, external gas exchange would appear to be the obvious function of the parichnos. For photosynthetic leaves and leaf cushions with stomata, the parichnos would appear to be an internal system of gas exchange associated with photosynthesis, corresponding more to recycling of CO_2 and O_2 than to external diffusion balances, which were presumably mediated by functional stomata on photosynthetic surfaces. This would be particularly true in genera such as *Paratycopodites* or *Diaphorodendron*, where the parichnos system was entirely internal

prior to leaf loss. The loss of laminae from most lepidodendrid leaf cushions is accepted as an abscission process, paralleling that of stigmarian appendages. However, if abscission in lycopsids were even roughly comparable to that of other vascular plants, the parichnos may have been obstructed at the abscission point in the leaf cushion and would not have functioned in external gas exchange, as analogized with lenticels. Two divergences from this *Diaphorodendron-Paralycopodites* parichnos pattern are evident. The first, represented by *Lepidodendron* and *Lepidophloios*, characteristically exhibited a lower pair of infrafoliar parichnos on the leaf cushion connected to the main parichnos system; this pair is hidden in *Lepidophloios* by cushion imbrication and has been identified (by us) only recently from anatomically preserved specimens. It is reasonable to assume that these external parichnos functioned in diffusion. The second is found in *Sigillaria*, which has the most prominent parichnos among the lepidodendrids. A pair flank the vascular strand and extend inward from the leaf cushion through thick periderm to form a single fusiform mass of highly distinctive, dense, almost resinous tissues. It is not really possible to distinguish sharply among parichnos that may have been aerating systems for deep-seated tissues, such as in *Sigillaria*, for functional exchange or venting as in *Lepidodendron*, or only internal recycling as suspected in *Diaphorodendron*. We can only raise the possibilities of differences, especially for the coal-swamp centered genera.

It is likely that some lepidodendrids may have been primeval photosynthetic giants in coal swamps. With limited water transport capacity, general xeromorphy and a variety of anatomical features that suggest CO₂ conservation, they may have utilized physiological attributes that resembled CAM (Crassulacean Acid Metabolism) plants in their aerial shoot systems. If this were the case, it follows that their stigmarian systems were also CAM-like if photosynthetic. Barring the potential role of stigmarian systems as being partially photosynthetic, it seems likely that they could have been major systems of CO₂ acquisition.

If stigmarian appendicular tissues could photosynthesize, CO₂ may have been obtained both from the organic-rich swamp water and from respiration. The concentrations of CO₂ could have been extremely high, minimizing photorespiration. In a sense, the possible design is most similar to a "submerged version" of a CAM plant that has no stomates to open at night and a surplus CO₂ supply. This may fit with the peculiar lacunar design of the stigmarian appendages where the inner wall

surface is about the same as the outer with the excentric vascular strand loosely connected with the outer cortex. Those stigmarian appendages that may have been photosynthetic would have been both major sources of food and aeration for the submerged system, while others provided anchorage and nutrients, functions dependent on the microenvironment in which they developed; these were expendable appendages of limited duration permitting the axis system to meet changing environmental circumstances. If stigmarian appendages utilized only a part of the high CO₂ concentration in photosynthesis, the water conduit would have been a means of moving dissolved CO₂ to aerial portions. This could have enhanced the photosynthetic capacity of the shoot with the parichnos perhaps mediating O₂-CO₂ physiological balance. While emphasis here is on the possibility of photosynthesis in the stigmarian system, the collective arguments for internal recycling of CO₂/O₂ in the pole system follow the same line of reasoning for a CAM-like physiology.

The high light penetration permitted by lepidodendrids is consistent with, but not necessarily demanding of, such interpretations. However, in a lepidodendrid dominated tropical-swamp forest with pole-tree canopies, light intensity would have been high enough to support floating or submerged vascular aquatics very near the surface. As far as we know, there were no such plants. Even in the shallow reaches, accessible to other trees and herbs, there may have been relatively little shading. There could have been an enormous mass of buoyant stigmarian appendages in many water surface areas. In fact, if you pursue the strategies of lepidodendrids in the coal swamps, it is the "light permissiveness," allowing light to reach their own trunks and branches, their reproductive offspring on the surface of the water or exposed peat, and perhaps their stigmarian appendages, that constitutes the ultimate anomaly in tree design.

The estimated biomass of stigmarian structure preserved in peat deposits are taphonomically biased by what happens after burial. However, of the stigmarian biomass preserved in coal balls, 75-90% of it is appendicular as opposed to axial. Only in a few "root peats" with repeated "rerooting" of stigmarian systems do the percentages drop to the 60% level. With that much biomass allocated to appendages, it is reasonable to suggest that perhaps such appendages were more than conventional "rooting" organs.

It is well beyond our scope to try to carry our ideas about CO₂ uptake and CAM in lepidodendrids to the living *Isoetes* (= *Stylites*). However, the

discovery of CAM in *Isoetes* (Keeley, 1981, 1982; Keeley et al., 1984) and further studies of the process in these plants (Boston, 1986; Boston et al., 1987a, b; Raven et al., 1988; Sandquist & Keeley, 1990, and references therein) should not be divorced from potential implications for both small and large rhizomorphic lycopsids of the geologic past. That stigmarian lycopsids suggest physiological attributes comparable to extant *Isoetes* is mostly a matter of their large size, excellent preservational integrity, and our ability to resolve their ecologies broadly. Perhaps the most pertinent speculation about the late Paleozoic rhizomorphic lycopsids would be, "What if they were CAM plants?" We should not bias relevant comparisons to just the smaller ones (Raven et al., 1988), nor continue to hold to the great reductional series (Thomas, 1985) with its implications about aquatic morphologies. This may aid in viewing *Isoetes* (*Stylites*) as a model system for how some lycopsids (vascular plants) invaded seasonally dry terrestrial environments (Keeley et al., 1985) as well as tropical swamps.

The evolutionary generalization we suggest about the open canopy of the lepidodendrids is that they probably radiated under such conditions, perhaps in the virtual absence of non-lycopsids and utilized diffuse photosynthetic distribution systems to permit their growth in height, while allowing sunlight to reach the full range of their organ systems. With their short-term strategies for reproduction this reemphasizes their "giant herb" status. This brings in a recurrent question about why lepidodendrids were so tall compared to their contemporary tree types in the tropical swamps. While actual sizes differed greatly between coal and clastic swamp lepidodendrids, and even among coal swamps with time and circumstances, they were consistently the tallest by far.

EARLY STAGE DEVELOPMENT

The early development of the lepidodendrid plant must have involved even closer coordination of stem and rhizomorph development than that projected for later stages. Briefly, the early stage may be considered as a temporally coordinated development, in which the pole and stigmarian shoots share resources during establishment growth. In order for expansion of the primary bodies in both systems, and increase in appendicular sizes and functions, there has to be a closer coordination of shared food supply than presumed in later stages. This mode of development is dependent upon some of the possibilities put forth about stigmarian pho-

tosynthetic potential. It depends, in part, on precocious branching of the stigmarian axis and attainment of a large primary body without a central pith or even a legitimate siphonostele.

If there is a "lepidodendrid" logic of developmental sequencing, it suggests that the pole trunk must be adequately stabilized, even if not necessarily well anchored, before achieving a massive apical plume of large leaves. In order to provide the mix of a stable platform and a large, perhaps domed or cone-shaped pole stage with a primary thickening meristem, one axial system has to develop somewhat ahead of the other. If both were photosynthetic, it is reasonable that it should be the stigmarian system (Fig. 2), with its early appendicular development and axial branching in the least demanding allocation strategy—the sparse "stele" of only appendage traces and a mostly hollow pith, that permits a rapid increase in circumference for appendage display. Also, stigmarias are more cheaply constructed than pole stages and lack the evapotranspiration limitations. The earliest formed appendages of stigmaria come from the transition region and may not have been indicative of the larger ones later produced. Nonetheless, the basalmost leaf cushions of the pole phase, while not necessarily indicative of the first leaves formed, give evidence of an enormous expansion capability reflective of a large apical meristem, primary thickening, and perhaps expansion processes that go beyond these.

If stigmarian systems developed more extensively than stems in the "early stages" of tree establishment, then there is a stronger case for the photosynthetic potential of some stigmarian appendages. This supposes that the primary phloem translocation worked well, at least for a while, to supply the pole stage development. As development of the two organ systems ensued, the separate photosynthetic capabilities and the high light penetration permitted by the pole design would become increasingly important. If a stigmarian system radiated outward before the pole stage expansion, there would be less self-shading. Considering the eventual primary-body expansion of the pole stage, it seems probable that the stigmarian system precociously assumed a prime photosynthetic, anchorage, nutrient, and water supply role in the critical establishment phase. If any or most of this proves to be the case, it is no wonder that stigmarian systems were the adaptive breakthrough of the mosaic lepidodendrid conquests of tropical swamps.

On a less speculative note, the relatively long-term growth and extensively ramified stigmarian

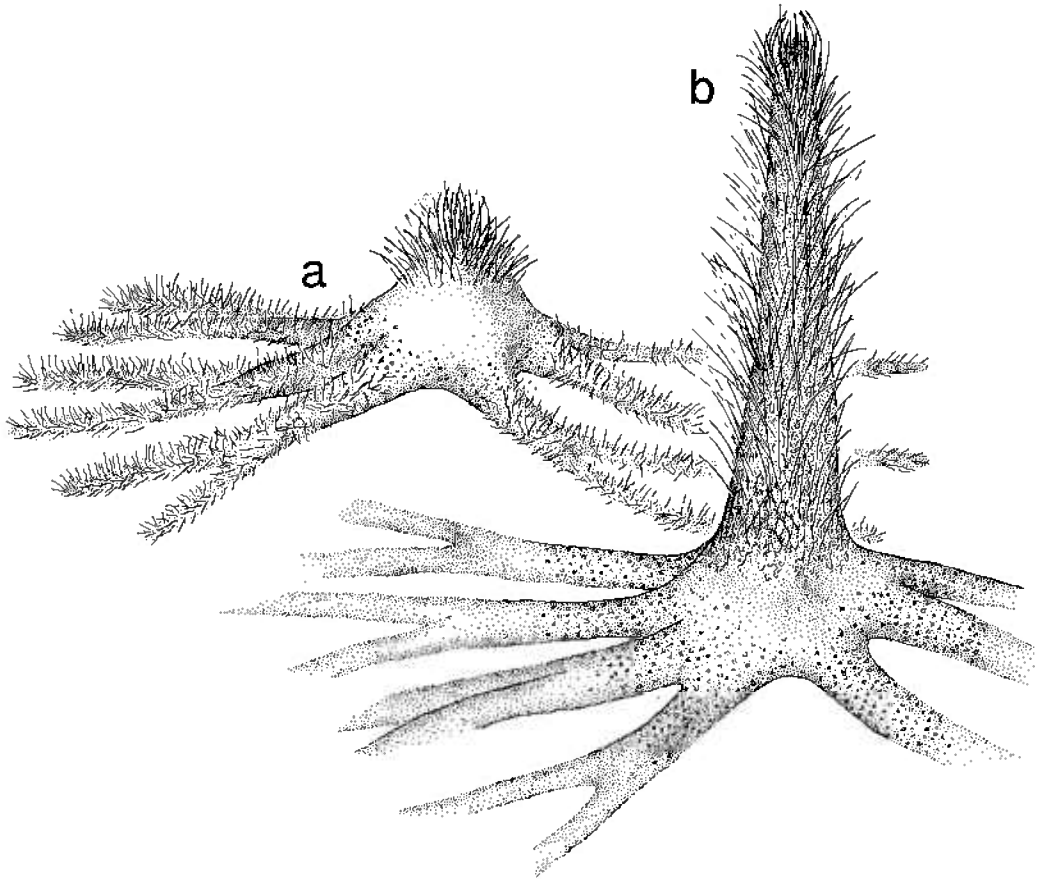


FIGURE 2. Hypothetical early growth stages of a lepidodendrid tree. Each reconstruction represents a successive stage, a, and b. In this hypothetical sequence, the stigmarian system is elaborated more rapidly than the trunk, made possible by an independent photosynthetic capacity. Early stages are rosettelike; once the stigmarian system is sufficiently elaborated to provide a stable base of support and supply of nutrients, trunk elongation occurs rapidly.

system was essential to the support and sustained or massed reproductive capacities of the lepidodendrids whether stigmarias were photosynthetic or not. The capacity to ramify and extensively permeate the substrates of soft sediment and water was crucial to longer lived and larger arborescent reproductive strategies; this is the critical distinction between lepidodendrids and the lepidodendropsids (*Lepidodendropsis*) and other isoetaleans that inhabited wetlands with them during the Early and/or Late Carboniferous.

PRINCIPAL GENERA

TAXONOMY AND COMPARATIVE MORPHOLOGY

Comparative morphological studies of the principal lepidodendrids in Late Carboniferous peat-swamp assemblages indicate very distinctive morphological groups corresponding to the currently

recognized genera (Bateman et al., 1992). The known assemblages of each genus exhibit markedly different megasporangium-sporophyll units (Phillips, 1979), which largely frame the accepted generic limits at present. In part, the megasporangiate morphology of genera seems so stereotyped in basic structure that it is not useful currently below the generic level for taxonomic delimitation, except in *Sigillaria* and perhaps *Paralycopodites*.

The microsporangia and especially the microspores provide sharp distinctions among *Sigillaria*, *Diaphorodendron*, and the three *Lycospora*-bearing genera (Courvoisier & Phillips, 1975; Willard, 1989a). Taxonomic distinctions among some of the *Lycospora* microspores correlate, in large part, with the different genera (*Paralycopodites*, *Lepidodendron*, *Lepidophloios*) and, in turn, permit separation of *Lepidophloios harcourtii* from *L. hallii* (Willard, 1989a, b).

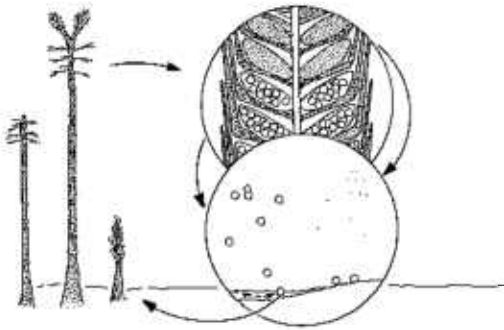


FIGURE 3. Inferred life history of *Paralycopodites* (= *Anabathra*) species. This was the only one of the lepidodendrid trees to produce a bisporangiate cone (*Flemingites*), freely releasing megaspores and microspores. Cones were produced on deciduous lateral branches. Plants appear ultimately to have been determinate, suggested by a limited number of apoxogenetic apical dichotomies.

Whereas each of the five lepidodendrid genera are now recognized to be quite distinctive anatomically, there is a paucity or lack of known vegetative characteristics to separate coal-swamp species within *Paralycopodites* and within *Lepidodendron*. Sigillarias are too poorly known in coal swamps to apply rigorous vegetative comparisons; however, the sigillarian stigmarian system certainly is the most distinctive of the lepidodendrid genera. By contrast, *Diaphorodendron* species, as very abundant lepidodendrids in peat swamps, are now separable only by vegetative morphology (DiMichele, 1979b, 1981, 1985).

Paralycopodites (= *Anabathra*)

Three species of *Paralycopodites* can be recognized in the Carboniferous, based on reproductive organs. One species producing a *Flemingites scottii* cone is known from the Lower Carboniferous of western Europe (Meyer-Berthaud, 1981). In Pennsylvanian peat swamps of the United States, two species have been recognized, one producing *F. schopfii* in the Westphalian C (Brack, 1970), and one with *F. diversus* in the Westphalian D (Felix, 1954). The vegetative organs of these species are indistinguishable; the leaves have enlarged bases but lack distinctions of a leaf cushion and lamina. All those species described produce *Lycopospora orbicula* microspores (Willard, pers. comm.).

Paralycopodites abundances are highest in ecotonal habitats marking the transition from peat to clastic substrates. In peat profiles, *Paralycopodites*-rich zones often occur adjacent to clastic partings or in parts of the coal seam enriched with

mineral matter (DiMichele & Phillips, 1985, 1988; Willard, 1989a). Similar patterns are suggested by spore data (Calder, in press; Eble & Grady, in press). Medullosan pteridosperms often are part of this assemblage in the Westphalian D. *Paralycopodites* appears to have been a colonist, preferring open, disturbed, but nutrient-enriched parts of peat swamps, probably not subjected to long-term flooding. Little is known of these kinds of plants from purely clastic deposits. The genus *Ulodendron* (sensu Thomas, 1967) may be the closest counterpart. A lepidodendrid that appears to occupy a comparable habitat in some clastic swamps is *Bothrodendron* (sensu Wnuk, 1989).

Paralycopodites trees bore opposite rows of small, deciduous, lateral branch systems on the trunk. At the ends of the lateral branches cones were produced in abundance. Trunks ultimately dichotomized, but apparently only in the later phases of determinate growth. Habit reconstructions can be found in Hirmer (1927, for *Ulodendron majus*) and in DiMichele & Phillips (1985). These reconstructions emphasize that the fundamental function of the lateral branch systems was cone display; as with monocarpic forms, branching formed a scaffold on which cone production occurred.

The reproductive biology of *Paralycopodites* in combination with its habit appear to have been the keys to its ecological success (Fig. 3). Cones were bisporangiate; microsporangia occurred in the apical part of cones, megasporangia in the basal portion. Multiple megaspores were produced within each megasporangium and were freely released into the environment. The prolific production of cones by *Paralycopodites* in the frequently disturbed ecotonal habits commonly resulted in the abundance of cones and cone fragments, many still containing spores, associated with their vegetative litter. Exceptionally well preserved endosporic gametophytes have been documented in phenomenal detail (Brack, 1970; Brack-Hanes, 1978; Brack-Hanes & Vaughan, 1978).

The nearly continuous production of cone-bearing branches, the overall large allocation to cones, and the assured presence of both male and female gametophytes provided by bisporangiate cones of *Paralycopodites* are consistent with its role as a colonizing, pioneer species. Continuous saturation of the local habitat with megaspores and microspores and the potential for some widespread water dispersal, even for cone fragments, during occasional floods, may have circumvented unpredictability of local conditions. This could have introduced some plants into a wide variety of settings, some favorable for establishment. In this sense,

Paralycopodites may have escaped the constraints of heterospory, which imposes an absolute need for separate male and female gametophytes to be present within a narrow spectrum of wet environmental conditions if sporophytes are to be produced; this is not the optimal life history for a colonizing species. However, modification of sporophytic architecture, so that megaspores and microspores were produced nearly continuously over an extended life span, permitted it to sustain prolific reproductive functions in a role not generally accessible to free-sporing bisporangiate plants of shorter life spans.

Sigillaria

Sigillaria is a diverse genus, comprising at least two subgenera. Nearly all of the species have been described from clastic environments, including a number of structurally preserved forms (Lemoigne, 1960). In peat-forming swamps, *Sigillaria* occurs throughout the Pennsylvanian, although no swamp-centered evolutionary lineages can be identified. Based on cone morphologies, sizes of plants inferred from the dimensions of preserved organs, and anatomies of the swamp species, it appears that sigillarians sporadically entered, became established, and then disappeared from peat swamps. They were generally a minor, but detectable part of most Westphalian and Stephanian swamp habitats. Relatively higher abundances occur in the late Westphalian A to early B and in the Stephanian. *Sigillarias* produced separate microsporangiate and megasporangiate cones; both were basically free sporing but with a complex megasporangiate dispersal pattern. Cones are assigned to *Mazocarpon* if preserved anatomically (see Benson, 1918; Phillips, 1979). Microspores belong to the dispersed spore genus *Crassispora*.

The sigillarians appear to encompass a range of ecological conditions that suggest drier habitats or lower water tables associated with wetlands. Although it is not possible to give specifics for such a large group, the hallmark of their ecology appears to be a preference for the more marginal wetland settings with entry into peat swamps following floods and dry downs. Their common occurrence in channel lag sandstones suggests growth of some species along stream margins. Others may have been part of wet levee communities (Gastaldo, 1987), or occupied freshwater, nutrient-enriched parts of swamps, close to channels, and perhaps intermittently in flowing water (DiMichele & Nelson, 1989). In peat swamps of the Westphalian, *Sigillaria* abundance was usually associated with abundant ground cover, medullosans, and sometimes species

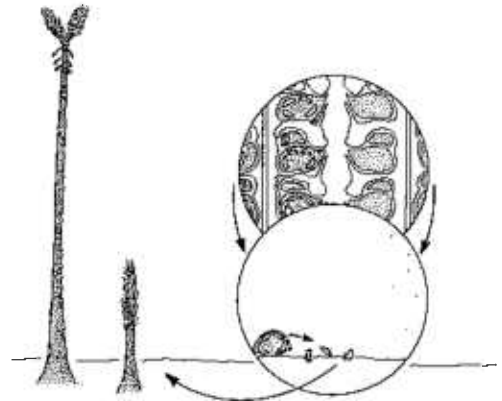


FIGURE 4. Inferred life history of *Sigillaria ichthyolepis* (= *S. approximata*), from the Late Pennsylvanian. All *Sigillaria* produced separate megasporangiate and microsporangiate cones assignable to *Mazocarpon*; *S. ichthyolepis* produced *M. oedipternum*. Megaspores of *M. oedipternum* had a thick subarchesporial pad covering the proximal face. We suggest in this reconstruction that this pad may have obviated sperm access to eggs, fostering apomixis as the link between sporophyte and gametophyte.

of *Diaphorodendron*; *Sigillaria* is less commonly associated with indicators of long periods of standing, possibly stagnant water (e.g., Phillips & DiMichele, 1981; Willard, 1990).

Several aspects of sigillarian architecture may provide some additional insights on their biology (Fig. 4). The trunks apparently were sparsely branched terminally at maturity, and some may not have branched at all except during cone-bearing phases (e.g., Hirmer, 1927). In coal-ball deposits it is most common to find accumulation of bark sheets or fragments of large stems without ever encountering twigs or smaller axes that could suggest a crown. These peats often show evidence of considerable exposure and decay. Stigmarian systems were smaller and more compact than those found in other lepidodendrids, and it is strongly suspected that they were the most distinctive, both in branching architecture and function. Lemoigne (1960) suggested that some branching of sigillarian stigmarias may have penetrated the substrate deeply. This would have strongly anchored these plants and could have tapped lower water tables and perhaps more aerated groundwater; in other lycopods the stigmarian systems were buried shallowly and formed a broader platform at the base of the tree. The small sigillarian stigmarian appendages contain a connective, a band of tissue linking the vascular strand to the outer cortex; small size and the connective also provide greater structural strength than is found in the balloonlike appendages of the other lepidodendrids.

Reproductively, cones apparently were produced intermittently and were borne by peduncles directly on the trunk in whorls. This suggests, in context of their habitats and habit, that they were tolerant of fluctuation in the relative wetness of the environments and perhaps responded to drier and wetter episodes to reproduce. Because sigillarians were basically free-sporing, this intermittent reproduction entailed the risk of mistiming spore release unless the local environments were wet, at least soon after dispersal.

The largest known sigillarians in peat swamps are from the Stephanian, a size feature shared with tree ferns, calamites, and medullosan seed ferns. Several sigillarian species were present, based on cone morphology (Schopf, 1941; Figg, 1983; Feng & Rothwell, 1989). Our reconstruction (Fig. 4) is of *Sigillaria approximata* and *Mazocarpon oedipternum*. The megasporangiate cones are the best known among the sigillarians, with the megaspores embedded in a subarchesporial pad of parenchyma, apparently a generic characteristic. Benson (1918) and Schopf (1941) suggested that the cones were deciduous and the contents were dispersed by sequential cone, sporangial, megasporangial fragment units. These units could have been disaggregated after or during dispersal by mechanical means, or germination may have occurred locally where the cones originally fell. The presence of megagametophytes and possibly embryos in *M. oedipternum* (Schopf, 1941) led us (DiMichele & Phillips, 1985) to suggest apomictic origin of the embryos. It is not the presence of putative embryos alone that leads to this suggestion, but rather the adherence of archesporial parenchyma to the proximal surface of the megaspore, obviating access of sperm to the eggs. Details of sigillarian reproductive organs are discussed in papers by Phillips (1979), Figg (1983), and Feng & Rothwell (1989). Sigillarian cone and megaspore morphology suggest evolutionary changes in mode of dispersal during the Pennsylvanian. Earlier megaspore types had barblike (apiculate) or similar appendages. The Late Pennsylvanian ones lack these and had adherent tissue protection.

Sigillaria may have made some ecologically significant, evolutionary modifications in timing of reproduction and dispersal mechanisms as a response to environmental variability. Morphological differences among cones provide evidence of changing circumstances within the Late Carboniferous peat swamps (Benson, 1918; Schopf, 1941; Figg, 1983). Considering evidence of frequent disturbances in peat-swamp environments, including fluctuations in water tables, sigillarians may have

tracked the most extreme dry-wet seasonal fluctuations or comparable changes in water tables caused by other factors. Morphological features of some megaspores may have been as important for prevention of desiccation, or for protection in flood transport (as proposed for *Porostrobus*, Leary & Mickle, 1989).

Diaphorodendron

Diaphorodendron species comprise two life-history groups, one polycarpic, the other monocarpic (DiMichele, 1979b, 1981). Three polycarpic species have been identified in Pennsylvanian-age coal swamps, but the similarity in morphology of many of these forms probably masks greater species diversity. *Diaphorodendron vasculare* occurs throughout the Westphalian except for the uppermost Westphalian D. It probably represents a species complex. *Diaphorodendron phillipsii* occurs in the Westphalian C-D, and *D. scleroticum* is known only from the Westphalian D. The monocarpic forms have been subsumed in a single species, *D. dicentricum*, which probably represents a group of related species. All species in this genus appear to have identical reproductive structures (Fig. 5). Cones are assigned to *Achlamydocarpon varius* (Leisman & Phillips, 1976). Megasporangiate cones had one functional megaspore (*Cystosporites varius*) per sporangium. Microspores are described now as *Granasporites medius* (Ravn et al., 1986) and were frequently dispersed as tetrads.

The *Diaphorodendron* species, individually and collectively, are the most difficult of the arborescent lycopsids for which to deduce ecological strategies because they have such broad ecological amplitudes. They occur in markedly different kinds of assemblages within peat swamps, as dominant to minor elements. Furthermore, both polycarpic and monocarpic forms occur in clastic as well as peat-forming habitats, an overlap that apparently extends to the species level (e.g., Wnuk, 1985). This is the only aquacarpic genus thus far recognized that appears to have undergone marked evolutionary change within the Westphalian. Much as the recognition of *Diaphorodendron* as a genus distinct from *Lepidodendron* was long delayed (DiMichele, 1985), so has there been delay in the separation of species ecologically. All species of *Diaphorodendron* appear to have the very same reproductive morphologies. This is in contrast to *Sigillaria* where there were differences in megasporangiate and megaspore reproductive morphology and in vegetative, and presumably physiological, strategies. Polycarpic species of *Diapho-*

rodendron appear to have favored areas of infrequent, irregular disturbance. Monocarpic forms appear to have been colonizers of disturbed areas, but apparently lived for quite a long time on these sites, attaining large size (Wnuk, 1985).

Diaphorodendron vasculare is characteristic of the ancestral condition in this genus. Its distributional history indicates a broad ecological amplitude. Trees produced deciduous lateral branches on an otherwise unbranched columnar trunk. Reproductive allocation appears to have been low at any given time. Even in coals where *D. vasculare* is the only lycopsiid tree, reproductive organs are not encountered frequently, and relative abundances of *Granasporites* in spore-pollen samples greatly underestimate the biomass of the parent plants (Peppers, in Eggert & Phillips, 1982). The lateral branches contain little wood or bark, were of quite limited sizes, and served largely to support the cone array. The extended, low-level reproductive output may have positioned these plants to recover rapidly from severe but unpredictable (irregular) disturbances. They are rarely fusinized and occur in some assemblages in association with marine invertebrates, so disturbances such as wind throw, storm surges of marine waters into peat swamps, or other causes may have been more important than fire.

Diaphorodendron scleroticum is built along the same plan as *D. vasculare*, except the amount of wood and bark is greater throughout the tree, extending even into the lateral branch systems (DiMichele, 1981). This suggests a longer life span than *D. vasculare* and retention of lateral branch systems, perhaps approximating the habit reconstructed by Walton (see Thomas, 1978). In this species the lateral branches may have formed a diffuse crown, the main function of which was light capture. Wnuk's (1985) discovery of whole trees indicates that lateral branches were distributed sparsely along the main trunk. As with *D. vasculare*, reproductive allocation in *D. scleroticum* appears to have been relatively low at any one time. Community ecological studies of several late Westphalian D coals (Phillips & DiMichele, 1981; DiMichele & Phillips, 1988; Willard, 1990) suggest great variation in the taxonomic and structural composition of assemblages associated with *D. scleroticum*. It is conceivable that these plants opted for tolerance of all but the most severe disturbances, leading to variable but taxonomically diverse, associated vegetation. This species of *Diaphorodendron*, more than any other lepidodendrid, somewhat approaches the status of a "conventional" (dicot) tree, with sustained structural support

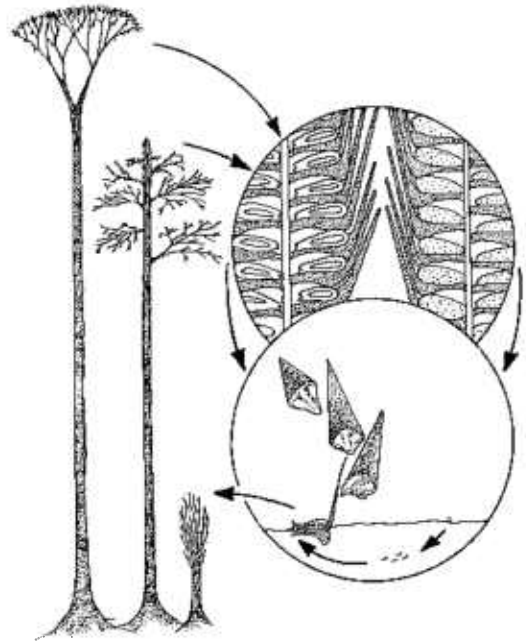


FIGURE 5. Inferred life history of the two major *Diaphorodendron* lineages, here represented by *D. dicentricum* (large tree to left, outside, with terminal crown) and *D. scleroticum* (center tree with crown of laterally borne branches). Innermost tree is a juvenile. Despite extensive differences in growth form and vegetative anatomy and morphology between these lineages, and even within some of the lineages, all species have indistinguishable reproductive morphology. Reproduction is characterized by separate megasporangiate and microsporangiate cones. The megasporangiate cones fragmented into aquacarp units composed of a sporangium with single functional megaspore and associated sporophyll tissues. Fertilization probably was aquatic.

and maintenance of a crown. It is noteworthy that *D. scleroticum* is presently known only in the Westphalian D.

The monocarpic *Diaphorodendron dicentricum* was also a large tree, nearly 30 m in height in clastic swamps (Wnuk, 1985). Structurally, the tree was cheaply constructed, with thin-walled cells in the periderm and broad bands of parenchymatous tissue in the wood (DiMichele, 1979b). The trunk was unbranched until the terminal phases of growth when a scaffold of branches was produced. Cones were borne on small side branches, derived from highly anisotomous apical divisions. Short-term, and perhaps lifetime, allocation to reproduction appears to have been much higher than in other *Diaphorodendron* species; very abundant *Achlamydocarpon varius* microsporangiate cones and megasporangium-sporophyll units typically oc-

cur in association with vegetative litter. The species can be found rarely as a codominant of intraseam assemblages (coupled with *Lepidophloios* near the end of the Westphalian D) and occurs widely at less than 10% biomass in assemblages from other late Westphalian D coals (DiMichele & Phillips, 1985). In these, its highest abundances occur in taxonomically and structurally diverse assemblages with a rich assortment of vines and ground cover (DiMichele & Phillips, 1988). We have suggested (DiMichele & Phillips, 1985) an invasive strategy for this tree, which is consistent with monocarpic habit and highly dispersed distribution. The cheaper construction and widespread but low density occurrence suggest *D. dicentricum* as a potential counterpart to *Lepidophloios* in longer-term monocarpic reproductive cycles. That is, *D. dicentricum* may be an ecological counterpart in longer-term life cycles for monocarpic lepidodendrids. The larger relative tree sizes and greater diversity-abundance patterns in some Westphalian D peat-swamp vegetation suggest temporal changes in disturbance frequencies.

The dispersal units of *Diaphorodendron* are apparently more stereotyped morphologically than those for any other genus of the five lepidodendrids, indicating that the sexual life cycle is extremely specialized in both microspore and megaspore dispersal and the linkage of these functions to morphology (Fig. 5). The tolerances of these linkages have been suggested by the distinctive morphology of a massa that was probably hydrophilic (Taylor & Brack-Hanes, 1976), an interlocking of microspores with the massa, and by the common dispersal of microspore tetrads. Leisman & Phillips (1979) noted that channels in the massa are about 65 μm in diameter, a dimension that would have allowed docking and entrapment of the microspores. It is interesting to note that the proximal faces of both the microspores, in persistent tetrads, and the functional megaspore with a massa were protected.

The dispersal units in *Diaphorodendron* morphologically fall between the relatively unspecialized free-sporing habit of *Paralycopodites* and the complex aquacarp of *Lepidophloios* (Phillips, 1979). *Achlamydocarpon varius* cones (Leisman & Phillips, 1979) may have been borne upright rather than pendent on the parent trees. Although monosporangiate, nothing is known about distribution of microsporangiate or megasporangiate cones among or within trees. That such widely differing life histories of the species are associated with the same set of morphological reproductive features suggests that evolution in the timing of reproduction, the tolerances of disturbance, and allocation to costly bark and wood, all features of

the sporophyte, were species-determining elements in *Diaphorodendron* ecological strategies.

Lepidodendron

Lepidodendron (sensu DiMichele, 1983) was the clastic-swamp counterpart to *Lepidophloios*. Many species have been described, primarily from the compression-impression record; many of these are *Diaphorodendron* or other as yet nonsegregated genera that may be distinct from *Lepidodendron* sens. str. in anatomy and reproductive biology. Nonetheless, *Lepidodendron* does appear to have been far more diverse and abundant in mineral substrate wetlands than in peat swamps. Two well-circumscribed species are known from peat-forming environments: the arborescent *Lepidodendron hickii*, which appears to be the anatomical counterpart to the compression *L. aculeatum*, and the scrambling ground cover plants *L. serratum* (Felix, 1952; Baxter, 1965), which Bateman & DiMichele (1991) have segregated as a new genus. Both occur throughout the Westphalian. At least one other form, similar to *L. mannabachense* (Thomas, 1970), occurs in late Westphalian D coals. *Lepidodendron* persisted into the Stephanian in western European clastic swamps (e.g., Lorenzo, 1979) and may have lasted until the end of the Permian in both clastic and peat swamps of China (see Chaloner & Boureau, 1967). The megasporangiate cones of *L. hickii* from peat swamps are assigned to *Achlamydocarpon takhtajanii* (= *A. belgicum*) (Snigirevskaya, 1964; Balbach, 1966; Schumacker-Lambry, 1966); microsporangiate cones are of the *Lepidostrobus* type and produced *Lycospora pusilla* microspores (Willard, 1989a).

Species of *Lepidodendron*, with the important exception of *L. serratum*, were monocarpic. Most arborescent growth occurred as an unbranched, columnar stem. Growth terminated with a determinate "crown" of dichotomous branches (Thomas & Watson, 1976). Cones were borne laterally in the crown on strongly anisotomous branches. The *Achlamydocarpon takhtajanii* megasporangium-sporophyll units are similar morphologically to *Lepidocarpon* in general shape, site of megasporangial opening, and morphology of the megaspore (Phillips, 1979). They are about one-half the size of *Lepidocarpon* and lack the lateral alations or integuments that enclose the *Lepidophloios* megasporangium. *Lepidodendron* aquacarp appear to have been suited for aquatic fertilization and dispersal (Phillips, 1979).

These aspects of reproductive biology suggest growth in environments with standing water and

sufficient environmental stability for completion of a monocarpic life cycle. However, *Lepidodendron hickii* appears to have been less tolerant of the low nutrient conditions of flooded peat swamps than *Lepidophloios*. Its observed dominance in peat swamps has thus far been limited to some Appalachian coals. Its occurrences almost never coincide with those of *Lepidophloios* in peat swamps (see Phillips & DiMichele, 1981; Gastaldo, 1987). There are exceptions, most notably in the vicinity of paleochannels and split coal. In clastic environments *Lepidodendron* is often a dominant in low diversity assemblages, frequently as preserved in organic-rich shales. In many instances it is a dominant in coal roof-shale assemblages, where it may represent a final swamp forest formed during drowning associated with rising water tables and clastic influx. Evidence of cohorts of trees in flooded, near channel backswamps, rich in clastic material (e.g., DiMichele & DeMaris, 1987), is consistent both with requirements for higher nutrients than offered by peat swamps, with dispersal in aquatic media, and with monocarpic habit.

Lepidodendron shares with *Lepidophloios* several anatomical traits that suggest tolerance of flooding. Large, highly lacunate stigmarian appendages suggest the ability to withstand long periods of flooding. The thick, yellowish resinous appearing bark is highly decay resistant. This decay resistance is associated with little root penetration of littered bark fragments. Where it occurs in peat-swamp floras, *Lepidodendron*-rich peats are poorly preserved, suggesting aerobic decay and high levels of activity by microorganisms.

The parallels between *Lepidodendron* and *Lepidophloios* are striking. Morphological similarities, most of which are highly derived, suggest close phylogenetic relationships. Ecological similarities suggest early partitioning or segregation of these lineages into very similar kinds of swamp habitats, but differing in basic mineral nutrient availability or the temporal-physical aspects of the environment associated with peat versus clastic accumulation. *Lepidodendron* appears to have been more diverse at the species and subhabitat level than *Lepidophloios*. The large number of species of *Lepidodendron*, as in *Sigillaria*, suggests more opportunities for speciation on a basic morphological theme in clastic environments than in peat swamps.

Lepidophloios

There are three known species of *Lepidophloios* in Pennsylvanian-age coal swamps: *L. harcourtii*, *L. hallii*, and *L. johnsonii* (Arnold, 1940; Di-

Michele, 1979a). *Lepidophloios harcourtii* has been identified in the megafossil record from the Westphalian A-C; its microspore, *Lycospora pellucida*, occurs throughout the Westphalian. Megafossils of *Lepidophloios hallii* have been found in coals of the Westphalian C-D; its microspore, *Lycospora granulata*, occurs throughout the Westphalian and into the Stephanian of Europe. *Lepidophloios "johnsonii"* was recognized by Winston (1988) from the late Westphalian D equivalent in the Illinois Basin. It could be conspecific with *L. johnsonii* (DiMichele, 1979a) from the Lower Pennsylvanian of Colorado, extending its known range, or be more closely related to *L. harcourtii*. This remains unresolved but no microspores have been correlated with *L. "johnsonii"* (Willard, 1989a) and *Lycospora pellucida* from *Lepidophloios harcourtii* does occur in the Westphalian D.

Lepidophloios abundance was centered in peat-forming environments. All species show the similar basic habitat preferences in their highest distributional abundances. They appear to have been more tolerant of longer periods of standing water than any other peat-swamp trees. Such tolerance is suggested by the frequent occurrences of high-dominance, low-diversity assemblages with little ground cover and few free-sporing components (Phillips & DiMichele, 1981; DiMichele & Phillips, 1988). The stigmarian systems of these plants were robust, with large appendages and substantial air cavities in both appendages and main axes. This is also consistent with their thick, highly decay-resistant bark, which is yellowish in color and may have been resinous and impervious to water. Such bark is often found relatively unaltered in peat litter and is almost never penetrated by roots in otherwise highly decayed peats. It appears that their range of tolerance permitted growth in some habitats from which other species were largely excluded and this is where they dominated. However, *Lepidophloios* species probably were not confined exclusively to such high-stress habitats. The plants also occurred more widely within peat swamps often in highly mixed assemblages, although these may represent the taphonomic effects of time averaging and a subsequent lack of temporal separation of successive forest stands.

One of the most striking aspects of the *Lepidophloios* life history (Fig. 6) is apparent monocarpy (DiMichele & Phillips, 1985). Two types of branching appear to have been confined to the final stages of growth. Isotomous dichotomies formed a crown scaffold in which cones were produced. The cones were borne laterally, terminating peduncles that were the product of strongly anisotomous

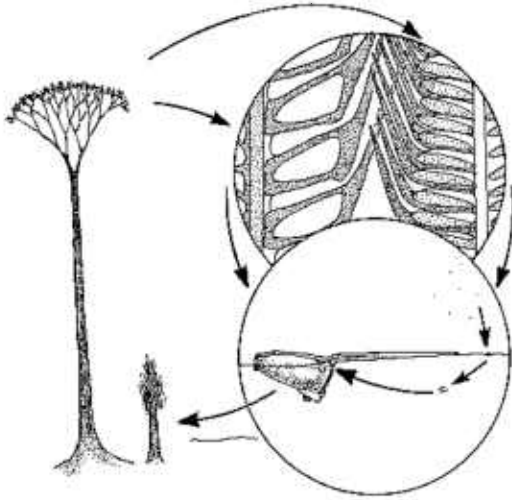


FIGURE 6. Inferred life history of *Lepidophloios* species. Major life cycle attributes include determinate habit and monocarpy of individual trees, separate megasporangiate and microsporangiate cones, and probable aquatic fertilization. Megasporangia were the largest ever to be produced by a lower vascular plant. With one spore per sporangium, and envelopment of the sporangium by sporophyll tissues, these aquacarp (*Lepidocarpon*) were the most complex produced by the lepidodendrids.

branchings. Microsporangia and megasporangia were produced in separate cones although their relative positions, or even if they were produced on the same tree, are unknown. This life history requires an environment free of major disturbances at least for the life of a tree. Given that, in some coals, *Lepidophloios* trees were abundant and *Lepidophloios*-dominated stands were common and repetitive in peat profiles, this tree may have reached its maximum abundance in peat swamps or parts thereof with relatively low disturbance frequencies.

The megasporangiate cones, *Lepidocarpon*, were constructed of a central axis bearing sporophyll units that abscised from the cone axis. These units were morphologically complex, containing a large single functional megaspore and a megasporangium encased in integumentlike outgrowths. The similarity of these structures to ovules has been a subject of considerable discussion (Thomas, 1981); to differentiate them, the term "aquacarp" is suggested to reflect functional aspects of the *Lepidocarpon* on megasporangiate units. Aquacarp morphology suggests aquatic-based reproduction and dispersal (Phillips, 1979). The large distal lamina would have served as a wing to aid in wind dispersal away from the parent tree (Thomas, 1981)

as well as a flotation device (Phillips, 1979). Juvenile sporophytes with exerted stigmarian axes (Phillips, 1979) suggest the potential for anchorage in a water-cover environment. The wide distribution of aquacarp in peat swamps (DiMichele & Phillips, 1985) and the density of *Lepidophloios* stands brings to mind the suggestion of Chaloner & Boureau (1967) that *Lepidocarpon* may have been carried by water and concentrated along margins of water bodies. Massive microspore and aquacarp production, the largely aquatic mode of dispersal, and tolerance of highly stressed physical conditions were the keys to the success of *Lepidophloios* in peat swamps.

ASPECTS OF REPRODUCTIVE BIOLOGY

Each of the lepidodendrid genera exhibited a distinctive combination of reproductive attributes including how cones were borne, cone structure, dispersal-unit morphology, and reproductive timing, as well as characteristic relative abundances of reproductive to vegetative biomass. As determinate and relatively short-lived, arborescent plants, lepidodendrids represent a spectrum of reproductive modes reflected directly in their architectures and autecologies.

Branching in lepidodendrids seems to be geared almost exclusively to reproduction or cone-bearing. The principal possible exception to this may be *Diaphorodendron scleroticum* with its extended branch development (DiMichele, 1981; Wnuk, 1985). Lepidodendrids are separated into polycarpic and monocarpic life histories by the types of branching, lateral versus terminal "crowns," and the associated timing of cone production. *Diaphorodendron* is the only genus that exhibits both polycarpy and monocarpy; aquacarpic *Lepidodendron* (except *L. serratum*) and *Lepidophloios* were exclusively monocarpic; free-sporing *Paralycopodites* and *Sigillaria* were polycarpic (Table 1).

REPRODUCTIVE ALLOCATION PATTERNS

As an approximate guide to relative reproductive allocations, biomass estimates of megasporangiate structures are divided by total aerial litter of a species. This is treated as the relative lifetime megasporangiate output. Despite many vagaries associated with such an indirect measure, based as it is on dispersed structures, these estimates provide a relative quantitative expression of differences. Relative microspore outputs are categorized as overrepresented or underrepresented, based on comparison of importance in peat versus palynological assemblages. It is well known from quan-

TABLE 1. Reproductive allocation patterns of Lycopside trees.

Taxon	Reproductive timing	Lifetime mega-sporangiate allocation (♀/total aerial biomass)	Microspore (♂)/vegetative biomass pattern	Ecology
<i>Diaphorodendron vasculare</i>	Polycarpic	2-4%	<i>Granasporites</i> : under represented	Site occupier; disturbance tolerant
<i>Diaphorodendron phillipsii</i>	Polycarpic	1-2%	<i>Granasporites</i> : under represented	Site occupier; disturbance tolerant
<i>Diaphorodendron scleroticum</i>	Polycarpic	1-2%	<i>Granasporites</i> : under represented	Site occupier; disturbance tolerant
<i>Sigillaria approximata</i>	Polycarpic	3-5%	<i>Crassispora</i> : under represented	Site occupier; disturbance tolerant
<i>Paralycopodites brevifolius</i>	Polycarpic	4-7%	<i>Lycospora</i> : over represented	Colonizer; disturbance tolerant
<i>Lepidophloios harcourtii</i>	Monocarpic	3-4%	<i>Lycospora</i> : over represented	Site occupier; disturbance intolerant
<i>Lepidophloios hallii</i>	Monocarpic	6-7% (19%)	<i>Lycospora</i> : over represented	Site occupier; disturbance intolerant
<i>Lepidodendron hickii</i>	Monocarpic	?	<i>Lycospora</i> : ?	Site occupier; disturbance intolerant
<i>Diaphorodendron dicentricum</i>	Monocarpic	7-8% (22%)	<i>Granasporites</i> : ?	Colonizer; disturbance intolerant

tative biomass estimates of peat assemblages, compared to quantitative microspore floras from the same coals, that certain lepidodendrid genera are consistently either over- or underrepresented in spore floras (Phillips & Peppers, 1984). Some quantitative comparisons have been made by Peppers in Phillips & DiMichele (1981), Mahaffy (1985), and Willard (1990, in press). The *Lycospora* producers are overrepresented and the *Crassispora* and *Granasporites* (*Sigillaria* and *Diaphorodendron*) producers with larger microspores are underrepresented in spore floras.

Polycarpic. Lifetime megasporangiate reproductive allocation in *Paralycopodites brevifolius* ranges from 4-7% in Westphalian-age coal balls. This species was the only bisporangiate, free-sporing type, but was the most prolific polycarpic cone producer, which is consistent with its inferred role as a principal colonizer of disturbed ecotonal sites. This estimate probably is enhanced by more local distribution of cone fragments and megaspores. However, it rivals the megasporangiate outputs of the monocarpic forms, which are generally higher than polycarpic ones.

Sigillaria approximata from the lower Stephanian has a 3-5% megasporangiate allocation, which is also high. This estimate probably is affected by local conditions of accumulation, which could vary markedly within the Stephanian swamps,

in which sigillarias were large and scattered; it may not be a typical estimate where cone fragments are aided in dispersal by sporadic sheet wash or intermittent floods.

Diaphorodendron species, except *D. dicentricum*, had lower reproductive outputs than the other polycarpic species: 1-2% in *D. phillipsii* and *D. scleroticum*, and 2-4% in *D. vasculare*. It should be noted that *D. vasculare* was typically a much smaller tree than any of the other *Diaphorodendron* species in the peat swamps sampled.

The estimates of reproductive allocations per relative units of time are portrayed graphically in Figure 7. *Paralycopodites* is thought to have begun cone formation earlier than other genera, rapidly attained a maximum reproductive output, and sustained that for variable but short life spans. Disturbances in its ecotonal habitats probably often altered the longevity of plants well below determinate limits. *Diaphorodendron* species exhibit the widest range of reproductive life spans; polycarpic ones probably started cone production slightly later than *Paralycopodites*. *Diaphorodendron* is the only genus containing a species with a continuous, low level of cone production over the life span of the trees; *D. scleroticum* represents potentially the longest sustained period of reproduction. Cone production by *Sigillaria* is the only distinctly sporadic or intermittent reproductive strategy detected; it is entirely conjectural how early reproduction

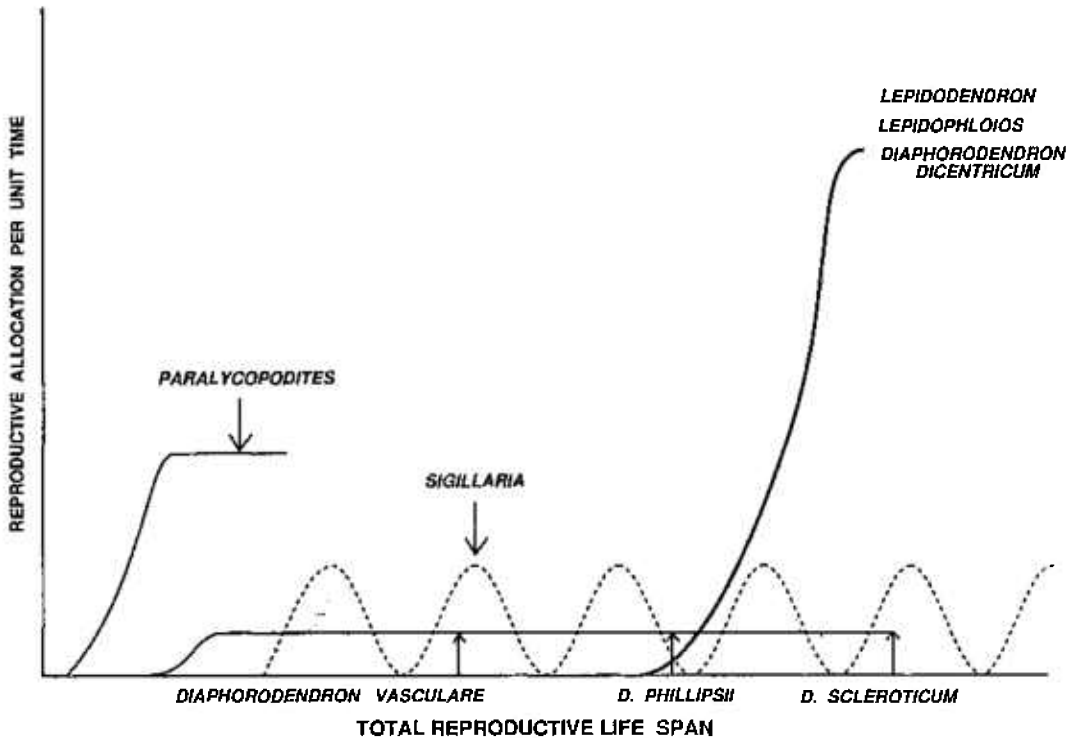


FIGURE 7. Reproductive patterns in the major lepidodendrid genera. Relative total reproductive life span is estimated from known maximum sizes of each species and the location and relative thickness of wood and periderm. *Paralycopodites*, *Diaphorodendron vasculare*, *D. phillipsii*, and *D. scleroticum* were all variants on a polycarpic life history with cones borne on lateral branch systems. The onset of branch production is thought to correspond to the beginning of reproduction. *Lepidodendron*, *Lepidophloios*, and *Diaphorodendron dicentricum* were monocarpic, with cone production limited to the determinate, terminal crown. Reproductive output appears to have been substantial in all of the monocarpic species based on quantitative analyses of coal balls and on morphological studies. *Sigillaria* was a diverse genus that cannot be summarized fully here; morphological evidence points to long life spans and periodic reproductive intervals, but qualitative evidence suggests only moderate productivity during any one event.

began and its establishment phase may have differed substantially from other genera. The symmetrical patterns of its reproductive cycles (Fig. 7) are intended to convey only repeated episodes of cone formation. While it is uncertain how *Sigillaria* cued reproductive cycles, it seems that they were likely geared to relative dry-wet conditions which could involve both seasonal and sporadic conditions of change. It is likely that *Sigillaria* had the potential for reproduction over a longer interval than most other genera. *Sigillaria* apparently produced only pedunculate branches until near its onset of determinate growth, and branching, then, was minimal at most.

Monocarpic. All the monocarpic lepidodendrids with essentially one terminal interval of cone production had aquacarps. They relied on determinate, terminal "crown" branching for cone formation

and dispersal of microspores and megasporangium-sporophyll units. This constituted a massed reproductive phase near the end of the plant's life span. The estimates of megasporangiate allocations are the highest in *Diaphorodendron dicentricum* with 7-8%. *Lepidophloios hallii* is similar with 6-7% and *L. harcourtii* is 3-4%. Data are inadequate to make an estimate for *Lepidodendron*.

In the monocarpic time-abundance curve shown in Figure 7 all the taxa are represented by a common plot because of the lack of a temporal guide for distinct differences in life spans. However, it is likely that life span and timing of reproduction in *Diaphorodendron dicentricum* was distinct from that of *Lepidophloios*, probably geared to colonizing scattered habitats within the less-wet reaches of the swamp, as opposed to those in standing deeper water. The *D. dicentricum* trees do not appear in abundance until Westphalian C and ap-

parently evolved monocarpic habit independently of *Lepidodendron* and *Lepidophloios*, perhaps rising in importance in large, variably disturbed planar swamps.

With the exceptions of *D. dicentricum* and the polycarpic *Paralycopodites brevifolius*, the lepidodendrids are termed site occupiers in the sense that they were generally capable of replacing themselves, conditions permitting. To a certain extent, all the polycarpic forms are regarded as disturbance tolerant because they could generally reproduce at least some before being killed by a major disturbance. The monocarpic forms were intolerant of disturbance levels that prevented the completion of their terminal reproductive phase.

It is not known whether all monocarpic species individually tended to be cohorts and, in turn, mass reproduced at about the same time. This is a cycle that certainly could have developed with *Lepidophloios* and probably differed within species. Despite the inherent drawbacks to such episodes and to monocarpy in general, it should be noted that this kind of reproduction was clearly related to a maximum mass dispersal capability from very elevated heights, utilizing both wind and water.

COMPARATIVE ECOLOGY: PERSPECTIVES AND IMPLICATIONS

At least five unusual circumstances provide important insights into and put constraints on our interpretations of stigmarian lycopsid ecology. The first and most important is that the lepidodendrids radiated within tropical wetlands and were confined to such habitats. That is to say, stigmarian lycopsids were the major trees in the tropical swamp-forests primeval. The pantropical distribution of principal genera resulted from tracking the expansion of the first coal age to its zenith in the Westphalian.

Second, the latest Devonian-earliest Carboniferous radiation of heterosporous arborescent lycopsids coincided with that of seed plants and apparently ferns. However, the lycopsids may have been the most conservative of these, establishing nearly all genera early in their radiation, rapidly in a geologic sense, attaining generic lines of remarkably distinctive bauplans and associated reproductive biology that persisted to extinctions, some over 100 million years later.

Third, only a small number of principal lepidodendrid genera spanned tropical wetlands. The five we have dealt with were widespread, although differentially abundant in different habitats. They occurred in both peat and clastic wetland environments and provide a means to contrast swamp types

(see Gastaldo, 1987), as well as a means of tracking swamp structure over time using dispersed spore floras (see Kosanke & Cecil, 1989; Eble, 1990).

Fourth, exceptional in situ occurrences of swamp plants make the Westphalian one of the highest resolution windows on plant paleoecology in the entire geological record. This includes some of the enormous compression and cast/mold fossils of clastic deposits, the basis for the reconstructions of the trees and forests, and the vast numbers of occurrences of anatomical preservation in coal balls.

Fifth and last, these combined fossil records emphasize the generic paucity of Late Carboniferous tropical swamp floras as a whole, despite their maximum diversity in the Westphalian. Although we have avoided discussing the other kinds of trees that lived in the coal swamps with lepidodendrids, they are vitally important to our perspectives of the comparative ecology of the lycopsids. Every major group was represented, but commonly only by one or two arborescent genera. Thus, there were more genera of lepidodendrids in coal swamps than almost all the arborescent genera of other plant groups combined.

The extinct lepidodendrids and sigillarias have no modern analogues. Yet, they partitioned and characterized nearly the full spectrum of tropical wetland habitats. This is particularly evident in the early Westphalian A of Europe where lepidodendrids totally dominated the vegetation, and where their greatest generic diversity is found in peat swamps. Because the established stratigraphic ranges of the five principal genera extend back to the Tournaisian and Viséan, it is reasonable to hypothesize that partitioning of swamp habitats occurred early in the Carboniferous and perhaps under circumstances where lycopsids were the principal or only arborescent occupants.

It was not until after the Westphalian A that other major groups (cordaites, ferns, pteridosperms) rose to codominant status or even as dominants (cordaites). Such vegetational changes may have taken place at the expense of lycopsids. However, in the late Westphalian D (uppermost Middle Pennsylvanian) of the United States, after most other plant groups had become well established in coal swamps, the five principal genera of lepidodendrids still dominated on a whole coal-swamp basis. Cordaites were the only other plants to hold a dominant ecological position within Westphalian coal swamps, but this was limited to the early Westphalian D and, as far as we know, to the western interior coal region of the United States (Raymond, 1988).

Late Westphalian D peat swamps indicate an

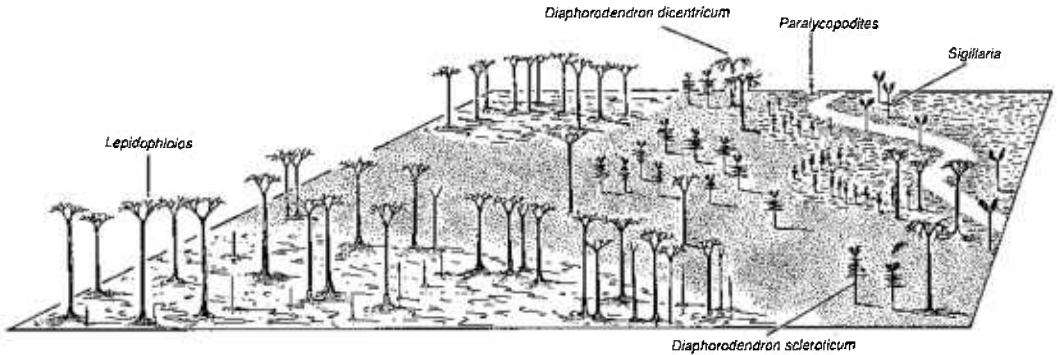
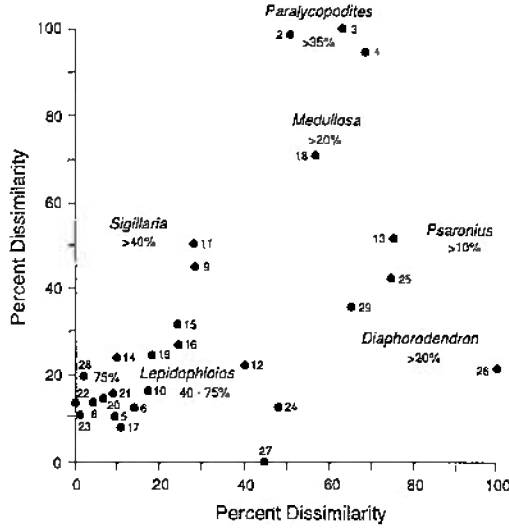


FIGURE 8. Patterns of distribution and association of major trees in the Herrin (No. 6) Coal of Illinois. Ordination, modified from DiMichele & Phillips (1988, fig. 10), is based on a profile of coal balls from the Old Ben No. 24 Mine (numbers refer to profile zones, beginning with 1 at the bottom of the seam). The lycopod distribution revealed in this ordination is characteristic of all late Westphalian D-age coals from the Illinois, Western Interior, and Appalachian coal regions studied to date. The distribution is depicted in the reconstruction: *Lepidophloios* occurred widely, but dominated flooded parts of the swamp (left corner). *Diaphorodendron* trees were site occupiers (*D. scleroticum*: center of diagram) or colonizers (*D. dicentricum*: top center, lower right corner) within parts of the swamp subject to minor disturbance. *Paralycopodites* (small trees along margin of drainage) occupied areas subject to clastic influx and disturbance; they frequently co-occurred with medullosan pteridosperms. *Sigillaria* may have grown along stream margins (sparsely branched trees along drainage margin).

increased diversity and abundance of non-lycopods. In addition, most of the arborescent genera tended to be larger than their antecedents in older swamp floras, including the lepidodendrids. Some lepidodendrid forests became more storied-structured with increased shading by columnar tree ferns and seed ferns in some stands. In the Springfield and Herrin Coals, the best known from coal-ball studies, the habitat partitioning is perhaps even more clearcut because of the associated non-lycopods that tend to cluster repeatedly in assem-

blages with particular lepidodendrids (Fig. 8; Phillips & DiMichele, 1981; DiMichele & Phillips, 1988). While *Lepidophloios* dominated the wettest and lowest diversity forest assemblages, *Psaronius* encroaches such habitats, as well as most others. *Diaphorodendron* species are associated with a variety of taxa but with a minimal overlap with *Paralycopodites* and *Lepidophloios*. *Paralycopodites* is often closely associated with *Medullosa*. In turn, *Sigillaria* is not generally a part of this array of coal-swamp assemblages. It rarely

appears in relative high abundance, and then either with diverse, more non-swamp assemblages of seed ferns and ferns, or as simply repetitive sigillarian debris sometimes mixed with *Diaphorodendron*.

Coal swamps were edaphic islands because of the stressful physical attributes of an organic substrate (DiMichele et al., 1987). The appearances of other tree genera in what were nearly exclusively lycopsid-dominated habitats may reflect exploitation of the "colonizable-space" present at nearly all times in these environments. Drop in relative lycopsid abundance could result simply from the gradual accrual of new taxa that evolved the capacities to live in peat swamps, environments with low interspecific competition.

Our interpretation of such ordinations of profile data as well as gradient traverses (unpublished data) indicates that the key shifts of lepidodendrids in coal swamps are between ecotonal *Paralycopodites* and either *Lepidophloios* or *Lepidodendron*. These end point assemblages appear to define a marginal to deep-water gradient that probably existed for millions of years. The intercalation of *Diaphorodendron* may represent an originally short-term aquacarpic expansion into frequently disturbed environments where other factors preclude effective fertilization and/or dispersal. Most of the *Diaphorodendron* species, including the monocarpic *D. dicentricum*, manifest occupation of habitats with variable frequencies and intensities of disturbances, factors more important than the environmentally restricted conditions that defined the habitat limits of the other major genera. *Diaphorodendron* was probably as important in coal swamps of the Westphalian as *Lepidophloios*, and perhaps more so than *Lepidodendron*. The genus had a broader ecological amplitude because of the species differences in tolerances and reproductive strategies. These differences are still on a theme largely within the more physiologically water-stressed environments, not related to deeper standing water but in conditions of possible brackish influence, frequent edaphic substrate exposure and repetitive dry downs, all indicative of physiological drought stress at different temporal frequencies.

The ecological inferences for *Sigillaria* are quite different from the other "array of four" lepidodendrids. *Sigillaria* was essentially a marginal escapee of wetland environments labeled "swamps" and yet undoubtedly it was one of the characteristic wetland genera. *Sigillaria* represents the most xeromorphic of the lepidodendrids, unless *Sporangiostrobus* turns out to be stigmarian as suggested in Wagner's (1989) reconstruction. *Sigillaria* is so closely associated with the wetland tropics that it has rarely

occurred to us that it may have occupied the drier, seasonally or intermittently wet habitats scattered along the streams and drainage areas where water availability was variable but subject to neither long-term flooding nor long periods of drought. In *Sigillaria* cone dispersal was apparently not so much a matter of high elevation, but of repeated dispersal in the same limited area.

ECOLOGICAL IMPACT ON SWAMP ENVIRONMENTS

The lepidodendrids may have altered their environments in profound ways. Here we consider how stigmarian lycopsids expanded their available habitats and contributed to stability of environments, how they may have affected nutrient and oxygen supply available to other plants, and how they contributed with litter and "self-burial" of roots to literally filling accumulation space and changing the water table of habitats.

The first and most striking comparative ecological feature of stigmarian lycopsids is how they dominated the available peat and water substrates and yet permitted extensive light penetration due to their open canopies. These two ecological patterns are compatible if our suggestions about diffuse photosynthesis are near the mark. They are compatible also with an extensive system of stigmarian axes and radiating appendages, which would act as both baffling and filtering systems in movement of transported sediment, modifying water flow itself. One might think of stigmarians as sort of botanical "beaver dams." If *Lepidodendron* and *Lepidophloios* were part of such a sediment baffling system they would constitute an important means of trapping mineral matter in the water and enhancing their nutrient supply, as well as ultimately adding to the stability of anchorage. The surficial flow of water in such swamps would have been more rapid along waterways unoccupied by impeding vegetation. The likely habitats of these genera extended to those waterways, no doubt utilizing them in reproductive dispersal. From the viewpoint of expanding lepidodendrid habitats, these open water areas were available for occupation up to depths that may have encroached the 2 m limits of semiaquatics and aquatics today. This would have been ideal for buoyant stigmarian appendages and potential exposure to sunlight. In this scenario; standing water is viewed as an area into which swamp plants encroached, particularly in clastic swamp settings. The lepidodendrids in these habitats impeded water and sediment flow, adding to swamp stability and garnering their resources into habitable substrates.

There are important consequences of such environmental alterations. If the flow of water were impeded by baffling and filtering, stigmarian lycopsids, with their dominance of many substrates, would have been a key nutrient filtering system. This amplifies the suspected differences in nutrient requirements between *Lepidodendron* and *Lepidophloios* with the latter more typical of lower nutrient, peat swamps, and the former centered in clastic-rich substrates.

The second aspect ties in with nutrient retention by stigmarian lycopsids. Surficial water, principally runoff from marginal watersheds, is apt to be quite varied in mineral nutrients, O_2 , and CO_2 . The effective acquisition of resources by stigmarian systems may have limited nutrients to other plant groups. In addition, lepidodendrids tend to tie up mineral nutrients with their large physical stature, extensive stigmarian systems, and decay-resistant litter. The most significant component is generally the periderm, parts of which are the most decay-resistant tissues found in peat deposits of the Upper Carboniferous. This sequestering of nutrients in organic matter prevents recycling in already very low nutrient environments, particularly in the *Lepidophloios* habitats and depositional environments. Coal geologists often associate high ash coals with most *Lycospora*-producing lepidodendrids and attribute this to planar swamp, eutrophic environments of habitation. This appears to be, in part, a circumstance of filtering out mineral matter and retarding its recycling by incorporating it into some organic matter that is highly decay resistant. This modifies the nutrient availability for plants that follow on these peat substrates.

Lepidodendrids may have partially structured the Westphalian coal swamps while serving their own peculiar adaptational strategies. The lush reconstructions of Late Carboniferous (Westphalian) lepidodendrid swamps are pictures of environmental uniformity and tranquility, not conveying that such an ecosystem may have been ever on the brink of disaster. These coal swamps were disturbance driven and abiotically controlled. The plants relied on highly dispersible sexual propagules for reproduction and colonization of available habitats. This system of reproduction was responsible for swamp persistence over short-term disturbances and following large areal disruptions where continuity had to be maintained from coal swamp to coal swamp.

We tentatively suggest that tropical Westphalian coal swamps defined a major coal age, in part, because of the ecology of the stigmarian lycopsids. Instead of being planar, eutrophic environmental

indicators, these lycopsids might better be viewed as environmental stabilizers and hoarders of resources. Without these environmental framework builders, Westphalian peat formation may have been substantially diminished. Lepidodendrids formed an important part of the framework of Westphalian coal swamps by contributing to the stability of the wetland habitats and expanding the area of peat accumulation. The extinction of the principal genera in North America is tied perhaps to climatic changes and the consequent collapse of the entire ecosystem. With increasing taxonomic refinement (e.g., Lesnikowska, 1989) extinction can be documented for many other swamp-centered, allied plants. It is reasonable to suggest that it was the environmental importance of lepidodendrids that sustained the Westphalian coal age, and that their extinction, as an array, probably resulted in the loss of the many dependent non-lycopsids.

AQUACARPS

The concurrent radiation of lepidodendrids in wetlands and seed plants almost everywhere else during the latest Devonian-earliest Carboniferous presents unparalleled opportunities for comparison of independent, contemporaneous evolutionary radiations based on different fundamental architectures. Unfortunately, gymnosperm morphology has served as a reference base for assessing organizational grades that relate to wetland ecology. As a consequence, we spuriously, or for brevity of comparison, suggest that lepidodendrids mimicked the seed habit, bipolar "shoot and root" design, and, for want of the concept of the "lycopsid tree habit," "tree" architecture. The last appellation is most justified because of sheer size and a pole frame that usually branched. However, most such comparisons miss the mark in the questions asked because they are framed from preconceived notions that such comparative morphology can be taken out of evolutionary and ecological contexts and reduced to a seed-plant based reference.

A classic example of this, shared by most of us at one time or another, is, "How close did *Lepidocarpon* come to the seed habit?" This diverts the focus from how did it work in the life cycle ecologically to how should it have worked from a seed-plant perspective. Many of us have been taught that the homosporous-to-heterosporous-to-seed habit was the evolutionary sequence and that heterosporous lower vascular plants were stymied at free-sporing heterosporous, a dead end. The dissections of this sequence (Sussex, 1966) indicated a slight spill over to heterangy by some heterosporous lower vascular

plants, but there was not enough compelling data to suggest an alternative concept to the seed habit, along wetland ecological and evolutionary lines. The lepidodendrids demonstrate the further evolutionary elaboration of heterospory in directions other than the seed habit, an elaboration that is best represented by lepidodendrid structures such as *Lepidocarpon* and *Achlamydocarpon*. We have suggested the term aquacarp for these structures, incorporating the propensity for "carpon" names of such structures in wetland habitats. In an evolutionary and ecological sense such structures evolved toward the use of water in ways not found in their lower vascular plant ancestors, just as seed plants escaped from the constraints of aquatically mediated life cycles. In this sense, seeds and aquacarps are similar in grade and convergent in morphology, but are widely divergent in ancestry and function.

Aquacarpic lepidodendrid trees are viewed as the most highly derived, heterosporous lower vascular plants ever to exist within tropical wetlands. Consequently, they offer exceptional perspectives to the importance of heterospory in such environments. A striking feature about the late Paleozoic tropical wetlands is the diversity and relative abundance of heterosporous plants, especially lycopoids of most lineages.

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ADDENDUM

Since this manuscript was edited, the following relevant publications have appeared:

- ROTHWELL, G. W. & J. S. PRYOR. 1991. Development dynamics of arborescent lycophytes—apical and lateral growth in *Stigmaria ficoides*. *Amer. J. Bot.* 78: 1740-1745.
- WINSTON, R. B. & T. L. PHILLIPS. 1991. A structurally preserved, Lower Pennsylvanian flora from the New Castle Coal Bed of Alabama. Geological Survey of Alabama Circular 157, Tuscaloosa. (Plant source of *Lycospora pellucida*.)