



Arborescent lycopsid productivity and lifespan: Constraining the possibilities



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ABSTRACT

One of the most enigmatic components of early terrestrial vegetation was the arborescent lycopsids. Because of the sheer abundance of their biomass in many wetland environments of the Late Paleozoic, they may have been an important variable in the global carbon cycle and climate. However, their unusual structure has invited extraordinary interpretations regarding their biology. One idea that has persisted in the literature for over forty years is that these trees had extremely short lifespans, on the order of ten years. Such an accelerated lifecycle would require growth rates twenty times higher than modern angiosperm trees (and at least 60 times higher than modern lycopsids). Here, we evaluate the morphology and anatomy of lycopsid trees—including aerenchyma, phloem, leaf base distributions, leaf structure, rootlet anatomy, and the demography of the preserved fossils—with comparison to modern plants with some similarity of overall form, most notably the palms. The environmental context of lycopsid trees also is considered in the light of the vegetation of modern water-saturated substrates. It is concluded that such rapid growth would violate all known physiological mechanisms. One hypothetical mechanism that had been proposed to provide for increased carbon fixation, a unique photosynthetic pathway, could not have been viable in these plants and there is no accounting for the increases in nitrogen and phosphorous uptake that would be necessary to sustain enormous rates of carbon fixation. Of the various aspects of lycopsid anatomy and ecology that might militate against this conclusion that productivity was not high, no line of evidence requires a uniquely rapid growth rate for the arborescent lycopsids and several lines of evidence seem to prohibit it. Thus, we conclude that the lifespans of arborescent lycopsids most likely were measured in centuries rather than years. These trees should not be expected to have been unique outliers with physiological function completely distinct from all other tracheophytes. Furthermore, they require no special consideration in the evaluation of Paleozoic biogeochemical cycling. Finally, the conclusion that lycopsid lifespans were an order of magnitude longer than previous expectations invites reconsideration of many other aspects of their ontogeny, physiology, and structure.

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1. Introduction

The largest and most significant evolutionary radiations into new environments or ecologies often have involved a rapid evolutionary turnover whereby the taxa dominant early in the radiation are replaced by a different, more persistent association of taxa. For example, such a pattern is repeated with the Cambrian fauna among marine invertebrates (Sepkoski, 1981), Paleozoic fish and tetrapods (Benton, 1998), and Paleocene mammals (Alroy, 1999) and is also seen in the earliest Silurian through Carboniferous vascular plants (Niklas et al., 1985; Knoll, 1986). This limited evolutionary continuity with later, better-known biotas can complicate dissection of the biology and ecology of the extinct lineages involved in these initial radiations. One of the last and most morphologically complex examples during the early history of vascular

plants was the arborescent lycopsids, often segregated from the Isoetales as the “Lepidodendrales” (DiMichele and Bateman, 1996). This group appeared in the Carboniferous and reached its maximal diversity in Pennsylvanian-age wetlands. The unusual morphology and anatomy of the arborescent lycopsids has invited speculation regarding many aspects of their biology that extends beyond the bounds of what has been documented in living plants. Here, the focus will be on evaluating suggestions of a highly accelerated lifecycle (Bierhorst, 1971; Phillips and DiMichele, 1992; Bateman, 1994).

Different taxa among the arborescent lycopsids varied from 10 to 50 meters in maximum height (Thomas and Watson, 1976; Wnuk, 1985, 1989) and from a decimeter to more than two meters in trunk diameter (Walters, 1891; Thomas and Seyfulla, 2015) (Fig. 1). They could be polycarpic or monocarpic (DiMichele and Phillips, 1985). Some bore serially produced, progressively abscised, lateral plagiotropic branches on their dominant orthotropic trunk (Wnuk, 1989; Thomas et al., 2010; DiMichele et al., 2013); others had an orthotropic trunk that remained

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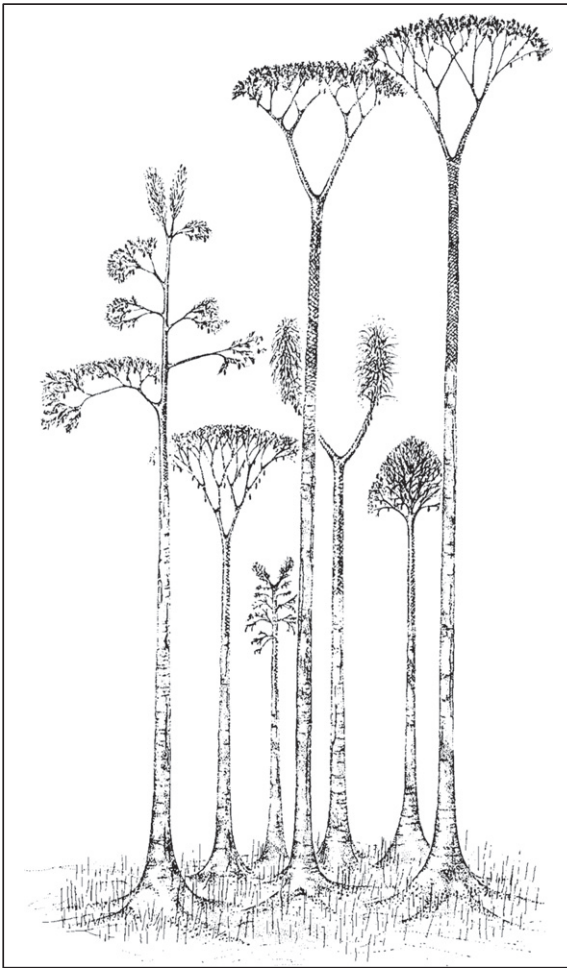


Fig. 1. Reconstructions of major arborescent lycopsid trees. Left to right, *Diaphorodendron scleroticum*, *Lepidophlois hallii*, *Paralycopodites brevifolius*, *Synchysidendron* sp. (note, later research has altered this reconstruction, see DiMichele et al., 2013), *Sigillaria* sp., *Diaphorodendron vasculare*, *Lepidodendron* sp. From Bateman et al., 1992, used with permission of the Missouri Botanical Garden. Mary Parrish, Smithsonian Institution, artist.

unbranched until a few distal dichotomies at the end of their ontogeny, associated with the onset of reproduction (Andrews and Murdy, 1958; Eggert, 1961; DiMichele and Phillips, 1985; Bateman, 1994; Opluštil, 2010). All taxa tended to have a relatively small amount of secondary xylem that was highly efficient in water conduction (Cichan, 1986) but played little role in stem support (Fig. 2). Instead, thick, peripheral secondary cortex, or periderm (Williamson, 1872) of possibly water-resistant chemical composition (Collinson et al., 1994; Boyce et al., 2010a) provided the structural support (Speck, 1994). None are known to have had secondary phloem (Eggert and Kanemoto, 1977; Cichan, 1985). Leaves were linear and varied among taxa, from small awl-shaped forms in plants such as *Paralycopodites* and *Bothrodendron* (DiMichele, 1980; Thomas et al., 2010), to narrow, elongate forms a meter or more in length borne proximally on the main trunk in most of the *Lepidodendraceae* and *Sigillariaceae* (Graham, 1935; Kosanke, 1979; Rex, 1983). Leaves had few stomata and were weakly vascularized. Some were anatomically simple while others had extensive sclerenchyma. Leaves were closely packed on the stem and their abscission left persistent, taxonomically distinctive leaf bases (Fig. 2B) that were diamond, lozenge, or hexagonally shaped (Bateman et al., 1992), although these leaf bases could be sloughed off in the largest/oldest stems of some species, leaving an exposed surface of periderm or other cortical tissues at varying levels (Thomas, 1970; Wnuk, 1985; Bateman et al., 1992; Gensel and Pigg, 2010; Opluštil, 2010). The rooting systems of these plants, referred to as *Stigmara*, were distinctly



Fig. 2. Lycopsid vegetative structure. A. *Diaphorodendron vasculare*, stem base cross section. Wood cylinder (W) is small but highly efficient at water conduction. Note the small primary xylem cylinder. There is no secondary phloem. Secondary cortex/periderm, the main support of the stem, is thick and somewhat collapsed and compressed. Murphysboro Coal, Middle Pennsylvanian, Indiana. USNM specimen 458251 (cellulose acetate peel of coal ball in the collections of the University of Illinois). From (DiMichele and Phillips, 1994), used with permission of Elsevier. B. Trunk of *Lepidodendron* sp. with leaf cushions surrounding the entire girth of the stem. Field Museum of Natural History specimens PP52325 and PP52326. Top scale bar increments in centimeters. C. *Stigmara ficoides* main axis with attached lateral rootlets. Underclay beneath the "Cottage coal", a presently informal name used for a coal bed above the Middle Pennsylvanian Baker Coal, Desmoinesian age, Illinois.

biartite (Fig. 2C), consisting of dichotomous major axes on which were borne helically arranged lateral appendages or "rootlets" (Frankenberg and Eggert, 1969; Eggert, 1972). At least in some cases, the rootlets were produced by a ring meristem located behind the immediate apex of the main axis (Rothwell, 1984). Because of this appendicular relationship to the main axis, the surficial rootlet attachment points on adpressed or cast specimens, and leaf-like rootlet anatomy

(Williamson, 1887; Stewart, 1947), rootlets and their parent axes frequently have been thought of in a manner paralleling—or directly homologous to—leaves on the stem. The entire root system was aerenchymatous (Fig. 3A). In the main axes, the pith region of the vascular core was either parenchymatous or hollow. In addition, the middle cortical region of the main axis was composed of thin-walled tissue that either broke down during the life of the plant or shortly after death (Fig. 3A). Cortical airspaces were continuous with those of the leaf. The cortical region of rootlets also was largely occupied by an air cavity, although rootlet and main-axis air cavities were not directly connected due to a complex pad of sclerenchyma and parenchyma, sometimes supplemented by secondary cortex/periderm (Stewart, 1947).

These trees could be so abundant in their environments as to represent a volumetric majority of the biomass in many wetland ecosystems (Calder et al., 2006), but especially peat/coal forming habitats (Phillips et al., 1985), particularly in the Carboniferous, a time when more coal was deposited than at any other point in Earth history (Bernier and Canfield, 1989; Bernier, 2003). Because of this abundance, understanding of their biology could appreciably impact understanding of coal accumulation, the carbon cycle, sedimentary processes, and perhaps even climate (Collinson and Scott, 1987; Collinson et al., 1994; Bernier, 2004; Cleal and Thomas, 2005; Boyce et al., 2010a; Davies and Gibling, 2011; Davies et al., 2011; Gibling and Davies, 2012). This abundance has left us with a rich tree-lycopsid fossil record; however, that record indicates a complicated and unusual biology that is not easily resolved and that possesses no modern equivalents (though comparison to modern *Isaetes* may be useful for some attributes, such as rootlet development).

Estimates of the lifespans of these trees serve as examples of the complex ambiguity that surrounds them. Lifespans of the large tree forms have been estimated to be extremely short—10 to 15 years (Phillips and DiMichele, 1992), if not even less (Bierhorst, 1971). Such fast lifecycles, however, would impose extreme constraints upon other aspects of the biology of these large trees. Here, we explore the viability of these estimates and consider other independent lines of evidence that might inform upon the lifespans and growth rates of the arborescent lycopsids.

2. Original argument for a short lifespan

The expectation that the arborescent lycopsid life cycle must have been unusually fast ultimately appears to come, albeit indirectly, from

the observation that there are almost no small or intermediate sized individuals linking known tiny embryos (Phillips, 1979; Stubblefield and Rothwell, 1981) with the widely known and reported large trees (e.g., Phillips and DiMichele, 1992; Thomas and Watson, 1976; Thomas and Seyfulla, 2015; Walters, 1891). From this observation, it was argued both directly and indirectly that an absence of small individuals indicates rapid growth, high productivity, and an accelerated life cycle (Bierhorst, 1971); a 10 to 15 year lifespan (Phillips and DiMichele, 1992) was presented as a general illustration, rather than as a firm quantitative estimate. [Other lines of argument that were considered in formulating this estimate are considered in later sections: 4.2, 4.3, 4.4.]

The empirical lack of growth stages between miniscule embryonic and gigantic mature phases of lycopsid trees (Fig. 4) need not reflect rapid growth, however. For example, such an observation may simply be a consequence of demography: local disturbance history, discrepancies between juvenile and adult mortality rates and reproduction/recruitment history will strongly affect the age structure of any given population. Such factors even may produce different age structures for different populations of the same species, as highly evident in human populations. Even if any demographic issues are put aside and two species are considered that do have profoundly different lifespans, then that would still provide no clear expectation of which species should involve more mature individuals; it would not be the overall length of the lifecycle that matters, but the proportion of the lifecycle spent as a juvenile. Thus, even if *Lepidodendron* were a “normal” tree in every way, aside from possessing a 10 year lifecycle, then still presumably the first year would have been as a recognizable sapling: yet 10% of the trees are not juveniles, as would be expected under such a model. A rapid lifecycle, therefore, would not resolve the problems of lycopsid biology. This does not require that the intuition of a rapid lifespan is incorrect, only that the lifespan of arborescent lycopsids cannot be constrained by the size distributions of fossils.

3. Can the productivity requirements of a short lifespan be satisfied?

Cleal and Thomas (2005) generated per tree and per hectare estimates of the total carbon budget of a Carboniferous swamp forest by combining volume calculations for an average lycopsid tree with empirical measures of tissue carbon densities (Baker and DiMichele, 1997) of the periderm and wood expected to represent the greatest proportion

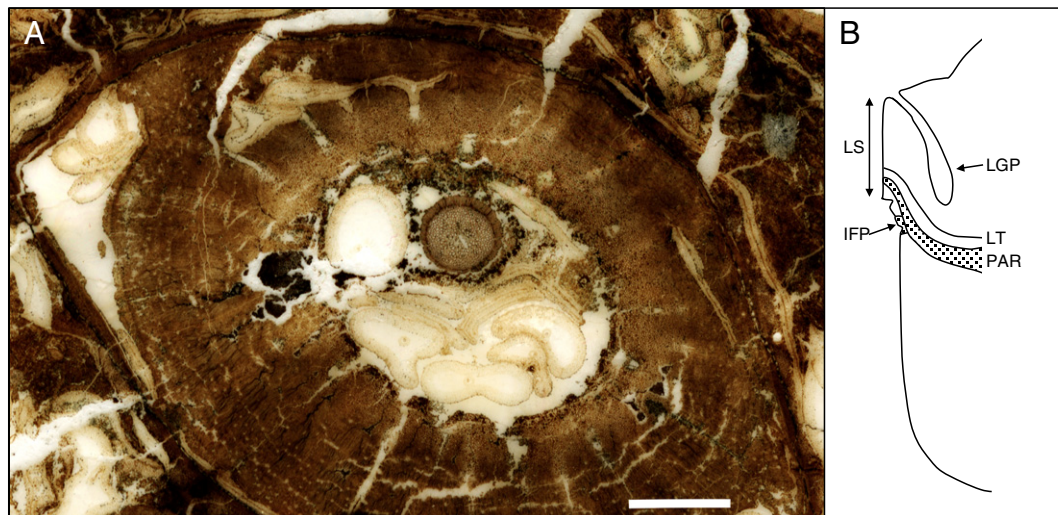


Fig. 3. Aerenchyma forming potential of lycopsid tissues. A. Cross-section of a *Diaphorodendron vasculare* deciduous lateral branch of aerial axis showing a prominent cortical cavity between central wood and peripheral periderm, although it is unclear how much cortical decay is *pre-* versus *post-mortem*. As part of a peat substrate, the air cavities in this stem were subsequently filled with the stigmarian rootlets of a later tree. The rootlet cross-sections, which are thin walled and preserved more faintly than the *Diaphorodendron* axis, are also distinctly aerenchymatous. From the Cayuga locality of the Murphysboro Coal, Indiana. B. *Lepidodendron hickii* longitudinal section of a leaf cushion showing external connectivity of parichnos aerenchyma system. LS = leaf scar, LGP = ligule pit, LT = leaf trace, PAR = parichnos, IFP = infrafoliar parichnos. Redrawn from (DiMichele, 1983).

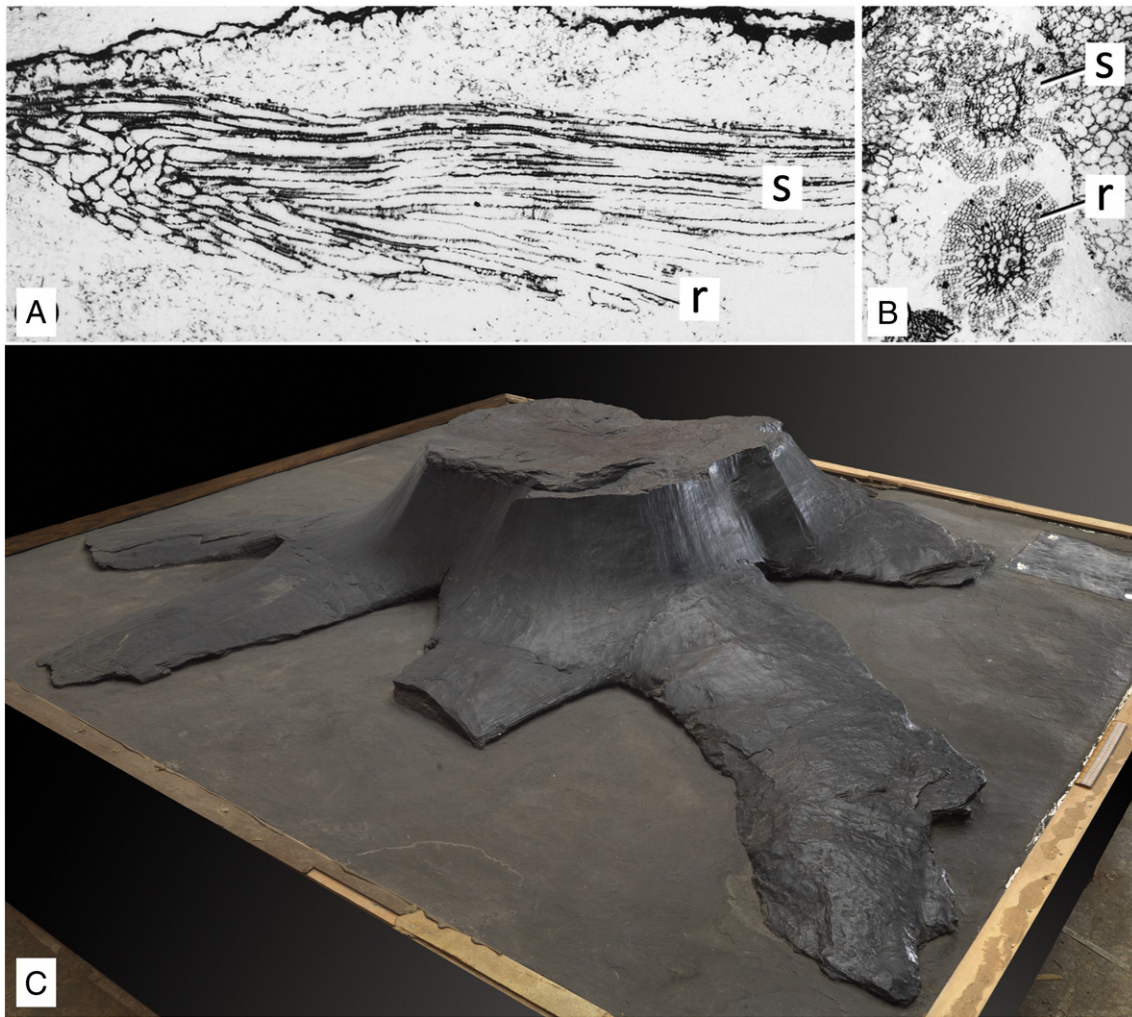


Fig. 4. The opposite ends of the tree lycopsid growth trajectory. A. Longitudinal section through an embryonic arborescent lycopsid of *Lepidophloios* sp. s = shoot, r = root. B. Cross section through an embryo of *Lepidophloios* sp., s = shoot, r = root, note the primary xylem present in the shoot and lacking in the root, and secondary xylem in both. C. Lycopsid tree stump formed following tree death, USNM specimen 34989. Scale bar is 12 inches. (A, B from (Rothwell et al., 2014), used with permission of the Botanical Society of America).

of tree carbon allocation. A ten-year lifespan was then assumed in order to calculate annual productivity from that total carbon content. The productivity value resulting from this calculation is high, almost 20 times higher than modern angiosperm-dominated tropical rainforests and almost two orders of magnitude higher than actual living lycopsids (Brodribb et al., 2007). This productivity estimate was then used to calculate that the waxing and waning of forest area occupied by such fast growing trees would have had a 2–5 ppm/year impact on atmospheric CO₂—an impact as large as that of modern anthropogenic forcing (e.g. Sabine et al., 2004). Such an extraordinarily high productivity estimate might be taken as a persuasive argument that the lifespan of these trees must have been considerably longer than ten years. Tree sizes are relatively well known. Tissue proportions are more speculative, but the carbon content is relatively uniform across the relevant tissue types—wood and periderm differed by only 20% and no sampled tissue differed from wood by more than 50% (Baker and DiMichele, 1997). Thus, changing the assumed proportions of lycopsid tissues could accommodate no more than a 50% decrease in productivity, not a 2000% reduction. The remaining variable in the productivity calculation is tree lifespan. Rather than ten years, a lifespan of hundreds of years would be needed if productivity requirements were to be brought down to a level comparable to even the most productive of living plants.

The short-lifespan interpretation, based on the above reasoning, would require a plausible mechanism for greatly elevated productivity. Productivity potential should increase when atmospheric CO₂ is high

and/or O₂ is low (Beerling and Berner, 2000; Boyce and Zwieniecki, 2012), however Carboniferous CO₂ concentrations are thought to be as low as they are now (McElwain and Chaloner, 1995; Berner and Kothavala, 2001; Beerling et al., 2002; Royer et al., 2004; Berner, 2006) and O₂ levels may have been higher (Beerling and Berner, 2000; Beerling et al., 2002; Berner, 2006; Glasspool and Scott, 2010) suggesting that Carboniferous productivity should have been comparable to modern levels or lower, not higher. Furthermore, even the most favorable atmospheric compositions are not expected to result in more than a factor of two or three increase in productivity over modern maximum levels (Beerling and Woodward, 1997; Franks and Beerling, 2009; Brodribb and Feild, 2010) and even that more modest degree of CO₂ fertilization may be limited largely to the angiosperms (Boyce and Zwieniecki, 2012). An increase in growth and assimilation rates by a factor of twenty or more would require a unique mechanism outside of any known physiological response common to other plants.

A mechanism for increasing primary production in arborescent lycopsids has recently been suggested: the scavenging of CO₂ from decay processes in the organic-rich substrates of these trees via a network of internal gas-filled channels allowing CO₂ absorbed by the rooting structures to diffuse up to the leaves (Green, 2010). This suggestion extrapolates from the demonstration of the build up of CO₂ in internal spaces during dark periods in aquatic and semi-aquatic species of the small living lycopsid *Isoetes* (Keeley, 1987, 1998), some species of which have no stomata and no visible means of CO₂ absorption from

the atmosphere. However, as important as diffusion is at the micron to mm-scale, such as within a cell or from stomata to mesophyll within a leaf, diffusion could not operate effectively over the forty or fifty meters of a lycopsid tree from the rootlets through the *Stigmaria* rooting system and aerial trunk up to the leaves. In the most generous of scenarios, one may assume that 50% of the cross sectional area of the trunk is dedicated to airspace for diffusion, that a continuous airspace existed between the rooting system spaces and the shoot (thus ignoring the tissue barrier between stigmarian rootlets and the main axis), and that there was a CO₂ concentration gradient of 100,000 ppm in rootlet airspaces (Barber, 1961) diminishing to 100 ppm in the leaf. Under these assumptions, and using the most simplified and idealized equation for Fick's Law of Diffusion,¹ an estimate of approximately 200 g of carbon would be made available to the leaves per year via diffusion. Using the Cleal and Thomas (2005) estimate of *Lepidodendron* carbon content, it would then take more than 10,000 years to grow a tree. Any correction of the relevant parameters—less than 50% of the trunk dedicated to airspace, less extreme *Stigmaria* CO₂ concentrations, less than 100% conversion to photosynthate of the CO₂ reaching the leaves—should only serve to increase that estimate of tree life span.

Convection through internal airspaces can be found among modern aquatic and wetland plants, with mechanisms including the negative pressures generated by the Venturi effect as external winds pass over the plant or the positive pressures generated by the humidification of drier atmospheric air entering via the stomata (Beckett et al., 1988; Armstrong et al., 1992; Vogel, 1994; Armstrong and Armstrong, 2009; Raven, 2009). In addition to stomata, however, the tree lycopsids also possessed internal aerenchymatous channels through the periderm and leaves, the so-called parichnos (Bertrand, 1891), generally presumed to be aerating strands (Jeffrey and Wetmore, 1926; Hook et al., 1972). These strands ran internally from the middle cortex of the stem through the leaves, and were exposed on the outer surface of the stem following leaf abscission. In addition, in the Lepidodendraceae s.s. (DiMichele and Bateman, 1996), the parichnos strands branched just before the point of leaf attachment to the leaf cushion, the lower channels appearing as external parichnos openings immediately below the point of leaf attachment (Fig. 3B). Thus, the open connection to the exterior presented by the external parichnos and by the post-abscission parichnos openings should have been compatible with Venturi effects. This open connection, however, would have likely violated a key requirement of humidity-induced convection, that positive pressures generated as atmospheric air is humidified in the photosynthetic tissues not be lost to immediate backflow to the atmosphere (Armstrong and Armstrong, 2009).

Despite the potential that parichnos offer for connection of the plant's interior to the atmosphere, any form of convection will ultimately depend on a through-flow of gases (Beckett et al., 1988), of which the arborescent lycopsids may not have been capable. In those modern plants where convection has been demonstrated, points of gas entry and egress are both required. This may entail flow in and out through different aerial stems or leaves, or even different areas of the same leaf (Große, 1996), but in no case does it resemble the closed circulatory system of an animal. For example, convective flow through *Equisetum* involves the venting of humidity-induced pressure developed in photosynthetically active axes through the broken off stubble of older axes, thereby ventilating the rhizome connecting successive aerial axes, but no convection is seen in those *Equisetum* species where their aerenchyma architecture does not provide for through-flow of air currents (Armstrong and Armstrong, 2009)—the mere presence of air channels

in all *Equisetum* does not mean that all experience convective airflow. Similarly, airflow may well have been possible out of (or in to) the parichnos of the distal parts of the arborescent-lycopsid aerial axis, and—if the disintegration of the middle cortex of the axes was during the lifetime of the plant—a continuous air space may have existed through the stem and rooting systems. *Stigmaria*, however, appears to have been a dead end with no capacity to provide the second vent needed for convective airflow. Stigmarian rootlets would be the obvious candidate capable of reaching to and venting to the atmosphere even if the stigmarian axes were submerged. However, a pad of tissue at the base of each rootlet, the so-called rootlet cushion, separated the rootlet airspace from that of the parent axis (Stewart, 1947), thereby preventing convective flow. Convective internal airflow would be required to bypass the inefficiencies of diffusion in order to have any CO₂ available in the substrate reach the leaves, but arborescent lycopsid anatomy is not consistent with that convection.

More problematic, regardless of how the CO₂ is transported once within the body of the plant, is the rate of CO₂ diffusion in water, which would mediate any transfer of CO₂ from the substrate into the root system. Diffusion of CO₂ is 10⁴ slower in water than in air (Vogel, 2012); all other things being equal, the last 3 mm of aqueous diffusion of CO₂ through the rootlet tissue into the plant would be as slow as 30 m of diffusion through internal air channels within the plant. [As with convection, the large total surface area of each tree's stigmarian rootlets might have mitigated some of the challenges of that aqueous diffusion to the internal airspaces, but the pad of tissue separating rootlet and axial airspaces (Stewart, 1947) would instead require an additional barrier of aqueous diffusion through that tissue for any transport between the two airspaces.] Thus, even if active convection through the air channels were available, this would not alleviate the difficulties attendant on CO₂ entry to the aerenchyma network in the first place. It is notable that this concern does not apply in the opposite direction: the widespread occurrence of aerenchyma in wetland plants is more typically thought to facilitate movement of O₂ down from the atmosphere rather than CO₂ up from the waterlogged substrate, so that the source does not involve an aqueous diffusive step.

Airspaces could plausibly have been involved in the local salvaging of metabolic CO₂ from the respiration of adjacent tissues within the plant (Raven, 1970). However, low net productivity would be indicated were such recycling to have provided a substantial fraction of the overall CO₂ used in photosynthesis. Consistent with living plants where the scavenging of metabolic CO₂ is important, such as CAM plants (Griffiths et al., 1989), the implication would be that the arborescent lycopsids were like other slow growing tolerators of stress, not exceptions to these general physiological rules. If any function ultimately can be assigned to parichnos, it may have to be something of such a limited extent as metabolic recycling. This is suggested by the anatomy of several phylogenetically basal groups of the arborescent lycopsids (Bateman et al., 1992) that had parichnos systems but had neither leaf abscission nor external (infrafoliar) parichnos. Their parichnos system therefore was strictly internal. Thus, the plesiomorphic function of the parichnos system—whatever it may have been—appears not to have been associated with exposure of the internal aerenchyma channels to the external environment.

All of the above only address the need for a twenty-fold increase in CO₂ assimilation rates in order for a short lifespan to be a possibility for arborescent lycopsids, but no organism is made only of carbon. If a hypothetical mechanism for vastly increased carbon fixation were available, it would not address the need for corresponding increases in nitrogen and phosphorous uptake, both often being limiting in wetland habitats (Mitsch et al., 1979; Day, 1982; Bowden, 1987). In part, wetland environments often can be stressful and unproductive for vascular plants specifically because of the limited availability of these nutrients to root systems growing in waterlogged, anoxic substrates, a problem exacerbated on peat substrates (Schlesinger, 1978) and in still water and ombrotrophic habitats (Mitsch et al., 1979; Brinson et al., 1980;

¹ $\frac{m}{t} = -DS \frac{C_1 - C_2}{x}$, where m is mass, t is time, D is the diffusion coefficient, S is the cross-sectional area of the diffusion path, C_1 and C_2 are concentrations of source and sink, and x is the path length. The use of this equation is an oversimplification intended only as an order-of-magnitude illustration of the inefficiency of diffusion at larger spatial scales. More complex calculations would be unwarranted given the poor constraint of parameter values. For detailed discussion of diffusion in plants, see: Vogel, S., 2012. The life of a leaf. Chicago: University of Chicago Press.

Page et al., 1999). The absorptive organs of arborescent lycopsids were rootlets that were a few millimeters to a centimeter in thickness and lacked root hairs entirely (Figs. 2C, 3A). Some potential for fungal symbiosis has recently been demonstrated (Kring et al., 2011), but appears to have been limited to middle cortical tissues lost to airspace formation early in rootlet ontogeny. As a result, for a rootlet that is 6 mm in overall diameter with a 4 mm-wide central air cavity, the surface area for absorption relative to overall volume would be at more than a 300-times disadvantage relative to a 10 μ -wide root hair and more than a 1000-times disadvantage relative to a 3 μ -wide mycorrhizal hypha. To be sure, root hairs and mycorrhizal associations are also less prevalent—although not absent—in modern wetland plants (Romberger et al., 1993; Smith and Read, 1997; Khan, 2004), but the anatomy of the arborescent lycopsids is consistent with this limitation rather than presenting any obvious anatomical solution. Thus, at least as much as is the case for other stress-tolerant vascular plants living in nutrient-poor wetland environments, carbon fixation likely would have been secondary to other, much larger nutrient limitations on growth.

4. Other potential constraints on lifespan

No known physiological mechanisms could approach the productivity rates necessary for arborescent lycopsids to have had a rapid lifecycle. This conclusion is supported all the more so by a low-CO₂/high-O₂ atmospheric composition that would have been unfavorable for carbon fixation and by stagnant, waterlogged substrates that would have limited phosphorous and nitrogen uptake. This argument is deemed adequate to reject rapid growth in the arborescent lycopsids. What remains to be seen is whether any aspects of lycopsid structure might militate against that conclusion. Do any aspects of their form, ecology, or environmental context require reviving the possibility of very rapid growth or are they consistent with being slow growing, stress tolerant plants?

4.1. Leaf base crowding

A 10 to 15 year lifespan for arborescent lycopsids would require 3 to 4 m of growth per year in the largest taxa. Where such rapid rates of extension do exist, they are typically associated with climbers freed from the need to provide their own structural support. Greater than 2 m of growth per year is known among living self-supporting plants, but rapid growth is typically accommodated by extensive internode elongation, e.g. bamboo, the bolting reproductive axes of rosette plants, the long shoots of *Ginkgo* relative to the short shoots. For example, the presence or absence of internode elongation is recognized to be of central developmental and ecological importance within the palms: rattan palms may grow 6 m in a year with that growth accommodated by only 3 or 4 fronds separated by internodes up to 2 m long, whereas slower growing palms without internode elongation may take 80 years to achieve the same stem growth (Henderson, 2002). Overall, a sampling of palms with internodes yields an average of 40 cm/year of stem growth, whereas those without internodes average only 10 cm/year (Henderson, 2002). Most arborescent lycopsids have no elongation at all between their persistent leaf bases. The one exception would be some forms of *Sigillaria*, which have zones of modest cm-scale elongation between leaf bases alternating with areas without elongation (Thomas, 1972). Although not providing any quantitative constraints on growth rates, the little to no separation of leaf bases in most arborescent lycopsids, including the largest forms (Fig. 2B), is qualitatively more consistent with slow stem growth, e.g. rosette plants, cycads, the short shoots of *Ginkgo*. The external morphology of arborescent lycopsids does not conform to what could be expected of plants with extremely rapid stem growth.

4.2. Absence of secondary phloem

Phloem cells are typically short-lived, lasting only a few years (Tomlinson, 2006). The lack of secondary phloem—as in the arborescent lycopsids—might be expected to limit the longevity of any single stemmed tree. Since the sieve elements must survive and remain functional over the entire lifetime of the plant, their inevitable failure might be expected to put a firm upper limit on lifespan. Palms, however, lack secondary growth, but provide examples of strikingly long-lived primary tissues nonetheless. Age is difficult to assess in palms without wood rings to count and where the continuous metabolic activity of living tissues would complicate any attempt to use ¹⁴C dating, but historical documentation of individual trees does exist. Whereas most trees may only live for several decades (Henderson, 2002), that does not present an upper limit. Although some of the oldest known palms (e.g. the *Chamaerops humilis* specimen, known as the “Goethe Palm” planted in 1568 in Padua) are multi-stemmed so that no individual stem lives very long, the documented lifespans of single-stemmed species can approach or surpass 200 years: a specimen of *Jubaea chilensis*, growing in a Kew Gardens greenhouse was planted in 1843 and a specimen of *Elaeis guineensis* at Bogor Botanic Gardens is slightly older (Tomlinson, 2006; Tomlinson and Huggett, 2012). Another long-lived single-stemmed palm is documented here to have lived exposed in an urban street setting at the Palm Tree Mosque in Capetown, South Africa. Already a substantial tree in 1840 and, presumably, at the mosque’s inception in 1807 (Toffa, 2004), this plant survived past 1988 (Fig. 5). Beyond the direct documentation of these long-lived individuals in cultivated environments, extrapolations from leaf scars and frond lifespans (discussed further in Section 4.5, below) suggest—albeit less directly—that individuals of some palm species may live more than 700 years in their natural environments (Uhl and Dransfield, 1987). Thus, palms demonstrate that individual plant cells can live a remarkably long time—at least 200 years, presumably much longer—indicating that the aging of these cells will not necessarily truncate potential lifespan (Tomlinson, 2006).

Even if phloem were to impose some minor constraints on maximum lifespan in palms, those constraints may not apply to arborescent lycopsids. The longevity of palm sieve tubes is all the more remarkable because they are enucleate, but living lycopsids including *Lycopodium*, *Selaginella*, and *Isoetes* maintain degenerate nuclei in their sieve cells that may presumably contribute to continued cell function (Burr and Evert, 1973; Kruatrachue and Evert, 1974; Warmbrodt and Evert, 1974). Although the phloem of the arborescent lycopsids is almost never preserved, their phylogenetic relationships suggest this characteristic of persistent phloem nuclei may well have applied to them as well, perhaps making phloem longevity even less of a concern. Furthermore, a lack of secondary phloem is thought to be a primary limitation preventing palms from occupying environments prone to frost (Tomlinson, 2006), but some early tree lycopsids may have lived in close proximity to the ice front of the Late Devonian glaciation recorded in Appalachian basin strata of the Eastern United States (Brezinski et al., 2009; Brezinski et al., 2010). As with certain New Zealand tree ferns known to grow in the immediate vicinity of modern glaciers (Lindsay, 1868), a lack of secondary phloem may provide less of a constraint on ecology and lifespan that often surmised.

A final consideration regarding the absence of secondary phloem in arborescent lycopsids is the observation that even their primary phloem is generally quite restricted throughout the body of the plant (Phillips and DiMichele, 1992). Arborescent lycopsids have either long, deciduous leaves, or short, permanently retained leaves, and nearly all have sporophylls with prominently leafy distal laminae. Given the limited amount of phloem (Fig. 6A, B), most of the photosynthate generated by leaves and sporophylls may have been used locally, either in apical growth, periderm production, or in sporangia and spores, with only limited longer distance transport. Such local use and limited translocation has parallels in other plants, where sepals, for example, have been shown to contribute substantially to flower development (Bazzaz



Fig. 5. Palm Tree Mosque, Cape Town, South Africa—Longest documented lifespan of a palm (taxon indeterminate). A. 1840, drawing by N. Gertse, as reprinted by Toffa (2006). The two large trees would date at least to the founding of the mosque in 1807 and may be older than the building itself, constructed in 1788, based on their sizes and growth rates over the subsequent 200 years. B. 1915, photo by A. Elliot. C. 1988, photo by J. Szymanowski. The shorter tree is a 1966 replacement of one of the original two trees. D. 2012, photo by Discott. The only tree remaining is the 1966 replacement (of a different, faster growing species than the original trees). A photo (not shown) on display inside the mosque shows both original trees in 1876 with heights appropriately intermediate between the 1840 drawing and 1915 photo. With the tree now dead (by 2008, based on other photos), species identification is not available. [All images available in the public domain or via Wikimedia Commons (<http://commons.wikimedia.org>).]

et al., 1979). The leaf-like anatomy of stigmarian rootlets has even led to the suggestion that the rooting systems of these plants may have been self-sustaining, with upwardly directed rootlets being emergent from the substrate and functional as photosynthetic appendages (Phillips and DiMichele, 1992). The trunk itself connecting proximal rooting system and the distal growing apex may have had relatively limited metabolic demands: wood was certainly dead at maturity, periderm also may have been (although this is not certain and may well have been variable given the variability of periderm structure: (Bateman et al., 1992; Eggert, 1961; Gensel and Pigg, 2010), and much of the intervening cortex appears to have been subject to degradation and aerenchyma formation. To the extent that these inferences are persuasive, the limited carrying capacity of the phloem system may have constrained *growth rates* throughout the plant but would not constrain *longevity*.

4.3. Survival until reproduction in monocarpic taxa

A determinate, monocarpic life cycle, characteristic of several major lycopsid taxa (Phillips, 1979; DiMichele and Phillips, 1985; Phillips and DiMichele, 1992) is one that entails considerable risk; pushing reproduction to terminal phases of a long life raises the possibility of pre-reproductive death; various lines of evidence (Gastaldo, 1986) suggest that lycopsid trees often grew in disturbed settings where blow downs, fires, and intense floods (DiMichele et al., 2009) might preclude

completion of a long life cycle. Yet, whereas prostrate lycopsid trunks are known in abundance, immature crowns or unbranched trunks with apices (Fig. 7A) are essentially unknown with very few exceptions (Goldenberg, 1855; Kosanke, 1979). This absence could be inferred to suggest that nearly all trees completed their life cycles prior to death (Bateman, 1994). Thus, the success of monocarpic lycopsid trees has also been taken as evidence of a highly accelerated lifecycle (Bierhorst, 1971). However, the trunks of the monocarpic taxa were unbranched until the reproductive phase at the end of their lifecycle (Fig. 7B, C). Thus, these trees would have presented, little profile to the wind (Niklas, 1998), and would have had low risk of blow-down prior to formation of the branched crown. Furthermore, it is the leaves of a tree in aggregate that provide most of the drag that can result in windfalls during storms (Vogel, 1994), and leaves abscised at some point in the larger monocarpic lycopsid taxa. Indeed, uprooted lycopsid trees are unknown to us from either the literature or field observation, although this does not preclude that their trunks would have been prone to fail and snap before wind speeds high enough to uproot them were reached (DiMichele and DeMaris, 1987).

In any case, both monocarpic and polycarpic taxa existed and, if survival until reproduction were a dominant selective agent, then the monocarpic taxa might be expected to be smaller than the polycarpic taxa. In fact, the situation is considerably more complex. Polycarpic trees come in both small (Fig. 8A) and large (Fig. 8C) growth forms,

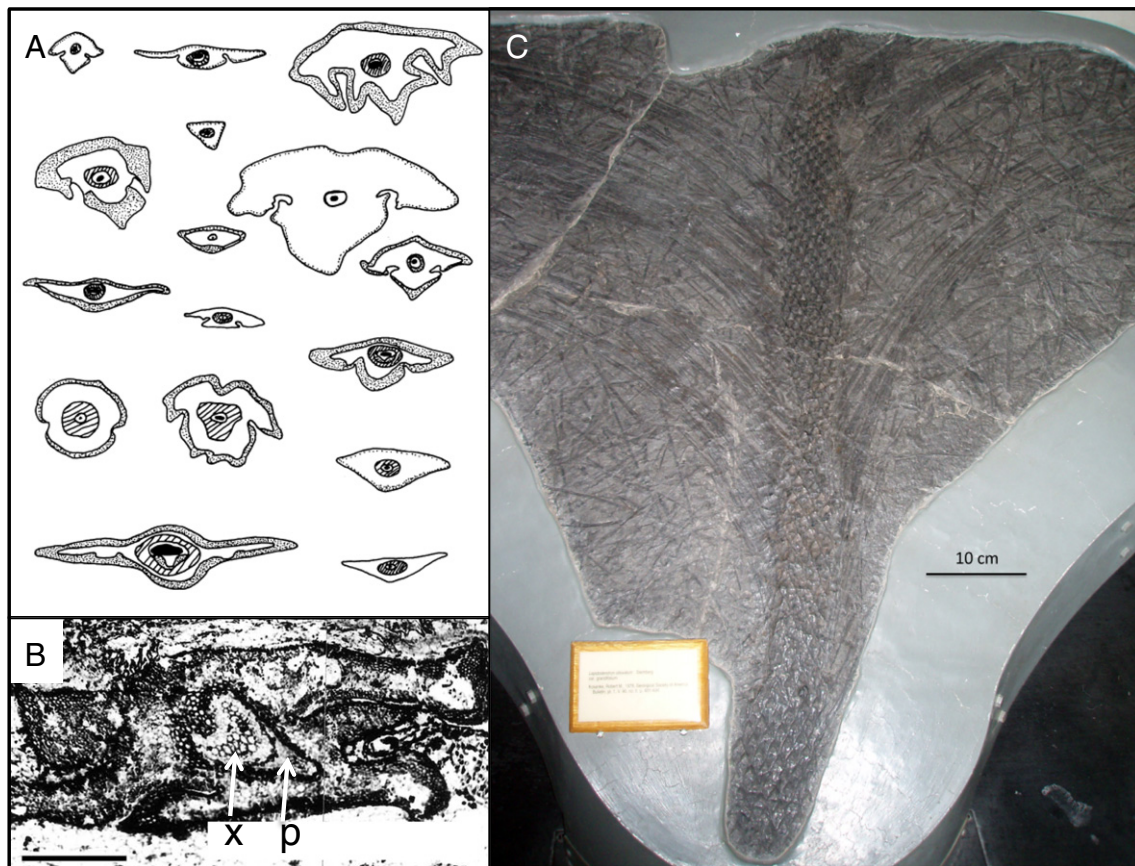


Fig. 6. The leaves of arborescent lycopsids. A. Outline cross-sections of various kinds of *Lepidophylloides*. Dotted area represents thick-walled fibrous cells; solid black area represents xylem; hatched area represents transfusion tissue. Magnifications vary, but note relative leaf thickness, peripheral sclerenchyma, and the relatively small area dedicated to vasculature. B. Anatomical cross section of *Lepidophylloides taiyuansensis* somewhat distorted by compression. Xylem (X) and phloem (P) labeled, scale bar is 500 μ . C. *Lepidodendron longifolium* Kosanke, type specimen on display at the Illinois State Geological Survey. Note long leaves in attachment to the stem. The leaf cushions are exposed along the fracture plane of the rock in which the plant specimen is preserved. (A, B from (Wang et al., 2002), used with permission of Elsevier).

and appear to be primitive/plesiomorphic among the overall tree lycopsid clade (Bateman et al., 1992; DiMichele et al., 2013). Monocarpic tree taxa, in contrast, are derived evolutionarily (Bateman et al., 1992), apparently reflecting developmentally mediated, heterochronic changes in the timing of reproduction (Bateman, 1994). There also are a number of smaller isoetalean forms, up to several meters in height, such as *Chaloneria cormosa*, a monocarpic form inferred to be derived on the basis of phylogenetic analysis (Bateman et al., 1992) and on the stratigraphically earlier occurrence of polycarpic *Chaloneria periodica* (DiMichele et al., 1979; Pigg and Rothwell, 1983). Thus, monocarpy may have been a derived developmental condition in various lycopsid lineages. This does not appear to reflect an acceleration of growth rate and an early onset of reproduction relative to polycarpic ancestral forms, but rather a delay in the onset of reproduction, pushing it into the period of crown formation, accompanied by the compression of ancestral, multi-strobilus deciduous lateral branches (Fig. 8B) to highly reduced branching systems bearing single cones (Bateman et al., 1991; Bateman, 1994). Given that all the large lycopsid trees appear to have undergone crown formation associated with growth termination, regardless of their overall size, monocarpy, *per se*, does not appear to have been a crucial factor limiting lycopsid lifespan.

4.4. Paleocology and sedimentology

The environments in which *in situ* tree bases are preserved typically indicate rapid, and in some instances catastrophic, burial of large stands of trees, the abundance and similar size of which may indicate monotypic lycopsid dominance and even cohort establishment (DiMichele

and Falcon-Lang, 2011; Thomas and Seyfulla, 2015). This could lead to the conclusion that these plants were highly productive ecosystem dominants that lived primarily in settings prone to sediment-laden floods or coastline progradation where rapid growth may have been required for lifecycle completion. In fact, it should be considered that such fossilized forests are uncommon and probably not representative of the habitats preferred by these species. Consider that the most common occurrences of lycopsid aerial remains are in peat swamp (coal balls) and clastic-swamp settings, floodplain environments, and even in carbonate muds, in all cases without being attached to upright stems. This is *prima facie* demonstration that the lycopsid trees were widespread and not confined, or even found most often, in environments conducive to rapid, aperiodic flooding and sediment deposition. Indeed, there is no guarantee the trees of frequently disturbed environments formed self-sustaining populations; they may have been dependent on propagule dispersal from more stable environments where reproductive potential was not repeatedly truncated by disturbance. Furthermore, partial burial need not have been lethal (DiMichele and Falcon-Lang, 2011). Finally, although some stands of fossil trees may appear to have been lycopsid-dominated, this is the exception rather than the rule; most stands consist of multiple species and genera, based on prostrate axes of such plants as tree ferns and pteridosperms amidst the standing trunks of lycopsids (DiMichele et al., 2007; Gastaldo et al., 2004; Opluštil et al., 2009). In one exceptional case (Willard and Phillips, 1993), two trunks of *Psaronius* and one of a calamitalean were found to extend from the underclay to the top of a >0.6 m thick mass of permineralized peat in the Late Pennsylvanian Friendsville coal of Illinois, USA. Thus, if *in situ* lycopsid trunks are presumed to indicate productivity many times

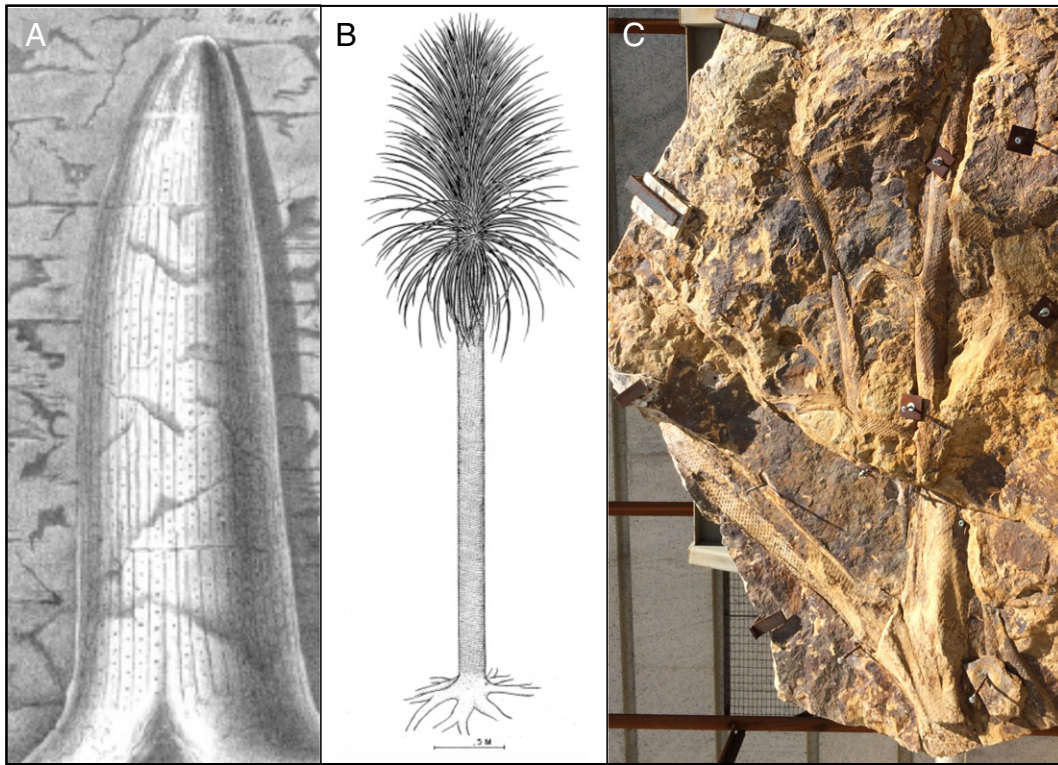


Fig. 7. Growth stages of arborescent lycopsids. A. Small, possibly juvenile plant attributed to *Sigillaria* by Goldenberg, (1855). B. Hypothetical reconstruction of a monocarpic lycopsid prior to crown formation with a thick, columnar trunk (From Andrews and Murdy, 1958, used with permission of the Botanical Society of America). C. Lower crown branches of *Lepidodendron mannabachense*. USNM specimen 528667.

higher than living plants, that uniquely high productivity must have applied across a broad swath of the vascular plant phylogeny during the late Paleozoic. Where monotypic stands do exist, they might be considered as likely to reflect high levels of environmental stress,

and exclusion of other taxa unable to handle the particular stresses of the environment, rather than high lycopsid productivity. In all cases, highly elevated growth rates may not be inconsistent with sedimentological evidence, but in no case is that answer a unique

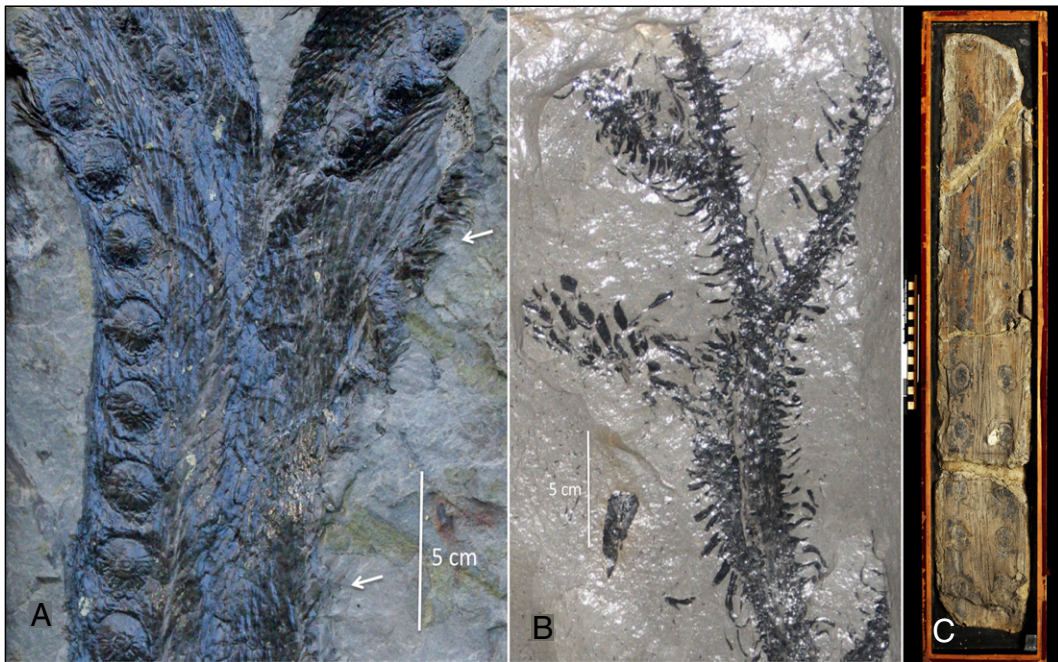


Fig. 8. Polycarpic arborescent lycopsid remains. A. *Paralycopodites* sp. main trunk with small, deciduous lateral branch scars, vertically disposed. Arrows point to attached leaves. Lower Pennsylvanian, Alabama, John Cooke Collection, USNM. B. *Diaphorodendron* sp. fragment of deciduous lateral branch system with leaves still in attachment (leaves are usually not found in attachment in this genus). Middle Pennsylvanian, Springfield coal, Indiana. C. *Synchronidendron* sp., main trunk with clearly marked deciduous lateral branch scars and still attached leaf cushions. On lower portions of this large trunk, of which this is the most distal portion, the leaf bases are not present, even though trunk diameter is approximately the same along the entire preserved length (see DiMichele et al., 2013, in which the full specimen is illustrated). USNM specimen 7304. Middle Pennsylvanian, Illinois. Scale bar is 18 inches.

requirement. High growth rates would at best be one potential explanation among several.

4.5. Direct measures of growth rates from fossil leaf characteristics?

In theory, fossil specimens with leaves in axial attachment can provide a rough estimate of tree lifespan as long as leaf lifespan can be estimated: length of axis with leaves (meters) divided by leaf lifespan (years) provides an estimate of axial growth rate that can then be compared to the overall height of the tree in order to estimate the tree's age. Such an approach has been used with a variety of living plants, such as palms, for which no tree rings are available, but leaf scars can be counted and leaf lifespan can be observed (Uhl and Dransfield, 1987). However, in practice, fossils present a series of challenges not faced when using this method with extant plants. The short, awl-like and permanently attached leaves of some arborescent lycopsids, such as *Paralycopodites* (Fig. 8A), do not allow for a determination of functional leaf lifespan. In those arborescent taxa that do have leaf abscission, axes with attached leaves (Thomas, 1970; Kosanke, 1979; Chaloner and Meyer-Berthaud, 1983; Rex, 1983; Leary and Thomas, 1989) are typically too fragmentary to determine an accurate length of a leaf-bearing stem segment. It does appear, however, that leaves covered at least a meter or so of trunk length within the crown of the monocarpic *Lepidodendron* (Kosanke, 1979) (Fig. 6C).

Research on the leaf economic spectrum (Reich et al., 1999; Wright and Westoby, 2002; Wright et al., 2004) cannot provide a direct estimate of leaf lifespan in the tree lycopsids—existing work has been focused on seed plants, specifically angiosperms—but can provide some general expectations: long-lived leaves with low photosynthetic rates tend to be thick and well defended via sclerenchyma or secondary chemistry, whereas short-lived leaves with high photosynthetic rates tend to be thin. Thick leaves will tend to have lower maximum photosynthetic rates because of the greater diffusive path lengths for CO₂ from the stomata through the mesophyll (Brodribb et al., 2007; Boyce et al., 2009; Zwieniecki and Boyce, 2014), requiring longer leaf lifespans for equivalent productivity in comparison with thin, short-lived leaves. Leaf laminae of the tree lycopsids are 1 mm or more in thickness. Such thick leaves would correspond to leaf lifespans of at least several years among living angiosperms (Wright and Westoby, 2002). For comparison, leaf lifespans among conifers range from less than six months to more than forty years (Reich et al., 1995). Data for lycopsids are scarce, but even the thin leaves of extant temperate species live for four to six years (Nauertz and Zasada, 1999), so the leaves of the main trunk in the lycopsid trees—more than 1 mm in thickness and up to a meter in length (Andrews and Murdy, 1958; Kosanke, 1979) (Fig. 6C)—would presumably have functioned considerably longer. If a ten-year leaf lifespan is chosen for illustrative purposes, then a meter of stem covered with living leaves would translate to a 10 cm/year growth rate and a 40 m tall lycopsid being 400 years old. All numbers involved in that calculation are order of magnitude estimates and the resulting whole-tree lifespan estimate could easily be pushed up to 800 years (e.g. if leaf lifespan were 20 years) or down to 200 years (e.g. if the distal 2 m of trunk bore living leaves). However, a tree lifespan of only one or a few decades would not be consistent with the large sizes of the trees in conjunction with the long leaf lifespans reflected by high leaf thicknesses and/or sclerenchymatous construction.

5. Implications

5.1. Productivity and lifespan

No line of evidence requires a uniquely rapid growth rate for the arborescent lycopsids and several lines of evidence appear to prohibit it. Of the various mechanisms that might be entertained to explain elevated rates of carbon assimilation, none appear to be viable. No mechanism has been proposed for the greatly increased rates of nitrogen and

phosphorous acquisition that would be needed to keep up with increased photosynthetic rates and no such mechanism seems forthcoming. Rather than ten to fifteen years or less, lifespans were more likely on the order of at least several decades for the smaller trees and a few hundred years for the largest. A reasonable starting point might be the expectation that these plants were no more productive than modern mesic angiosperm trees, leading to at least a 200 year lifespan for a *Lepidodendron* of the dimensions considered by Cleal and Thomas (2005). That baseline expectation might increase to 800 years or more with allowances for the low productivity of modern lycopsids or, more generally, the depressed productivity that can accompany permanent substrate flooding (Talbot et al., 1987; Armstrong et al., 1994; Lopez and Kursar, 1999; Pezeshki, 2001; Kozłowski, 2002), although that baseline might be brought back down to approximately 400 years with lower tissue densities than assumed by Cleal and Thomas (2005). The spacing of leaf bases and likely leaf lifespans of lycopsid trees are consistent with these baseline calculations.

5.2. Ontogeny and architecture of arborescent lycopsids

Of most direct relevance to paleobotany, the amount of fossil data regarding the arborescent lycopsids is enormous (Taylor et al., 2009), but much of it is not easy to reconcile. The suggestion of extraordinarily high productivity was an attempt to account for some of the complexities of arborescent lycopsid biology, but recognizing the impossibility of a ten-year lifespan invites reconsideration of those issues. A prime example is the original evidentiary basis for suggesting a rapid lifespan: if the seeming absence of juvenile specimens is neutral regarding the matter of lifespan, it nonetheless leaves us with the problem of the “missing” juveniles, undergirded by thousands of person-years of examination of outcrops and mine exposures, with eyes on tens of thousands of arborescent lycopsid specimens.

Why are trees that might be characterized as “juvenile” or “immature” so rare as to be virtually unknown among the arborescent lycopsids? Several possibilities present themselves. One explanation might be that the absence could be strictly taphonomic: either small trees lacked the secondary tissues that gave large trees high preservation potential, or old, long-dead trunks remained intact so that the large trees end up overrepresented relative to little plants in any sample, or both. However, although preservation biases are always a concern, they are unlikely to explain fully an absence of clearly identifiable juveniles when even arborescent lycopsid embryos are well known (Phillips, 1979). An alternative explanation would be simply that we don't know how to recognize young trees. The expectation that young trees should be small trees comes from an expectation of extensive secondary growth, i.e. the expectation of a sapling stage. However, a sapling stage cannot be preserved if a sapling stage never existed. Large slabs of intact, unseparated leaf bases indicate a large primary body and the preservation of non-abscised leaves on large stems demonstrates that full trunk diameter was achieved close to the apex. The only examples of which we know that illustrate such specimens are the engravings of juvenile *Sigillaria* stems (Fig. 7A) in Goldenberg (Goldenberg, 1855). Useful analogues to consider may be the primary thickening meristems of palm and cycad taxa that establish their full diameter immediately below the apex and do so early in ontogeny by the time the trunk emerges from the substrate. Thus, large lycopsid stump casts e.g. (Thomas and Seyfulla, 2015) may easily be assumed to have represented tall, mature trees, but a cast 0.8 m wide and 2 m tall may only require that the tree was taller than 2 m, not a full 30 or 40 m.

The fossil record of *in situ* occurrences of arborescent lycopsid trees, including tree stumps and prostrate trunks, (DiMichele and Falcon-Lang, 2011) is broadly consistent with the possibility that large fossils need not represent mature trees. First, the most commonly preserved, autochthonous remains of lycopsid trees are tree stump casts (Thomas and Seyfulla, 2015); although the length of trunk associated with bases is variable, most specimens are truncated close to the stem base.

A complete buried sexually mature tree has not been reported, to our knowledge, although fragmentary tree crowns preserved under nearly autochthonous conditions have been reported (e.g. Opluštil, 2010). Second, the great majority of prostrate trunks are partial specimens without base or crown. Trunks exceeding 30 m in length are rarely reported in the literature. Consequently, it cannot be ruled out that partially preserved tree bases and trunks are juveniles, particularly in the case of monocarpic taxa (e.g. *Lepidodendron*, *Lepidophloios*, and perhaps *Sublepidophloios*). As an additional consideration, however, to our knowledge there are no reports of prostrate trunks of those forms with deciduous lateral branches (e.g., *Paralycopodites*, *Diaphorodendron*, *Synchysidendron*, *Bothrodendron*) in which such branches are preserved in attachment to the main stem (see Fig. 8 A, C for examples of such stems). Thus, the problem persists: young plants of this polycarpic growth form should be highly recognizable based on attached branches, yet there are no such specimens reported in the literature, to our knowledge.

As a final consideration, we propose that it may be unrealistically optimistic to expect juvenile trees to be well represented in the fossil record. Juveniles of *Psaronius* and *Calamites* are also not known, or at least not recognized as such. There are exceptions (Beck, 1967), but fossil juveniles are rare in general. Juveniles may represent a demographic bottleneck, particularly in the stressful wetland environments that provide much of the fossil record. Megaspore-bounded embryos may be abundant, adults may persist for long lifespans once established, but few individuals at any one time may be in the transitory stage in between. Saguaro cacti are a modern example of such population dynamics in a stress tolerant plant for which a century may pass between successful recruitment years (Drezner, 2014). Leaves can provide a final comparison: the number of *Spiropteris* croziers that have been described (Kidston, 1884; Crookall, 1925; Diéguez and Meléndez, 2000; Bomfleur et al., 2011) is vanishingly small when compared to the total number of fossil fern and pteridosperm leaves that have been observed. As with investigation of the evolution of leaf development (Boyce and Knoll, 2002; Sanders et al., 2007; Boyce, 2008), the mature forms preserved as fossils may be a better starting point for considering the ecology and structure of juvenile arborescent lycopsids than the unrepresented (or unrecognized) juveniles themselves. The implications for classic interpretations of arborescent lycopsid anatomy, ontogeny, and establishment (Andrews and Murdy, 1958; Eggert, 1961) are the subject of continuing investigation.

5.3. Geobiology and the physiology of fossil plants

Plants are active participants in the creation of their environments, not just passive recipients (Algeo and Scheckler, 1998; Odling-Smee et al., 2003; Scheffer and Carpenter, 2003; Boyce et al., 2010b; Davies and Gibling, 2013). In any geobiological consideration, they cannot be lumped as a single homogenous vegetation; the evolution of ecology, architecture, and physiology matters on a lineage by lineage basis as has been demonstrated for extant ecosystems (Prinzinger, 2001; Webb et al., 2002; Wiens et al., 2010) and inferred even for those of the late Paleozoic (Scheckler, 1986; DiMichele and Phillips, 1996; DiMichele et al., 2001; Hotton et al., 2001). That being said, even when the structural novelty is extensive, the attribution of any particular environmental or ecophysiological impact to that novelty must be evaluated critically—as with, for example, suggested feedbacks between angiosperm evolution and marine productivity (Boyce and Lee, 2011)—and within the context of all available evidence. Similarly, the structure of the arborescent lycopsids consists of a series of challenging novelties, but all of these innovations are housed in plants limited to saturated substrates that likely were prone to nutrient limitations and low productivity. There is no reason to expect that these trees were immune to those stresses. Arborescent lycopsids require no special attention as an outlier in discussions over the role of vegetation and plant evolution in climate/biogeochemical cycling or in arguments over the productivity of plants

through time (Cleal and Thomas, 2005; Frank et al., 2008; Birgenheier et al., 2010; González and Díaz Saravia, 2010; Horton et al., 2012; Greb, 2013) and any calculations or models directly requiring such an expectation should be reconsidered as suspect.

The plants of the Silurian through the Carboniferous may be composed almost exclusively of lineages that either are now extinct or possess highly dissimilar modern members, but they are all just plants and plants all operate under similar physical constraints. There should be no expectation of anything shockingly different in these constraints during the early evolution of terrestrial vegetation. A variety of evolutionary novelties, such as angiosperms, C₄ grasses, CAM succulents, epiphytes, and secondary aquatics, have indeed been transformative—as were the parallel evolutions of leaves, roots, and secondary growth earlier in Earth history—but these transformations involved expansion into less productive environments or increasing productivity in the productive environments. Such advances would have been marginal compared to what has been attributed to the arborescent lycopsids: the maximum differences in productivity through time, when the fossil record is considered more broadly, are of the order of a factor of two or three (Beerling and Woodward, 1997; Brodribb et al., 2007; Franks and Beerling, 2009; Boyce and Zwieniecki, 2012), not twenty. When evaluating the biology of Paleozoic fossil plants and the transitions to terrestrial environments, the physiological possibilities exhibited by the diversity of living plants should be a guide. Direct and extraordinary evidence is needed for any argument for a substantial expansion of that range.

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