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PALEOBOTANY SUPPORTS THE FLOATING MAT MODEL FOR THE ORIGIN OF CARBONIFEROUS COAL BEDS

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ABSTRACT

A review of the history of the debate on origin of Carboniferous coal shows the priority that autochthonists have placed on paleobotanical data and interpretation. New data and methodology are offered here for interpreting the paleobotany and paleoecology of dominant Carboniferous coal plants: tree lycopsids and the tree-fern *Psaronius*. Lycopsid and tree-fern anatomies are characterized by air-filled chambers for buoyancy with rooting structures that are not suited for growth into and through terrestrial soil. Lycopsid development included boat-like dispersing spores, establishment of abundant buoyant, photosynthetic, branching and radiating rhizomorphs prior to upright stem growth, and prolonged life of the unbranched trunk prior to abrupt terminating growth of reproductive branches. The tree fern *Psaronius* is now understood better than previously to have had a much thicker, more flaring, and further spreading outer root mantle that formed a buoyant raft. Its increasingly heavy leaf crown was counterbalanced by forcing the basally rotting cane-like trunk and attached inner portion of the root mantle continually deeper underwater. Lycopsids and tree-ferns formed living floating mats capable of supporting the trunks. Paleobotany of coal plants should now be best understood as supporting a floating raft that deposited the detritus that now forms Carboniferous coal beds.

KEY WORDS

floating mat model, origin of coal, Carboniferous paleobotany, paleoecology, tree lycopsids, *Lepidophloios*, *Stigmaria*, tree fern, *Psaronius*

INTRODUCTION

Among geologists, two broad categories of depositional models for Carboniferous coals have been debated for three hundred years. The prevailing uniformitarian explanation of coal formation supposes coal beds to be authigenic and autochthonous (manufactured through a soil-forming environment from plants grown in place) and deposited within coastal swamps, delta plains or river levee environments. The enduring catastrophist explanation, never silenced during hundreds of years, supposes coal beds to be detrital and allochthonous (water-borne detritus transported to the submerged surface of sedimentation) and, likely, associated with rafts of floating vegetation. Our accompanying paper concerned the history of depositional models for the origin of Carboniferous coals (Austin and Sanders 2018). We sketched the familiar autochthonous versus allochthonous coal debate and argued that there are actually three depositional models for the origin of Carboniferous coals: (1) swamp model, (2) drift model, and (3) floating mat model.

ROOT OF CONTROVERSY

Advocates of the swamp model for Carboniferous coal devised paleoecological interpretations of plant fossils, especially rootlike structures of lycopods. These paleobotanical ideas are placed within strata sequences to assign the different rock layers to terrestrial swamp, floodplain and levee environments. Among the most famous early advocates of autochthony of Carboniferous coals (arguing from paleobotany through stratigraphy and petrology to paleoenvironment) were the field geologists Charles Lyell and John Dawson. Lyell (1855) and Dawson (1854) examined the rootlike fossil named *Stigmaria* in sandstones and shales at Joggins in Nova Scotia. They also described fossil lycopod trunks

standing upright in shale strata, but they didn't find them within coal beds. These upright trunks were interpreted to have formed *in situ* within fossil soils containing *Stigmaria*, and the associated coal beds were considered to be autochthonous, formed in large, topographically elevated, freshwater mires. Later at Joggins assemblages of upright trunks were supposed to represent *in situ* "fossil forests" on an elevated area. Among the autochthonous modelers of the origin of Carboniferous coal, the priority is coal paleobotany, not coal petrology. The autochthonist explanation of the origin of coal became the dominant view in the Twentieth Century following the methodology of Charles Lyell. Gastaldo (1984), McCabe (1984), Scott (1998), and O'Keefe et al. (2008) are modern advocates of autochthony using the "paleobotany-strata-petrology-environment" methodology.

Advocates of the drift model for Carboniferous coals focused on coal petrology. They studied coal composition, structure and texture under the microscope from coal thin sections. Two classic drift modelers were the French petrologist/paleobotanists Cyrille Grand'Eury (1882) and Henry Fayol (1887). A vigorous "French School" of allochthonist thought continued through the Twentieth Century and remains with us today. Interpretations made on fine-textured cannel coal (lithotype durain) were extended into what are called coarser-textured and banded humic coal (lithotypes clarain and vitrain). Coal did not compare texturally well with modern *in situ* swamp peat. Advocates of the drift model saw detrital textures, oriented plant structures and very thin shale partings dominating coal microstructure without rooting evidences within the original peat. Strata associated with coal beds also seemed to indicate submerged conditions. According to the drift model,

eroded plant detritus was transported in rivers as dispersed grains and settled through water in lakes, submerged parts of deltas or marine estuaries. Both early and later allochthonists of the French School used the “petrology-strata-paleobotany-environment” methodology to understand the origin of Carboniferous coal.

The floating mat model has a robust three-hundred-year history that was summarized for the first time by Austin and Sanders (2018). About the same time as the French School of allochthonists was developing subaqueous notions for coal deposition and elaborating the drift model, another group of allochthonists already had an alternate understanding. This second group of allochthonists was uneasy about coal plants being grown on upland terrain and then transported as debris by rivers to lakes or deltas. This group proposed coal-forming plants existed on large floating rafts of vegetation and that coal was deposited as vegetation sank, either *en masse* or as broken detritus. Assigning only secondary importance to the paleobotany, these early allochthonists understood *Stigmara* to be a solitary, prone-floating rhizomorph with water leaves, that when tangled with floating debris, became able to sprout an upright lycopod trunk. Three prominent early advocates are German botanist Otto Kuntze (1884, 1895), the British-American engineer and geologist William Gresley (1894a,b), and the Cambridge University paleobotanist Albert Seward (1895a,b). Later advocates are petrologist Steven Austin (1979, 1991), paleontologist Joachim Scheven (1981, 1996) and paleontologist Kurt Wise (2003). Paleobotanical observations favoring the floating mat model appear in the following pages. Austin and Sanders (2018) observed that historically the drift model and the floating mat model of allochthonists used the “petrology-strata-paleobotany-environment” methodology to understand the origin of Carboniferous coal.

What about those lycopod “roots” in strata above and below coal beds? Is the iconic coal fossil *Stigmara* really indisputable evidence for growth in place of roots in fossil terrestrial soils? Robert Gastaldo (1999) defends autochthony calling it “Empirical science versus the diluvialists.” How strong is the evidence from upright fossil trees grown on elevated terrestrial surfaces? Even creationists Tim Clarey and Jeff Tomkins (Clarey 2015, Clarey and Tomkins 2016) are persuaded that lycopod trees within Carboniferous strata in Glasgow, Scotland grew as a forest on terrestrial soils. Are the evidences straightforward observation? Examples of Carboniferous forests supposed to have grown in place have appeared in the literature (surveyed in DiMichele and Falcon-Lang 2011, Thomas and Seyfullah 2015). Could those “forests” instead be floated and grounded mats of vegetation? All these questions show us that there is a critical need to revisit lycopod and tree fern anatomy. Paleobotany needs to be considered in detail, and attention needs to be directed at alternate depositional models. That will focus our clear thinking to make progress in understanding the origin of coal.

Therefore, given the pervasive acceptance of the autochthonous origin of Carboniferous coal in coastal mires or swamps among conventional scientists, and given the objections to the floating forest biome within the creationist community (Clarey and Tomkins 2016), we examine here the biology of the dominant coal plants in the post-1940 conventional paleobotanical literature

to provide sound support by the scientific literature for a floating lifestyle. Detailed documentation and extensive, in-context quotes are provided for lycopsids in Appendix A and for the tree fern *Psaronius* in Appendix B.

ARBORESCENT LYCOPSIDS

The basic structure of arborescent (tree and treelike) lycopsids has been widely discussed and illustrated in the creationist literature, especially Scheven’s (1996) Figures 1, 3, and 8, which have been reprinted by various authors. Therefore, a basic description of these plants is unnecessary. The interconnections of the fragmentary fossils of these plants are well enough known now for the organs of each biological species to go under a single name instead of separate form-genera and species. One exception is that the rootlike horizontal axes of most species are identical and cannot easily be assigned to a particular trunk genus and species. These are assigned to the form genus *Stigmara*, and usually to the form-species *S. ficoides*. Hence these organs are often referred to as stigmarian axes or systems, though recent paleobotanists usually use the term rhizomorphs or rhizomorph axes. The structures radiating from these axes are usually called stigmarian/rhizomorph rootlets or appendages, depending on how the author is interpreting their homologies. The overall anatomy of the rhizomorph axis and appendages is shown in Figure 1.

The arguments that we make below are better understood using certain technical terms. Concerning stem and rhizomorph anatomy when these growing organs first matured, they consisted only of tissues generated by the apical meristems and, thus, were considered to be all primary tissues. At this stage, the primary tissue between the stele (the thin central core of primary xylem) and the outside of the organ is termed the cortex, which consisted of three zones. The inner cortex was a thin layer of fairly delicate parenchyma cells surrounding the stele. The middle cortex was a fairly wide cylinder, of which the composition has been debated as discussed below. The outer cortex consisted of fairly tough parenchyma cells that provided initial external support for the organ. Secondary tissues, giving extra support, were formed when certain cells of the primary tissues began to divide and generated radially aligned rows of cells. Thus, secondary xylem produced by and surrounding the stele made up most of the internal wood cylinder. (Because of the limited amount of secondary xylem and its similarity to primary xylem in these plants, paleobotanists often include the secondary xylem when speaking of the lycopsid stele, which we will follow in this paper.) Periderm was secondary cortex arising and growing in the mid-regions of the outer cortex and became much thicker and more supportive than the outer cortex. The colloquial term “bark” is usually applied to the periderm (secondary cortex) and cells of the outer cortex (primary tissue) that closely adhered to the periderm.

Concerning the diversity of arborescent lycopsids, there are six major genera. The plants of three (*Lepidodendron*, *Lepidophloios*, and *Synchysidendron*) were quite tall and distinguished by the trunks being unbranched except at the top, where the apical meristem was dissipated by successive dichotomous branching. These differed primarily in the degree by which the sporophyll base flanked and enclosed the megasporangium, which contained a single permanently encased megaspore (thus, monosporic).

Two genera (*Paralycopodites* and *Diaphorodendron*) sequentially produced well-branched lateral branches along the trunk which terminated in a single dichotomy, but each branch persisted only briefly before abscising and falling off. *Diaphorodendron* was monosporic, but *Paralycopodites* produced multiple megaspores that dropped from the sporangium (i.e., polysporic). *Sigillaria* was similar to *Paralycopodites* but its lateral branches were simple stalks producing a single cone each (Bateman 1994).

Bateman and DiMichele (1991) and Bateman (1994) argue that the structure of seed plants cannot be used as an analogy to understand that of lycopsids. That is, lycopsids are unique in their embryology, development, and anatomy. Furthermore, lycopsid structure and taxonomic diversity arise from their being made up of architectural modules. The modules (rhizomorph, trunk, crown branches, and lateral [cauline] branches) have similar anatomies (see also Eggert 1961 and Phillips and DiMichele 1992) but different growth trajectories and are combined in different ways in different genera (including non-trees, i.e., trailing shrub species, columnar species, and diminutive living *Isoetes*). Therefore, one has to be careful in the assumptions one makes in interpreting fossils of these extinct

species.

Actually, the floating, aquatic nature of the aborescent lycopsids is based, not only on the interpretation of hollow stems and rhizomorphs (Austin and Sanders 2018), but on a suite of consilient lifestyle traits which are documented in Appendix A.

1. Trunks and rhizomorphs contained hollow central cavity.

We argue that the trunks and rhizomorphs (as well as rhizomorph appendages) were hollow between the outer cortex/periderm and stele + inner cortex; that is, the region denoted as “middle cortex” actually was a zone lacking tissue. In contradiction, creationists Clarey and Tomkins (2016) assert,

In fact, this basic non-hollow anatomy is well established in arboreal lycopod stem tissue, which is typically well preserved. The problem lies in the fact that very little of this internal cortex tissue is well preserved in the large trunks and stigmarian roots....three layers of internal parenchymatous cortex tissue existed that became preferentially degraded over the other intervening layers and central vascular stele.

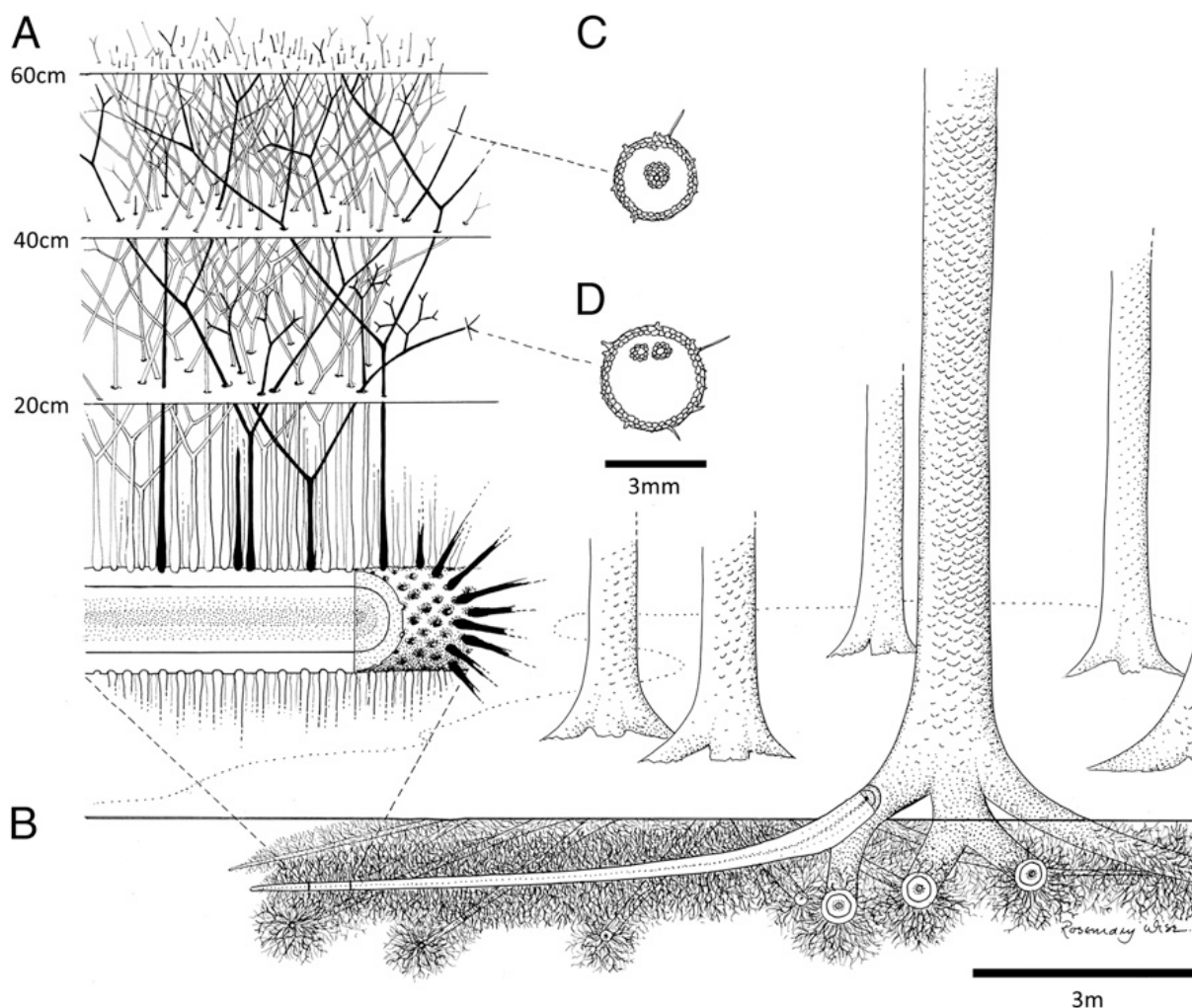


Figure 1. Anatomy of the submerged part of a mature arborescent lycopsid. (A) Frequently branched, spirally arranged floating water leaves (appendages) surround the partly hollow rhizomorphic axis (*Stigmaria*). (B) Floating rhizomorphs with ~25,000 leaf terminations per meter of rhizomorph axis. Rhizomorph apices incorrectly taper as drawn; see text. (C) Cross section of a water leaf (appendage) with vascular bundle within hollow space. (D) Cross section of water leaf at the branching point where the vascular bundle divides. (Figure from Hetherington et al. 2016, but we use our own terminology to describe anatomy).

This argument, of course, has been used by the autochthonists to debunk floating lycopside. We recognize what Clarey and Tomkins found in the literature, but we provide additional data and a different interpretation. Our studies showed that either cellular tissue is lacking from the middle cortex or the middle cortex and external tissues are missing entirely, presumably in cases where the bark has been ripped off, with paleobotanical authors since 1990 recognizing the hollow air chambers (Andrews and Murdy 1958; Bateman et al. 1992; Bateman 1994; DiMichele 1979a; Eggert 1961; Pannell 1942; Reed 1941; Rothwell and Erwin 1985). Statements by these paleobotanists are reviewed in Appendix A. Bateman (1994) indicates that the weight to volume ratio of the trees is low, which could not be obtained if the middle cortex consisted of water-filled aerenchyma cells (as interpreted by Clarey and Tomkins). Indeed, the only cellular middle cortex tissue of stems that is “typically well preserved” is in small twigs less than 3 cm diameter in the branching, reproductive module of the plant, while occasionally one finds larger crown or cauline branches 4 to 6 cm diameter which contain cellular middle cortex (DiMichele 1979a, 1979b, 1981; Eggert 1961; Taylor and Eggert 1967).

We understand that the horizontal branches were working against gravitation pull and needed the “filler” tissue to keep from collapsing, whereas the erect trunks did not have the gravitational problem. Not only did the distal branches produce limited secondary xylem and periderm, relying on outer (thus, primary) cortex for support, but the tissue in the middle cortex appears to have been histologically different from that in small twigs (DiMichele 1981; Eggert 1961), as were the sheaths surrounding the leaf traces crossing the air chambers in stems without cellular middle cortex (DiMichele 1979a, 1981; Eggert 1961). Eggert (1961) suggested that cells of middle cortex retained the ability to undergo cell division and proliferate secondarily (which is different from the development of the secondary cortex, *i.e.*, periderm, arising in the center of the outer cortex).

Thus, we suggest two possible growth outcomes: (1) Mature middle cortex parenchyma/aerenchyma was not formed in the trunk and larger to middle sized horizontal branches due to the shape of the primary thickening meristem (see below in section on development). That is, the apical meristem either did not directly make cellular middle cortex or cells that were produced broke down before they matured. Thus, primary middle cortex cells were formed or persisted only in the smallest twigs. Rather, initially formed air-chambers were filled when remnant cells (those remaining after most broke down during stem maturation) divided to make the secondary parenchyma as support tissue in the space of the original lacuna. (2) Some larger branches were never completely filled with middle cortex tissue but developed strong support from thick radial series of parenchyma around leaf traces. Thus, one would expect some larger-than-twig-sized branches to contain (a) only secondarily thickened leaf traces traversing lacunae that could as well characterize trunks, (b) secondarily thickened leaf traces and peripheral secondary parenchyma, possibly from the division of immediately adjacent inner or outer cortex cells, encroaching the lacunae, or (c) secondary parenchyma instead of lacunae.

Concerning both trunks and rhizomorphs, Clarey and Tomkins (2016) conclude:

The idea that the more resilient central stele tissues inside the stems and particularly within roots somehow stayed situated in the center of these structures in defiance of gravity during normal growth, and without the aid of any supportive tissue besides the vascular rays, is patently absurd and not observed in any known plant species today. (p. 120).

Not only have Clarey and Tomkins missed the point that arborescent lycopside cannot be compared to gymnosperm and flowering plant trees, they undervalue the supporting strength of the unusual secondary cortex and leaf/appendage traces (which they call “vascular rays”) of lycopside. Not only were these traces very numerous and closely adjacent in tight spirals, but also, they were reinforced with secondary parenchyma. Thus, they acted as tie-wires to help prevent the steles in the upright trunks (which themselves were supported against downward gravitation by the thick periderm) and water-buoyed rhizomorphs from collapsing. They also missed the point that there are two basic types of apical meristems in these plants: 1) primary thickening apical meristems (PTAM) in the trunks, branches, and rhizomorphs, and 2) normal apical meristems in the twigs. Therefore, the anatomy of the trunks, branches, and rhizomorphs cannot be determined or extrapolated from the anatomy of twigs due to dissipation of the PTAM.

Therefore, the argument by Clarey and Tomkins (2016) and some paleobotanists that the hollow chambers are simply a result of rapid differential decay after the death or fragmenting of the tree is unconvincing. The report of discovery of a well-preserved whole rhizomorph and connected stem base in the shrub species of *Paurodendron* (Rothwell and Erwin 1985) clearly contradicts the argument. Even though this rhizomorph is unbranched and small, Rothwell and Erwin argue that the anatomy was comparable to larger, branched rhizomorphs. The middle cortex was hollow and suspended in it was a cylindrical veil of delicate parenchyma only two cells thick! We suggest that the hollow chambers formed either because no parenchyma was produced behind the apical meristem or the parenchyma/aerenchyma that did form broke down and was digested as the stems and rhizomorphs matured to full size. Indeed, in the context of catastrophic events afflicting mats, while many trees would be ripped apart or float long enough for tissue decay, many samples would be buried rapidly revealing the anatomy of the living state.

2. Rhizomorphs incapable of penetrating clay soils.

Clarey and Tomkins (2016) argue that arborescent lycopside were rooted in rich clay soils of coastline swamps. We believe that the lycopsid’s rhizomorphs were incapable of growing through even dense peats or peaty soils. Scheven (1996) and Woolley (2011a, b) have already pointed out that the bottle-brush arrangement of the appendices attached at radiating right angles (see also Frankenberg and Eggert 1969; Hetherington et al. 2016) suggests that the rhizomorphs were suited to water not soil, analogous to roots of modern aquatic plants.

Until Hetherington et al. (2016) conclusively demonstrated that rhizomorph appendages are long (at least 0.5 m) and dichotomously branched four to five times, it was assumed that the appendages were straight, or branched no more than once. Their

rhizomorph illustration is Figure 1. This adds more difficulty to rooting in soil but implies even greater mesh strength and stability to a hypothesized basal mat. Because Hetherington et al. (2016) demonstrated homology between rhizomorph appendages (they call them rootlets) and rootlets of living *Isoetes*, one might argue that by analogy, because *Isoetes* is rooted in mud, then so were the arborescent lycopsids. However, *Isoetes* is a tiny emergent aquatic of shallow, permanent pools and probably represents a recent innovation. Its rootlets are much shorter than those of fossil lycopsids, oriented downward to horizontal, and are variously bent as they grow through mud.

However, the real problem with rhizomorphs growing through soil

is not the appendages as much as the axes themselves. The apex of rhizomorphs was unknown until documented by Rothwell and associates (Rothwell 1984; Rothwell and Ervin 1985; Rothwell and Pryor 1991). The apex is not a tapering point, as in seed plants, but is only slightly smaller diameter than the mature rhizomorph, is blunt, concave, with a raised peripheral ring from which the appendages emerge. It simply is not designed to push through soil. Finally, Bateman (1994) notes that evidence of soil mycorrhizal associations has not been found in the rhizomorphs, and he even admits that the capability of these organs penetrating soil has been questioned.

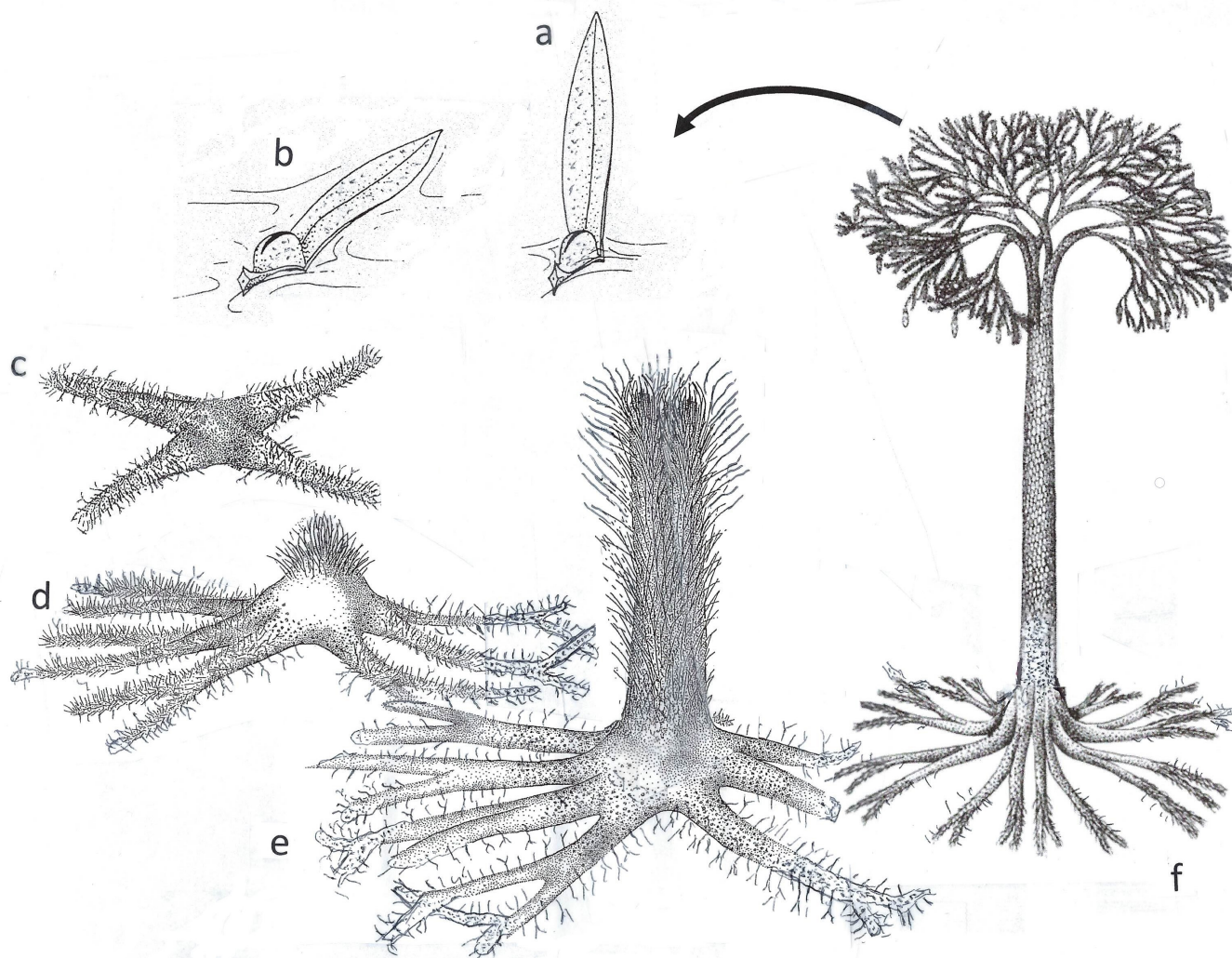


Figure 2. Life history of the arborescent lycopsid *Lepidophloios*. Ecology and life history follow suggestions by Phillips and DiMichele (1992). (a) Three-cm-long sporophyll *Lepidocarpon* (Phillips 1979) is shed from a cone of the mature tree (f). The sporophyll lands on water and is dispersed by wind resembling a boat with a sail. (b) The single megaspore within floating *Lepidocarpon* is fertilized by the microspore *Lycospora*. The embryo within the sporophyll germinates as a rhizomorph with a stem, but development of the stem is suppressed. (c) Juvenile plant has less than one-meter diameter and floats with hollow, buoyant, rhizomorphic arms (*Stigmara*) surrounded by hollow, branched, photosynthetic water leaves. (d) Precocious growth occurs due to photosynthesis forming an eight-meter-diameter “green air-filled starfish” that floats within the uppermost one meter of water. Buoyancy of the juvenile *Lepidophloios* is provided by the multitude of hollow, branched, half-meter-long water leaves (appendages) that surround the hollow, branched rhizomorphs (*Stigmara*). Stem phase of the plant is still suppressed within the central crown (see Phillips and DiMichele 1992). (e) After the floating juvenile plant becomes stabilized within a mat by tangling with other floating rhizomorphs, the trunk (“hollow pole”) grows vertically out of the water. The diameter of the trunk is approximately one meter. (f) The mature tree forms after branching of the trunk and has male cones (with microspore *Lycospora*) and female cones (with sporophyll *Lepidocarpon*) at the tips of branches. Height of mature tree could exceed 20 meters. Important question to ask, “At what stage of the life history of *Lepidophloios* does the floating plant become a tree rooted in terrestrial soil?” The answer could be “Never.”

3. Development and life history consistent with floating plant bodies and light-weight aerial structure.

As noted by Woolley (2011a) in her review of the paleobotanical literature, shortly after germination, the rhizomorph grows precociously and quickly forms its radiating architecture (substantiated by Bateman 1994; Phillips and DiMichele 1992; and Wnuk 1985). Thus, we understand the young tree-lycopsid plant to have been an air-filled “starfish,” floating along until the rhizomorph axes were long enough with enough appendages to become enmeshed with other rhizomorphs (Figure 2). Atop the radiating rhizomorph, the trunk at this point was just a latent dome, enlarging laterally to the diameter that the trunk eventually would be (that is, the primary thickening apical meristem was established before the trunk grew). The rhizomorphic axes and appendages apparently were photosynthetic and independent of the food supply produced by the latent trunk dome because there was almost no phloem connecting the two modules (Bateman 1994; Phillips and DiMichele 1992). Hence, we refer to these rhizomorphic appendages as water leaves.

When the latent apical stem dome did begin to grow after the rhizomorphic base was stabilized, it grew into an unbranched pole with very densely spiraled leaves in the top few feet (Andrews and Murdy 1958; Bateman 1994; Eggert 1961; Phillips and DiMichele 1992; Wnuk 1985). The formation of branches (along the stem or dichotomously in the crown) was brief and occurred only at the end of the life to produce spores (Bateman 1994; Eggert 1961; Phillips and DiMichele 1992; Wnuk 1985). Because branching was at the end of life, the forest consisted mostly of upright, unbranched poles, not a continuous canopy of branches and leaves (Bateman 1994; Bateman et al. 1992; Opluštil 2010; Phillips and DiMichele 1992; Wnuk 1985). In fact, because of the lack of phloem connections, the rhizomorph had to remain photosynthetic, as would the periderm on trunks and branches below the point of leaf abscission, both of which would be facilitated by the openness of the forest (Bateman 1994; Phillips and DiMichele 1992). Thus, such a forest would have been very light weight compared to present-day forests.

4. Propagules of dominant trees were water-dispersed “boats.”

Lepidodendron, *Lepidophloios*, *Diaphorodendron* and *Synchysidendron* all reproduced by propagules that resembled seeds but were quite unlike seeds and/or fruits of seed plants. The propagule consisted of a single very large female spore (i.e., megaspore), the only one produced by its sporangium. The spore remained encased in the sporangium, which in turn was attached to and shed with its sporophyll, a modified leaf that produced the sporangium. The base of the leaf formed a narrow to wide platform or, in the case of *Lepidophloios*, wrapped around and enclosed the sporangium. In all cases the sporophyll blade bent at right angles and, when the whole complex fell into the water, appeared to form a sail. Thus, these propagules were designed to be dispersed, fertilized, and germinated while floating and have even been termed “aquacarps” to distinguish them from true seeds (Phillips and DiMichele 1992). While, this could have happened in a swamp, it is consistent with the process occurring in open bodies of water, not part of a coastal, land-based swamp. The remaining genera produced smaller megaspores that were released

individually (free sporing). In a floating forest scenario, this latter type of megaspores would have fallen on free-floating rhizomorphs or enmeshed mats where they were fertilized and germinated, becoming part of a growing vegetation mat.

Therefore, there is ample evidence that arborescent lycopsids could have served as a source for Pennsylvanian coal not only as post-mortem vegetation debris mats, but also because they grew and floated on the surface of open water.

PSARONIUS TREE FERNS

Psaronius occurs throughout the Carboniferous and even in Permian strata, but this tree fern dominates Upper Pennsylvanian coal such as the Pittsburgh Coal Bed. These plants were not as tall as the tree lycopsids. Their stems were upright and unbranched, each bearing a crown of large, lacy fern leaves at the top. The stems were slender for the size of the plant and incapable of supporting the plant. However, shortly below the living leaves, adventitious roots grew down over the stem so that the lower on the stem, the thicker the mantle of roots, thus providing the needed support to keep the plant upright. As the roots were covered by newer ones above, they became embedded in secondary parenchyma produced by their own cortex and that of the stem. These roots are termed inner roots or bound roots. As the inner roots grew downward they were pushed outward by the underlying inner roots and were forced outward outside the bound root zone faster than the embedding parenchyma could grow and, thus, they became free. These and the topmost new roots were part of the outer root mantle and are termed outer roots or free roots (Ehret and Phillips 1977; Millay 1997; Morgan 1959; Weiss 2011).

Whereas Clarey (2015) and Clarey and Tomkins (2016) did not address the floatability of *Psaronius*, presumably they, as do most autochthonists, consider it to have been rooted in coastal swamps, as well. However, there are several lines of evidence that these tree ferns, like tree lycopsids, were capable of floating on the surface of water (see Appendix B). Figure 3 is a sketch of *Psaronius* as a floating tree following the proposal of Weiss (2011).

1. Roots and stems of some species contain air spaces.

All roots of the free-root zone, and in some species, the inner root zone have an aerenchymatous cortex between the stele and sclerenchymatous outer cortex (Ehret and Phillips 1977; Morgan 1959; Weiss 2011). Although the stem is small diameter compared to the root mantle, hollow air chambers are formed in one species by the breakdown of parenchyma (Ehret and Phillips 1977; Morgan 1959), and in a second species, the cortex is aerenchymatous (Ehret and Phillips 1977).

2. There is no evidence that anchorage in the soil of the stem or root existed.

All known specimens of *Psaronius* lack the very base of a stem and none show roots penetrating or encased in soil (Ehret and Phillips 1977; Mickle 1984; Millay 1997; Morgan 1959; Stidd and Phillips 1968; Weiss 2011). Mickle (1984) discovered that fossils of the stem-mantle segments farthest from the stem apex either had the stem and bound roots rotted away, leaving a thick free-root “doughnut,” or the “doughnut” was plugged by the stem and bound root layer only on the upper side of the “doughnut.” Thus, it is clear that the stem and attached bound roots rotted away

while the free root zone remained as the structural support at the base. Recent authors (Ehret and Phillips 1977; DiMichele and Phillips 2002; Rössler 2000) recognize that the flaring free root mantle at the base was much wider than illustrated by Morgan (1959), which is usually the reconstruction reprinted by many authors. Furthermore, significant numbers of fossils of sheet-like layers of free-roots completely detached from stem or bound roots are known suggesting these lay over the substrate and were not involved in anchoring to soil (Weiss 2011).

3. Weight of plant increased with age.

As the plant grew from a sporeling to a large plant, the diameter of the stem increased gradually, the stele became more complex, and the leaves in the crown became more and more numerous, and the basal root mantle continued to increase in thickness (Ehret and Phillips 1977; Mickle 1984; Millay 1997; Morgan 1959; Stidd and Phillips 1968; Weiss 2011). Thus, the stem of *Psaronius* was a narrow, upwardly thickening cane that was supported entirely by a downward thickening buttressing jacket of adventitious roots (Figure 3).

4. Reproduction was typical of marattialean ferns

Like living members of Marattiales, *Psaronius* was free-sporing, producing wind dispersed microspores all the same size (Millay 1997). Weiss (2001, cited in Steur 2016) reported fossils of young sporophytes germinating from free-living gametophytes which were found together with fertile spore-bearing leaves of *Psaronius*. This suggests these sporelings are very young *Psaronius* plants.

Taking all these life traits together, Weiss (2011) proposed the life

history of *Psaronius*, with which we concur. Once the sporeling was established (we presume by the spores germinating and being fertilized after landing on floating debris or existing free-root mats) it began to produce free roots as the wire-diameter stem elongated and produced more leaves. As the stem apex enlarged, became more complex and produced more leaves, and bound-root zone developed, the stem base was forced downward into the water or water-saturated mud. The stem base rotted and the loose, floating free-root skirt began to develop and enlarge. Continued enlargement of the stem apex, leaf crown and root mantle forced the base of the plant deeper under the water surface (as a counterbalance), where rotting continued and the free-root skirt became a large encircling raft that stabilized the upright stance (Weiss' Figure 4 that is redrawn here as Figure 3). Buoyancy was achieved not so much by the upright plant being light-weight, but by the free-root skirt and raft containing aerenchyma enough to float on the surface of the water. In fact, Weiss (see his Figure 3) argues that the raft would keep the upright tree from toppling, even in a wind storm or choppy water.

Thus, it appears to us that, as with the arborescent lycopsids, there is ample evidence that forests of *Psaronius* could have served as a source for Carboniferous and Lower Permian coal not only as post-mortem vegetation debris mats, but also because they floated on the surface of open water prior to burial.

CONCLUSION

Autochthonous and allochthonous explanations on the origin of Carboniferous coal in the Nineteenth Century showed how scientific methodology becomes involved in coal interpretation.

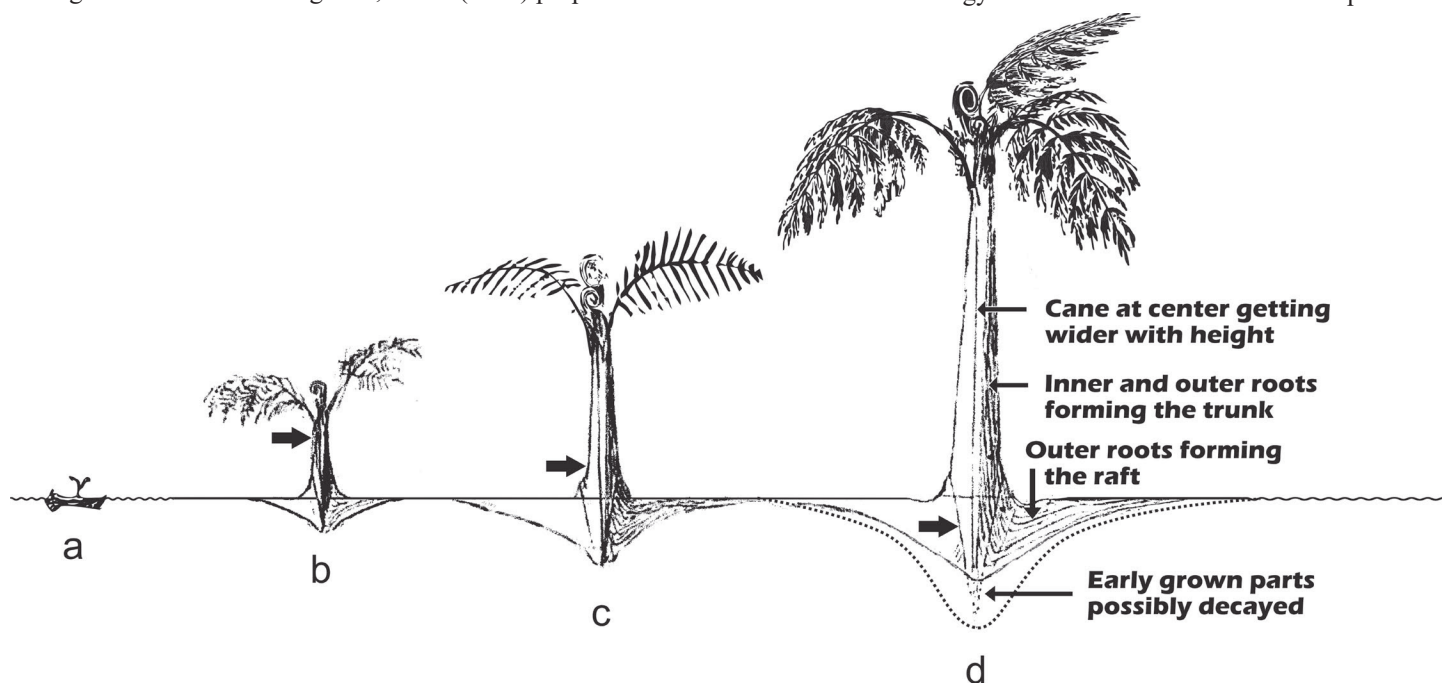


Figure 3. Life history of the tree fern *Psaronius*. Drawings suggest how the juvenile plant develops into the adult by being a free-floating tree (after Weiss 2011, with his comments on the drawings). (a) Spores of *Psaronius* land on floating vegetable debris and produce the sporeling. (b) Juvenile part of the fern's stem is composed of the "cane" surrounded by inner and outer roots. Outer roots are outspreading as a bundle forming a floating raft. (c) As the fern grows and the mass of the crown and trunk increases, the juvenile part of the stem is forced downward as indicated by positions of the arrows. (d) Mature tree fern has enlarged trunk and massive raft of outspreading, outer roots. Cutaway drawing suggests how the juvenile part of the stem becomes submerged and rots away as the raft of outer roots flares horizontally to enlarge the raft. As the draft of the raft increases with tree growth, it could become grounded in shallow water, be docked to other floating mats, or continue to float. Note that the basal structure of *Psaronius* offers no permanent attachment to a substrate. Mature tree may exceed three meters in height.

Autochthonous modelers used the paleobotany-strata-petrology-environment method, while allochthonous modelers used the petrology-strata-paleobotany-environment method. The two methodologies are best displayed at the end of the Nineteenth Century in the consensus autochthonists versus the French School allochthonists. Are coals terrestrial or subaqueous? Three explanations have been offered for the origin of coal: (1) peat swamp model, (2) drift model, and (3) floating mat model. Many paleobotany questions about lycopods and tree ferns had not been solved at the end of the Nineteenth Century, but the “floating mat model” offered a very robust path to direct research.

Although a strong sedimentary case can be made for the floating mat model for prominent Carboniferous coal beds, many geologists resist this way of thinking because (1) the scale of mat sedimentation is colossal and associated with marine flooding, and (2) the coal-forming plants are supposed to have been adapted uniquely to the terrestrial swamp environment. This second supposition is now challenged by an improved paleoecology of tree lycopoids and the dominant coal-forest tree-fern *Psaronius* (extensive literature review and documentation are provided in Appendix A and Appendix B). Lycopoid and tree-fern anatomies are characterized by air-filled chambers for buoyancy with rooting structures that are not suited for growth into and through terrestrial soil. Lycopoid development included boat-like dispersing spores, establishment of abundant buoyant branching and radiating rhizomorphs prior to upright stem growth, and prolonged life of the unbranched trunk prior to abrupt terminating growth of reproductive branches. The tree fern *Psaronius* is now understood better than previously to have had a much thicker, more flaring, and further spreading outer root mantle. Its increasingly heavy leaf crown was counterbalanced by forcing the basally rotting cane-like trunk and attached inner portion of the root mantle continually deeper underwater.

Important progress has been made during the three-hundred-years that geologists have been considering the question. Lycopoids and tree-ferns formed living floating mats capable of supporting the trunks. Paleobotany of coal plants should now be best understood as supporting a floating raft that deposited the detritus that now forms Carboniferous coal beds.

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APPENDIX A

Rhizomorphic lycopsids -- detailed documentation of observations and interpretations from conventional paleobotanical literature. Comments in square brackets are our insertions. Literature cited in the quotations, but not by us, are not included in the References list.

1. Rhizomorphic lycopsid bodies are composed of discrete modules.

Bateman and DiMichele (1991) label these modules on a drawing of a stylized composite lycopsid tree in Figure 2 (p. 198), saying:

...determinate growth distinguishes lepidodendraleans from most other tracheophyte lineages,... Thus it is reasonable ...to speak of a developmentally highly constrained, genetically imposed body plan.... This is further constrained by the limited number of major structural units available to the lepidodendraleans. We recognize four: rhizomorph, stem..., crown branches..., and lateral branches/cauline peduncles.... All units are modules of determinate growth. (pp. 197-198).

Bateman (1994) elaborates the concept of the modular growth of lycopsids and provides graphical drawings of the modules and their variations in his Figure 5 (p. 546).

Determinate, modular growth distinguishes the rhizomorphic lycopsids from most other tracheophyte lineages;...(p. 544).

... four fundamental, large-scale growth modules (axial units of determinate growth: Fig. 5). Here, the four units are recircumscribed and formally defined:

(A) rhizomorph: the entire axial system generated by the positively geotropic product of the initial embryonic vascular dichotomy.

(B) stem: that part of the negatively geotropic product of the initial embryonic vascular dichotomy that precedes the first isotomous [equal] division of the stem apical meristem.

(C) terminal crown: non-repetitive, isotomous aerial axial branch system terminating the stem and initiated by the first isotomous division of the stem apical meristem.

(D) lateral branches: repetitive aerial axial systems, each initiated by a strongly anisotomous [unequal] division of the stem apical meristem (cauline lateral branches: D1) or of the apical meristems of its isotomous products in the crown (crown lateral branches: (p. 545).

2. Understanding of rhizomorphic lycopsids is not to be based on analogy with spermatophytes

However, the arboreal lycopsids and spermatophytes share little more than a large body size and erect stem, which in turn necessitate bipolar growth, a robust centralized rootstock subtending the stem, and extensive production of structural support tissues. Each recent study has added to the lengthening list of fundamental differences in growth architecture, anatomy, ontogeny and physiology that separate lycopsid from spermatophyte trees. (Bateman 1994, p. 537).

Bipolar growth typically involved an initial dichotomy of the embryonic vasculature, analogous to that in spermatophytes but essentially by shoot-shoot rather than shoot-root dichotomy. Thus, the aerial axial system was, to a large extent, replicated in the subterranean system. (Bateman 1994, p. 539)

3. Rhizomorphs (stigmarian axes) contain prominent air-filled chambers

It has long been recognized that fossils of rhizomorph axes (form-genus *Stigmaria*) have a cylindrical area between the stele (plus inner cortex) and the outer cortex which does not contain cellular structure (usually referred to as the middle cortex). Paleobotanists, who look for analogies with seed plant trees, often argue that the empty cavity is due to rapid degradation of thin-walled parenchyma cells after the tree died or was toppled. Other paleobotanists have been more forthright in recognizing air chambers as part of the developmental pattern of the rhizomorphic lycopsids even though they hold that the plants are rooted in swamp peat and/or water-logged soils. They posit that the presence of air chambers would be adaptive in stagnant watery substrates. Could pervasive decay of parenchyma cells of the middle cortex allow adjacent parenchyma cells to remain?

Reed (1941) assumed rapid postmortem decay in saying, "The [rhizomorph] inner cortex is incomplete and there is no preservation beyond it" (p. 672).

Frankenberg and Eggert (1969), concerning the rhizomorph axes recognize that cell frass, not intact cellular tissue is sometimes preserved in fossils. The broken cell frass likely washed into the normally hollow space -- it did not require time for the rhizomorph to die, fragment and the middle cortex to deteriorate before frass washed in.

Cortical zone C₃ [middle cortex] is very seldom preserved, and is generally represented by a hollow space (Plate 3, Fig 12, Plate 14, Fig. 76) When preserved, the C₃ zone consists of a dark brown mass of broken cell-wall material (Plate 14, Fig. 79, Plate 16 Fig. 94) with scattered appendage traces and extraneous material intermixed (p. 24).

Frankenberg and Eggert (1969) note also that where the appendage traces traverse the middle cortex going from the stele to exit the axis that a parenchyma sheath around the trace was preserved, while the space it traverses lacks preserved parenchyma. "In *Stigmaria ficoides* the lateral appendage traces are enclosed by a parenchyma

sheath as they pass through the C₃ zone (Plate 14 Fig 76, Plate 18 Fig 106).” (p. 24). Also, they illustrate their conclusions of the hollow nature of the axis in Text Fig. 3. (p 36).

Stigmarian axes in *Sigillaria* are distinguishable from those of the more typical lycopsids trees. Eggert (1972), however, found the same basic hollow construction in the rhizomorphs of *Sigillaria*, which he illustrates in his Text Figures 1 and 2.

A narrow inner cortex made up of parenchyma surrounds the stele, outside of which a poorly preserved, possibly aerenchymatous or fistular [i.e., hollow], and relatively broad middle cortical region is present. The histology of this middle cortical tissue is still poorly known due to extremely poor or total lack of preservation present in specimens at hand. (p. 93).

Likewise, Eggert (1972) found in *Sigillaria* the same construction of appendage traces through the hollow middle cortex of the rhizomorphic axis as in the typical tree lycopsids. Note that he points out that the traces were oriented perpendicular to the axis stele as emphasized by creationist Woolley (2011a, b) by saying,

The lateral appendage traces had a horizontal course within the xylem zones and outer cortex Representation by some authors showing these traces arching acropetally in the middle cortex appear to be due to their interpreting displacement of these traces prior to preservation as a natural feature of the living organ....The appendage trace is surrounded by a parenchyma sheath where it extends across the middle cortex. (p. 97).

Rothwell and Erwin (1985) sectioned and described an exceptionally well-preserved fossil *Paurodendron*. This genus is considered a pseudoherb that is more like a shrub with a short unbranched rhizomorph, no trunk, and woody twigs. The fossil preserved the structure from rhizomorph apex through rhizomorph-stem transition zone to base of the stem. They found a hollow air-filled cylinder extending throughout the rhizomorph through the transition zone into the lower stem. This air chamber corresponds to the middle cortex of other stigmarian rhizomorphs. The only cells of this middle cortex are perfectly preserved and prove to be a single thin layer forming a cylindrical veil suspended in the air chamber. They suggest the veil is the inner cortex that does not form in direct contact with the stele. Thus, the middle cortex either does not form cells in the rhizomorphs and lower stems, or it consists of only a thin layer of cells within the air-chamber.

In the transition zone, the xylem is separated from a solid layer of cortex by a space within which there is suspended a delicate cylinder of 1-2 layers of thin-walled cells (Fig. 1, 12). This is the inner, aerenchymatous cortex (Fig. 9; p. 87).

Furthermore, Rothwell and Erwin argue that the rhizomorph of *Paurodendron* and those of other rhizomorphic lycopsids in their anatomy are similar. In particular they refer specifically to the specimen of Fig. 76 in Frankenburg and Eggert (1969):

We suspect that this specimen represents a segment from the proximal region of a stigmarian system that was preserved at a state when little secondary growth

had occurred. If true, then a single stigmarian axis of a sporeling was remarkable similar to the rhizomorph of *Paurodendron*. (p. 89).

Phillips and DiMichele (1992) acknowledge that the middle cortex of rhizomorphs is air-filled at maturity.

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. (p. 565).

Further in their paper they say, “The stigmarian systems of these plants [*Lepidophloios*] were robust, with large appendages and substantial air cavities in both appendages and main axes.” (p.577).

Phillips and DiMichele (1992) also point out the interesting fact that, unlike seed-plant trees in which secondary growth produces an outward expansion of stem and root diameter, secondary growth produces an inward expansion. A logical deduction that can be made from their observation is that rhizomorphs and trunks *had* to be hollow because secondary growth of periderm was to the inside.

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 externally 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.

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. (pp. 566-567).

Bateman et al. (1992) recognize the central air-chambers of rhizomorphs, as well as stems and suggest a possible function.

The persistent inner cortex may have provided a barrier of live cells along the outer margin of the phloem, protecting this delicate tissue from exposure to the central void created by the presumed in vivo disintegration of the thin-walled parenchyma of the middle cortex (p. 541).

4. Rhizomorph appendages (water leaves) contain prominent air-filled chambers

Because broken sections of rhizomorph appendages are such common features of coal-ball preservation, it has long been recognized that most of the length of appendages contains a central air-filled chamber.

Stewart (1947) explains that delicate parenchyma cells of the middle cortex are preserved in the appendages, but these occur only at the base of the appendage. Either the cells develop and

persist (or do not break down during development) only there.

The cells of the middle cortex of the [stigmarian] appendage remain intact for only a short distance after the appendage becomes free from the tissues of the main axis (fig. 16). They then give way to an open crescent shaped cavity devoid of tissue (fig. 16 and 18) which is typical of free stigmarian appendages. (p. 319).

Again, Stewart states, “The middle cortex of the root persists for only a short distance. It gives way to a horseshoe-shaped cavity as can be seen in fig. 23, 22 and 27” (p. 321).

Steward (1947) conducted a comparative study of *Stigmaria* and *Isoetes* (a living lycopsid) and concluded that structures called roots in *Isoetes* and the stigmarian appendages are equivalent structures including the central hollow air-space making up the middle cortex. However, there are differences between Paleozoic rhizomorphic lycopsids and *Isoetes*. Roots of *Isoetes* are much smaller, arranged in rows, and actually are known to penetrate soft mud underwater. Moreover, the much-reduced stem/rhizophore corm of *Isoetes* does not have a hollow middle cortex, but *Isoetes* does not float but is emergent from the bottom of a shallow pool.

However, from the evidence presented it appears more reasonable to regard the roots of *Isoetes* and the appendages of *Stigmaria* as strictly comparable. Even the minute anatomical structure of the phloem, inner cortex, middle cortex, outer cortex, etc., show many similar features. (p. 324).

Frankenberg and Eggert (1969) document the hollow nature of rhizomorph appendages, especially by the micrographs in their Plate 23. They diagram the structure in Text Figure 3 (p. 36).

In the appendages of *Stigmaria ficoides* the middle cortex is preserved only near the appendage base. This lack of preservation of the middle cortex in distal parts of the appendage is responsible for the general conclusion presented in the literature that this portion of the appendage consisted of a hollow region in the living organ....At the extreme base of the appendage lacuna a rather dense aerenchyma occupies the region of the middle cortex (Plate 21 Fig. 122 in the upper right hand portion, Fig 124 above the indication AL₁, Plate 26 Fig. 147). As one progresses distally, this tissue becomes more spongy in appearance and the cells take on a somewhat stellate form (Plate 20 Fig 116, Plate 21 Fig. 123).... Oftentimes, only a small amount of the basalmost middle cortex is preserved (Plate 20 Figs 118, 119, Plate 22 Fig 125)....The middle cortex intergrades below into the compact dome previously described, which has been referred as the rootlet cushion by some authors....our observations suggests that this tissue was confined to the relatively basal portions of the appendage....the vascular bundle and its enclosing sheath were free in the hollow middle cortical region throughout most of the length of the appendage. (pp. 32-33).

Eggert (1972), concerning lateral appendages of *Stigmaria* (see his plate 1, fig. 18, 19),

The monarch vascular bundle is surrounded by a parenchyma sheath (inner cortex of some authors) and is attached to the outer cortex by means of a relatively narrow bridge of tissue often called the connective. A broad hollow region occurs between the bundle sheath and the outer cortex except where the connective is found. (p. 94).

Eggert (1972), found the same anatomy as did Frankenberg and Eggert (1969), “...a spongy middle cortex is present at the base of the appendages and becomes progressively disorganized distally coming to be represented by a prominent lacuna” (p. 97).

Phillips and DiMichele (1992) emphasize the buoyancy and size of rhizomorph appendages by saying, “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” (p. 561). They also note the hollowness of the appendages in describing the main axes.

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. (p. 565).

Bateman (1994) suggests a possible function for the air-chambers in rhizomorph appendages, “The aerenchymous nature of the stigmarian rootlets... (lacunae...) in the...cortex indicate a need for local aeration, perhaps to maintain an optimal O₂ : CO₂, balance” (p. 543).

Hetherington et al. (2016) reiterated the hollowness of the appendages.

This analysis was possible because stigmarian rootlets are ubiquitous in coal balls ([footnotes] 49, 50), and can be readily identified because of their unique cellular anatomy composed of three zones of cortex, the middle of which rapidly disintegrates, leading to the formation of a large air space containing the inner cortex and central vascular strand (17, 21). (p. 4).

Hetherington et al. (2016) also pointed out that stigmarian rootlets of *Sigillaria* were differentiated from those of other tree lycopsids, but still possessed central air chambers.

There is a “connective” of cortical tissue between the vascular trace and the outer cortex in sigillarian rootlets (4, 17, 18, 21, 48; Fig. S10A). By contrast, there is no connective in the central cavity of the nonsigillarian rootlet and the central vascular trace is free within the rootlet cavity (4, 17, 21; Fig. S10B). (p. 3).

5. Stems contain prominent air-filled chambers

As with rhizomorph axes, stems of rhizomorphic lycopsids usually lack cellular structure in the middle cortex. Although paleobotanists who hold to the swamp forest model generally posit that the tissue simply rotted after the tree died or was toppled, recently some paleobotanists have gradually come to accept air-chambers, which are documented at least in the trunks. The only definite evidence of a tissue-filled middle cortex is in the small twigs and

horizontal branches in the dichotomously branching crowns. This appears to be related to preventing the horizontal branches from collapsing from lateral gravitational pull. Evidence suggests that the parenchymatous middle cortex is secondary, proliferating into the hollow air chamber from remnant cells or adjacent parenchyma of the inner or outer cortex after the initial growth of the branch (see section 6).

Reed (1941) describes what we interpret as hollow, air-filled stems into which fragmented stigmarian rootlets flowed.

Almost everyone who has worked with coal ball material has commented upon the abundance and frequency of stigmarian rootlets. They are found not only intermingled with other vegetable debris, but they penetrate tissues as the pith region of stems of any and all genera of contemporary plants. (p. 672).

Pannell (1942), who describes *Lepidodendron scleroticum* as a new species, notes that in the fossil stem segment, “The remaining cortical cells, separated from the inner cortex by a cavity caused by the decay of that tissue, are well preserved” (p. 254).

Andrews and Murdy (1958) describes the cortex of a lower stem of young *Lepidophloios pachydermatikos* and notes that tissue in the middle cortex was lacking, “Aside from the leaf traces which traverse and the band of presumed secretory cells, only the outermost part of this region is preserved” (p. 553).

Eggert (1961) confirms earlier reports of a hollow trunk in which the central stele fragmented and pieces from different vertical levels fell down inside the trunk to be fossilized at the same level in trunk.

These specimens (*Lepidophloios wuenschanus*) consisted of upright calcified trunks, about one-meter high containing one to several steles inside of the hollow cylinder of periderm composing the outer portions of the trunks. The steles are oriented vertically and various other plant parts abound in the mineral matrix filling the surrounding cavity between the steles and the periderm cylinder (Pl. 14, fig. 37; p. 60).

In this article Eggert (1961) conducted an extensive analysis of the development of lycopoid trees with dichotomously branched crowns. Most of the figures and images of branch cross sections, even very small ones, show either an obvious hollow cylinder, or show the stem collapsed with the outer cortex from two sides pressed together around the inner cortex and stele. He cites only two specimens with continuous cellular tissue in the middle cortex (pp. 69-70), without a cylindrical air chamber or lacuna. In his Plate 11 (Figure 1) is shown a tiny distal branch only about 5 to 10 mm in diameter with a middle cortex of primary isodiametric parenchyma cells. Based on a specimen of about 15 cm diameter (Plate 13 Figure 34), he suggests that in crown branches that cellular middle cortex that differed in appearance from that of the small twigs occurred. However, he also mentions that in a larger branch [diameter about 17 cm, without image] the only cells in the middle cortex are those radiating cells sheathing the leaf traces through the empty middle cortex.

Regardless of the size of the branch, there are three

recognizable cortical zones. In many of the specimens the cells of the middle cortical zone are not preserved so that a circumstellar lacuna results. Whether this is due to some natural loss of the tissues during development or is only due to the preservation remains uncertain. (p. 69).

The middle cortical zone makes up a larger proportion of the mass [i.e., volume] of the branch. The histology of this zone is quite variable, but unlike the inner zone, the tissue makeup seems to be related to the size and age of the branch. Unfortunately, we lack a sufficient number of specimens of any single species in which this zone is preserved, to arrive adequately at the changes from one level to another in the plant and to distinguish such changes from those arising as part of the aging process at any given level. (p. 69).

The developmental changes in the middle and outer cortex at the base of the tree remain unknown. Generally large trunks are found with a hollow zone around the stele, which extends to the periderm cylinder and which may have small amounts of old outer cortex along its inner margin. Whether the middle cortex was able to expand by cell proliferation and enlargement to keep up with the expansion of the secondary cortical cylinder is unknown. It is possible that the middle cortical tissues might have been torn apart by the expansion, to produce a circumstellar lacuna as Beck (1957) has suggested for the lowest levels of *Levicaulis arranensis* (p. 70).

The exact changes occurring in the inner and middle cortical tissues remain unknown; they are generally represented by the presence of a wide circumstellar lacuna between the outer margin of the stele and the fragments of outer cortex adhering to the periderm cylinder. (p.82).

Taylor and Eggert (1967, p. 415 and Figure 1) describe an aerial stem (minus leaf bases) ca. 2 cm diameter with well-preserved spongy middle cortex.

DiMichele (1979a) describes fossils of *Lepidophloios* (all tentative names he uses are synonyms of *Lepidophloios hallii*) upper stem and crown branches, and middle cortex is observable only in distal twigs. The branch in Plate 2, figure 7 is approximately 4 to 6 cm in diameter.

The cortex of most arborescent lycopods, including *Lepidophloios*, consists of three zones (Plate 2, fig. 7). These are recognizable only in branches from the upper parts of the plant in *Lepidophloios* (*L. pachydermatikos*), where secondary vascular growth has not disrupted the two inner zones.... Middle cortical tissues are rarely preserved. (pp. 62-63).

DiMichele (1979a) notes the missing cells in middle cortex of another species, “Although the inner and middle cortical tissues are not known in *L. kansanus*, the structure of its outer cortex is identical to that of *L. pachydermatikos*” (p. 66).

DiMichele (1979b) described twigs and larger dichotomizing branches proximal in crown of *Lepidodendron*. All showed middle cortex consisting of isodiametric cells and up to 2.5 mm in thickness.

These are the horizontal branches in which parenchyma cells of the middle cortex are needed to maintain the turgidity that keeps gravity from sharply bending the branches. This is consistent with reports of reduced secondary xylem and cortex (i.e., periderm) in these parts of the plant (see section 6 below). See his Plate 1, figs. 2, 4, 5; Plate 3, figs. 12, 13. He says, “The middle cortex is a zone of thin-walled parenchyma, up to six times as broad as the inner cortex. Cells are isodiametric 30-16-μm diameter, with a random size distribution and arrangement except around the leaf traces.” (p. 126).

DiMichele (1981) described twigs and larger dichotomizing branches proximal in the crown of *Lepidodendron* (including later segregated genera, especially *Diaphorodendron*). For *L. vasculare* he provides micrographs with cellular middle cortex in branches 2 to 5 cm in diameter (Plate 2). In others images of similar size, tissue appears to be lacking. Apparently, he did not describe the cortex of trunk sections. He says,

Most specimens of *Lepidodendron. vasculare* obtained from coal balls are <5 cm in diameter...and apparently represent deciduous lateral branches (Plate 1, Figs. 1-8). (p. 92).

The middle cortex is composed of thin-walled, isodiametric cells about 60 μm in diameter (Plate 2, Figs. 13, 14). They are randomly arranged, except around leaf traces where they form radially aligned rows up to 10 cells long around the traces. There are few or no secretory-like cells in the middle cortex of most stems. At the outer edge of the middle cortical zone cells are frequently radially aligned, and superficially resemble a secondary cortical layer. The middle cortex is the cortical zone that is usually not preserved. (p. 94).

DiMichele (1981) also describes cortex of *Lepidodendron scleroticum*. The stems illustrated (Plate 6 Figure 51; Plate 7 Figures 53, 54, 56, 57, 58) ranged in size from 0.3 cm to 5 cm in diameter. His description of *Lepidodendron phillipsii* is similar and the illustrated stems (Plate 10 Figures 84, 88) are 1.5 to 3 cm in diameter.

The middle cortex is up to five times the width of the inner cortex, its preservation is variable. Thin-walled parenchyma cells, 40-70 μm in diameter, are randomly arranged, except around leaf traces where they form files over 10 cells long that radiate around the traces. (p. 101).

Concerning the several species he studied, based on the twigs and small branches DiMichele (1981) says,

The cortex is three-zoned in all *Lepidodendron* species. The inner zone is a narrow layer of small diameter cylindrical cells and the middle cortex is composed of thin walled isodiametric cells. In all species, cells of the middle cortex are preferentially oriented in radiating files around leaf traces. (p. 114-115).

See report by Rothwell and Erwin (1985) above concerning air chambers in rhizomorphs. Their specimen included the transition zone into the stem base, which showed the same structure of the middle cortex.

Bateman et al. (1992) speaking of stems (as well as rhizomorphs, see above) of rhizomorphic lycopsids generally say,

The persistent inner cortex may have provided a barrier of live cells along the outer margin of the phloem, protecting this delicate tissue from exposure to the central void created by the presumed in vivo disintegration of the thin-walled parenchyma of the middle cortex (p. 541).

See quote by Phillips and DiMichelle (1992) under air chambers in rhizomorphs that stated that periderm growth was to the inside of stems, as well as rhizomorphs, supporting the idea that the inward growth was into the cylindrical air chamber in trunks.

Bateman (1994), who recognizes air channels in stems, proposes a functional adaptation related to gas exchange. He then goes on to suggest this gas exchange anatomy was due to an unusual physiology of plant photosynthetic modifications rather than design for aquatic habitats. The pertinent passage is, “The aerenchymous nature of the stigmarian rootlets and radial air channels (lacunae and parichnos) in the leaves and/or cortex indicate a need for local aeration, perhaps to maintain an optimal O₂ : CO₂ balance” (p. 543).

In an insightful note, Bateman (1994) points out that the rhizomorphic lycopsids were unusually light weight for their size. While admitting “local aeration” in the quote above and a “central void” in 1992, he says,

The weight : volume ratio was well below that of any similarly-sized extant spermatophyte -- the main benefit of using circumferential periderm for support, restricting wood to a transport role, and packing the rest of the axial interior with unlignified tissues composed largely of thin-walled parenchyma. (p. 543).

Therefore, it is not clear whether he means that thin-wall parenchyma occurs except in the “central void” or that the in vivo disintegration to form the “central void” occurs late in the life of the stem. However, if the middle cortex were really filled with thin-walled parenchyma (or even a spongy aerenchyma), that is, water-filled cells with thin walls, then the weight to volume ratio would not be lowered as much as he suggests. It would require extensive hollow air channels, which are best fit by the middle cortex lacking cells as soon as the cell maturation occurs behind the apical meristem.

6. Primary outer cortex and primary/secondary parenchyma in middle cortex important for support of stem branches.

Eggert (1961) recognizes that parenchyma cells from adjacent cortex or remnant from cellular degeneration in early development of the middle cortex lacuna (air-space cavity) dedifferentiate to divide and produce a type of secondary parenchyma different from secondary cortex (periderm). This secondary parenchyma encroaching upon or traversing the middle cortex lacuna is seen in horizontal branches (crown or cauline branches) in which the proportion of secondary xylem and periderm to primary xylem and primary cortex becomes increasingly smaller as the branches are more and more distal. In small twigs, primary parenchyma of the middle cortex apparently either persists at twig maturity or develops there in contradistinction to larger branches. He says,

The middle cortical zone makes up a larger proportion

of the mass [i.e., volume] of the branch. The histology of this zone is quite variable, but unlike the inner zone, the tissue makeup seems to be related to the size and age of the branch. Unfortunately, we lack a sufficient number of specimens of any single species in which this zone is preserved, to arrive adequately at the changes from one level to another in the plant and to distinguish such changes from those arising as part of the aging process at any given level....The smaller specimen [5-10 mm in diameter], a protostelic branch of the same species as the larger one, has a middle cortical zone made up of relatively large, isodiametric parenchyma cells (Plate 11, fig.1), while the larger stem [ca. 17 cm diameter], representing a more basal level, shows a comparable cortical zone *with a very different histology* [emphasis by RWS & SAA]. In the larger stem the middle cortex possesses lacunae with radiating series of parenchyma cells about the leaf traces. This lacunar middle cortex of *Lepidodendron vasculare* may have arisen from continued cell division and expansion of a more homogeneous tissue [emphasis by RWS & SAA] lacking lacunae. However, lacking sufficient specimens, we cannot correlate the changes in the middle cortex with aging. In this regard, we may mention that the middle cortices of large branches of other species of *Lepidodendron* which appear to be relatively advanced in age show extremely large amounts of radially seriated parenchyma surrounding the leaf traces. Usually the intervening cells between these cylinders of what appears to be secondary parenchyma are not preserved. Occasionally, other indications of proliferation of secondary parenchyma occur and are evident as radially aligned rows of cells in the outer portion of the middle cortex. The evidence at hand, therefore points to the ability of the middle cortex to undergo cell division and to produce secondary tissue with age. (pp. 69-70).

The developmental changes in the middle and outer cortex at the base of the tree remain unknown. Generally large trunks are found with a hollow zone around the stele, which extends to the periderm cylinder and which may have small amounts of old outer cortex along its inner margin. Whether the middle cortex was able to expand by cell proliferation and enlargement to keep up with the expansion of the secondary cortical cylinder is unknown. It is possible that the middle cortical tissues might have been torn apart by the expansion, to produce a circumstellar lacuna as Beck (1957) has suggested for the lowest levels of *Levicaulis arranensis*. It is clear that later in the development of the plant, massive branches possessed very extensive middle cortical zones (e.g. LD-1, Pl. 13, fig. 34 [stem ca. 15 cm diameter]), and that this zone was relatively compact and non-lacunar, even after considerable secondary cortical proliferation had occurred. It therefore seems unlikely that the crown branches developed circumstellar lacunae with age, at least in some of the species. (p. 70).

DiMichele (1979a) describes fossils of *Lepidophloios* (all tentative

names he uses are synonyms of *Lepidophloios hallii*) upper stem and crown branches, and middle cortex is observable only in distal twigs. Apparently, the middle cortex, where observed, was added support for the primary outer cortex because secondary cortex (i.e., periderm) was not as well developed in crown branches as in the trunk.

Although the inner and middle cortical tissues are not known in *L. kansanus*, the structure of its outer cortex is identical to that of *L. pachydermatikos*. The tissue zone [vis. outer cortex] is usually very thick in relation to other primary tissues. The cells are more decay resistant than most other types except the tracheids and the secretory cells of the periderm. The outer cortex was a supportive tissue and the major support in the crown where periderm development was markedly reduced and secondary xylem was lacking. (p. 66).

DiMichele (1981) describes what can be interpreted as secondary parenchyma derived from the dedifferentiation of residual middle cortex cells, "At the outer edge of the middle cortical zone cells are frequently radially aligned, and superficially resemble a secondary cortical layer" (p. 94).

7. Early development and establishment of basic growth pattern.

Germination resulted in an early formed rhizomorphic system, latent truck meristem dome followed by growth of upright unbranched, densely leafy trunk.

Andrews and Murdy (1958) described young trunks of *Lepidophloios* and developed an understanding of the development of those trunk, including a reconstruction illustrated in their Figure 13.

There seems to be no reason to doubt that the part of the plant represented by our specimens grew by means of massive apical meristem comparable in a general way with the mode of growth found in modern palms and tree ferns in which a large stem diameter is reached rather early in ontogeny and then tends to remain constant. If this concept is correct we suggest that many of the *Lepidodendron* and *Lepidophloios* trees in a Carboniferous landscape consisted of a tall (in some cases extraordinarily tall) unbranched trunk.... Also the evidence from many specimens indicates that the leaves were not retained for any great length of time so that a primary trunk of 40 to 50 ft high probably held its leaves only on the uppermost few feet. (pp. 557-558).

Andrews and Murdy (1958) summarize this development as:

It is therefore our conclusion that the ontogeny of the aerial parts...in the arborescent lycopods in general was essentially as follows: 1. In early stages the sporeling possessed a small protostele which enlarged rapidly in an obconical fashion....2. The primary trunk soon attained a diameter which remained essentially constant and continued growing upward to a considerable height...3. When the apical meristem started to divide, it continued doing so with the primary wood becoming progressively

smaller to a point at which longitudinal growth was terminated. (p 559).

The apex presumed by these authors in points 1 and 2 was actually found later, which Opluštil (2010) described. Possible creationist explanations for rarity of trunk apices are 1) that the establishment and death of whole forests were synchronized resulting in large single-aged stands, and the Flood occurred at the time when most forests had already entered the brief terminal reproductive phase, or 2) the apices were more likely to have been simply ground up and sunk with the bark to become part of the coal, as opposed to floating like the small twig fragments.

Eggert (1961) agrees essentially with Andrews and Murdy (1958). The quotes below and his Text Figure 60 summarize his ideas. First, he points out that the size of the stems can be deduced from the size and spacing of leaf bases. Then he points out that initially the earliest stem of the sporeling is small but rapidly increases through some sort of primary thickening meristem to form in the young plant an arrested apical dome, which he thinks is unique rather than like that of palms.

Concerning leaf-base size, Eggert (1961) says, “Large branches have large leaf bases and smaller branches have progressively smaller leaf bases...As branch diameter decreases, leaf base size decreases...as the branch became smaller, the number of leaf bases sectioned at a given level became less...a progressive reduction in length and width of the leaves is encountered as one moves toward the branch apices.” (pp. 67-68). On page 69 Eggert mentions young plants with leaves about 80 cm long. Then he summarizes, “Leaves of some species were small at the base, larger above, and again smaller at higher levels” (p. 77).

Concerning the sporeling stem and its enlargement Eggert (1961) concludes, “The stelar series above does allow us to suggest that the development of a plant of *Sigillaria* was essentially like that of *Lepidodendron* and *Lepidophloios*, growing from a small sporeling rather than from a massive bulbil or bud” (p. 74).

The early stages of development of the aerial portion of an arborescent lycopod witnessed the production of an increasingly more massive primary body.... The exact changes occurring in the inner and middle cortical tissues remain unknown; they are generally represented by the presence of a wide circumstellar lacuna between the outer margin of the stele and the fragments of the outer cortex adhering to the periderm cylinder. (p. 82).

From the presence of leaf traces at the very base of the trunks...it appears that the young sporeling was leafy. Although a great deal of lateral tissue production occurred to create the massive primary body of the trunk as it developed, elongation of the stem tissues after differentiation was probably very slight, since we find no evidence of any vertical separation of the leaf bases, nor any disruption of the protoxylem strands. As the stem developed, we may imagine it becoming increasingly larger and larger in diameter as well as in height, with progressively larger leaf bases in more and more orthostichies on the stem surface. Secondary cortical tissues would be developing meanwhile, causing

expansion of the lower levels so that the stem would remain columnar even though the successively formed primary systems would be increasingly larger.

The culmination of the expansive phase resulted in a stem with a massive primary body and with a siphonostelic vascular cylinder, exceeding 5 cm in diameter in at least some of the species, and with a large pith. The trunk was clothed with large leaf bases, which probably bore long, and relatively wide leaves at least in some forms.... Progressive increase in the dimensions of the primary body probably continued until the trunk underwent the first dichotomy...we may tentatively estimate the range as being at least from 40 to 114 feet above the base of the plant. (p. 83).

We lack specimens that give us any information regarding the actual size of the shoot apex in an arborescent lycopod at any stage in the development. Furthermore we lack information concerning the presence or absence of some sort of an organized lateral primary thickening meristem or of the distance behind the apex in which occurred such processes as cell elongation and primary thickening prior to differentiation of the tissues.

It should be pointed out that an organized primary thickening meristem, such as that of some palms and cycads, need not be present to produce a relatively massive stem of primary nature....It is clear, therefore, that a number of possible methods could have resulted in the type of primary body found in the arborescent lycopods, and that we cannot determine the specific type which was present from the mature specimens we possess. (pp. 85-86).

Wnuk (1985) in describing *Lepidodendron rimosum* reaffirms the establishment of an arrested, large-diameter apical dome of the trunk and maintenance of that diameter as the trunk grows upward. See his Figure 12, p 168, for “hairy telephone poles.”

Andrews and Murdy (1958) and Eggert (1961) both suggest that the meristem could have continued enlarging until the tree’s first branching, but in the mature trunks 3, 6, 8, etc. there is relatively little change in [leaf] cushion size over long trunk sections suggesting perhaps that the meristem reached a constant, steady-state size much earlier in the plant’s ontogeny than previously thought.... Perhaps the juvenile state could best be defined as the time during which the apical meristem is actively enlarging, and not the period during which the trunk is unbranched.... (p. 167)

In his discussion, Wnuk (1985) says, “Pigg & Rothwell (1979) suggest that laterally extending root systems were required to prevent the massive arborescent lycopods from uprooting and toppling in the soft, incompetent sediments,” implying that the rhizomorphs would need to be established before trunk growth could progress (p. 179).

Phillips and DiMichele (1992) argue for the early establishment of the rhizomorph while the stem remains as a latent meristematic

dome and the eventual growth of the trunk as an unbranched leafy pole. See their Figure 2 (page 571).

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. Such a large apex may have been supplemented by some kind of primary thickening meristem, particularly important in the establishment growth phase. (p. 564).

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.... 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. (p. 565).

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.... 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. (p. 570).

Bateman (1994) further explained how the initial growth from the embryo developed. See especially his Figure 4.

In *Lepidophloios-Lepidocarpon*, rapid radial expansion of the stem and rhizomorph apical meristems followed the primary embryonic dichotomy as resources were shared between the first-formed leaves and rootlets, creating the ‘ transition zone ‘ that links the two axial systems. Two closely spaced, isotomous apical divisions then produced the radially symmetrical stigmarian rhizomorph (thereby

severely disrupting the pith). Both the stigmarian branches and stem possessed large, domed, determinate apical meristems that emitted in tight helices more-or-less terete, hispid, monarch appendages (undivided microphylls and often once-divided rootlets respectively: Fig. 4b). Exarch centripetal maturation of the primary xylem was followed by rapid development of secondary xylem immediately behind the apical dome. (p. 540).

Xylem maturation differed between the stem plus aerial branches (exarch, medullated protostele or siphonostele) and the rhizomorph (arguably the product of a primary thickening meristem, with wide rays dissecting the wood into wedges to give the false impression of a dictyostele). Nonetheless, as growth proceeded in the branches of both the stem and the rhizomorph, the apical dome gradually increased in diameter (reflected in increasing medullation), whereas the amounts of wood and periderm decreased (Figs 4c, 5 left: Walton, 1935; Eggert, 1961; Frankenberg & Eggert 1969). Rothwell & Pryor (1991) plausibly suggested that these observations imply a significant modification in the behavior of the apical meristems during ontogeny. Beyond the transition zone, the first-formed unifacial vascular cambium behaved as a primary thickening meristem, analogous to those of monocotyledonous angiosperms such as palms.

Indeed, other aspects of rhizomorphic lycopsids ontogeny parallel those of palms (Figs 4a-c vs. d-f). Common sense suggests that stem elongation was preceded by extensive development of the rhizomorph, to provide firm anchorage and a reliable nutrient supply. Subsequent stem growth was rapid and confined to a narrow zone immediately below the huge apical meristem. Only limited radial expansion could be accommodated by the rhombohedral leaf-bases cladding the stem, either by passive inter-cushion fissuring or by active inter- or sub-cushion cortical expansion (DiMichele & Phillips, 1985). Similarly, neither leaf bases nor leaves were capable of substantial post-meristematic enlargement. (p. 541).

8. Reproductive phase short lived compared to the pole phase of growth.

Following from the understanding that the trunk developed after the rhizomorph was established and then grew as a uniform diameter pole is that the aerial branching systems developed only for a relatively brief period to form spores at the end of the life of the plant. Further, if sections of forest were of single age class due to germinating spores dispersing into a recently cleared area, then those sections would be forests of poles for an extended period and have a forest canopy for a brief period followed by collapse of the forest section. These general ideas are developed by the following authors.

Wnuk (1985) concerning *Lepidodendron* says, “Since all branchings are dichotomies in *L. rimosum*, this species has a determinate growth strategy. The high number of supposed juveniles in this population suggests that these plants were monocarpic, reproducing and dying when growth had been completed.” (p. 179).

Phillips and DiMichele (1992):

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.... Most constructions show lepidodendrids in late to terminal reproductive or “death” stages. (p. 561).

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 [because of much reduced leaf size] permitted high light penetration. (p. 567).

Bateman (1994):

Branches resulting from anisotomies [thin branches coming off of thick branches] also tended to be shed as units (Jonker, 1976), reflecting their primary function of rapid cone production and propagule dispersal rather than photosynthesis *per se* (DiMichele & Phillips, 1985; Phillips & DiMichele, 1992). (p. 543).

A. Species with many, large multiforking crown branches and no cauline branches

This delayed, short-lived, terminal reproductive phase is especially evident in the three genera (*Lepidodendron*, *Lepidophloios*, and *Synchysidendron*) that have all branches formed at the top of the tree by sequential dichotomous forkings of the trunk apical meristem.

Eggert (1961) in summarizing his work on *Lepidodendron* and *Lepidophloios* says,

It remains a possibility that the entire crown portion might have been produced at the apical meristem of the trunk, with rapid elongation of the branches prior to the differentiation of the leaf bases, leaves, and vascular system. As was mentioned previously, the structure of the mature branches does not favor the presence of any extensive elongation of the branch after the differentiation of the protoxylem and leaf bases. (p. 86).

Bateman et al. (1992):

The first subgroup includes the classic arboreal genera *Lepidodendron* and *Lepidophloios*, together with *Synchysidendron* (fig 1). Throughout much of their life history, these trees consist of a rhizomorph and telegraph polelike stem capped by a massive primary body, undergoing frequent dichotomous branching to form a determinate crown only during the final phase of growth and subsequent monocarpic reproduction. (p. 543).

Bateman (1994) researched this concept further. His Figure 6a. (p. 547) shows allometric projection of rapid initial rhizomorph growth followed by steady prolonged trunk growth, and abbreviated terminal crown branch growth. His Figures 10 and 12 (pp. 556, 558) show relative time of module growth. In *Lepidodendron*, *Lepidophloios*, and *Synchysidendron*, trunk growth lasts three

times as long as crown growth.

The dominantly crown-branched trees *Synchysidendron*, *Lepidodendron* and *Lepidophloios* (Fig. 6a) produced large, repeatedly and isotomously branched ‘stigmarian’ rhizomorphs. The stem then grew rapidly (in effect it ‘bolted’) to produce a ‘telegraph pole’, which greatly exceeded the rhizomorph in size and lacked cauline lateral branches. At an approximately predetermined height the domed apical meristem divided isotomously, terminating stem growth and initiating extensive crown development. Repeated lower-order isotomous branching in the crown was followed by anisotomous divisions to produce crown lateral branches. Together these axial systems generated an extensive physical framework, transient and with poorly developed secondary tissues, to display the abundant reproductive cones. Because crown production exhausted the products of the stem apical meristem, reproduction was rapid and immediately preceded the death of the individual (monocarpism).” (Bateman 1994, p. 548).

Opluštil (2010) concurred with Bateman. See his Figure 7.

[*Lepidodendron mannebachense*] started as an unbranched tall columnar stem before branching occurred.... Although these lateral branch systems occur throughout the tree crown, this final (apoxogenic) phase of tree development represents relatively short period of time when reproduction occurred. (p. 314).

B. Species with few, small crown branches and well-developed lateral trunk branches:

The remaining three genera of tree lycopsids produced reproductive lateral branches along the trunk before terminating in a single dichotomy (*Sigillaria*) or a small crown of unequal branches (*Paralycopodites* and *Diaphorodendron*). In all cases the production of lateral reproductive branches occurred during the latter part of the plant’s life. Also, these lateral branches abscised quickly after producing spores, such that only a few branches, not a dense heavy crown, were on the tree at any given time. In *Sigillaria*, the lateral branches were more or less unbranched, forming peduncles for single strobili.

Bateman (1994) shows in Figure 6b (p. 547) allometric projection of rapid initial rhizomorph growth followed by steady prolonged trunk growth and later short bursts of cauline branch and crown branch growth. His Figure 11 and 12 (pp. 557, 558) show relative time of module growth. *Sigillaria* has four times longer trunk growth than crown branch growth; cauline peduncles begin only in last half of trunk growth. *Paralycopodites*, and *Diaphorodendron* have eight times as long trunk growth as crown growth with cauline branch growth only in last half of trunk growth. He states,

Early growth stages resembled those of the dominantly crown-branched genera, though their stems contained more secondary tissue, sequestering photosynthate and therefore indicating less rapid development....In most of the species [*Sigillaria*, *Paralycopodites*, and *Diaphorodendron*] that possessed them, cauline lateral branches were ephemeral, containing little secondary tissue and being shed as cohesive units following cone

maturation....Cauline lateral branch production is assumed to have gradually diminished the stem apical meristem, so that the terminal phase of dominantly isotomous crownbranching was small-scale and heralded death....Reconstructed species of *Paralycopodites* were relatively small-bodied, and *Sigillaria* had a small, compact rhizomorph relative to its robust stem. (pp. 549-550).

9. Rhizomorphs were photosynthetic, capable of autotrophy independent of stem leaves.

Because the development of phloem was very limited in rhizomorphic lycopsids, the trunk and branches could not supply the rhizomorph with sugars for food. In fact, sugars could not be transported up and down the stems, so that all sugars were produced and used locally. Therefore, rhizomorphs had to be photosynthetic, as were the rhizomorphic appendages, which makes sense if the rhizomorphs developed and became established before the trunk grew.

Phillips and DiMichele (1992) were instrumental in developing the idea of photosynthesis of the rhizomorph:

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.... How could lepidodendrids attain such large sizes, even as shortlived plants, if they had limited capabilities to translocate photosynthate between aerial and subterranean systems, as well as within the shoot?... These may be described generally as diffuse photosynthesis with limited translocation and with tissue growth and maintenance derived from local sites of photosynthesis. (p. 565).

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 (p. 567).

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; ... in a lepidodendric dominated tropical-swamp forest with pole-tree canopies, light intensity would have been high enough to support [with photosynthesis] floating or submerged vascular aquatics very near the surface. (p. 569).

Bateman (1994) reiterates the concept:

The least intuitive feature of the rhizomorphic lycopsids is their lack of secondary phloem, a severe physiological constraint. The apparent paucity and radial distortion of primary phloem in the transition zone imply that the rhizomorph and aerial axes endured near-independence in terms of photosynthate transport potential, prompting suggestions that the rootlets may have been photosynthetic. (p. 541).

10. Tall unbranched pole-like trunk also photosynthetic below where leaves have dropped.

Eggert (1961) emphasized that leaves persisted and functioned only in the upper portion of the pole-like trunk and crown branches as these grew. “Secondary cortical development led to the separation and eventual loss of the leaf bases. The outer surface of older portions of the stems consisted of a ridged bark” (p. 77).

If the production and transport of photosynthetic sugars was only local, then the bark of the trunks and larger branches would also have to be photosynthetic.

Phillips and DiMichele (1992) recognized this fact by saying,

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. 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. (p. 567).

Bateman (1994) supports this contention by saying, “Moreover, leaves were shed during ontogeny, leaving distinct ‘abscission scars’ in the more derived tree genera. The presence of stomata on the more persistent leaf cushions suggests that they were capable of continued photosynthesis following leaf loss.” (p. 543).

11. Rhizomorphs parallel branching of stems in crown

Eggert (1961) says that as rhizomorphs branched, they also decreased in diameter and size of appendages:

...the evidence now at hand suggests that the stelar morphology underwent a series of changes which paralleled those found in the crown portion of the plant....As regards rootlet size, one may observe the gradual decrease in size of the rootlets and their scars as one moves distally along the surface of stigmarian casts. Furthermore, the greater amounts of secondary development in the forms of large rootlets and steles tends to point to these levels as being more proximal parts of the underground system. (pp. 75-76).

Phillips and DiMichele (1992):

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. (p. 561).

12. Rhizomorphs not capable of penetrating soil.

Frankenberg and Eggert (1969) provide compelling evidence that the rhizomorph appendages emerged from the axis at right angles completely around the axis, not some bent downwards and some bent to be vertical into the air above soil as is often portrayed in reconstructions.

...the primary vascular system of *Stigmaria ficoides* is dissected into bar-shaped strands of primary xylem as the result of the bending outward of the appendage traces and their associated LA [lateral appendage] gaps. The vertical orientation of the lateral trace within the inner part of the axis can be recognized when serial radial sections are made through the stele (Plate 5 Figs. 22, 24, Plate 11 Fig. 62). The initiation of the trace in the primary vascular tissue is first recognized by the outward bending of a complete strand of primary xylem, which assumes an arc shaped configuration. A short distance outward from the point of initiation the trace bends downward toward a true horizontal position placing it at a right angle to the stele for its remaining course through the stele and cortical tissues (Plate 11 Fig. 62 at arrow).... Fragments of traces are commonly seen in the middle cortex lying in a vertical position which is probably a secondary effect of the breakdown of the middle cortex tissues and the subsequent displacement of the traces [during fossilization]. (p. 27).

Rothwell and his associates have extensively researched rarely found apical meristems of rhizomorphic axes. Rothwell's (1984) Figures 1-5 make it clear that the apices were truncated, blunt, and round with a concave depression at the tip and could not push its way through soil or dense peat, nor could its rootlets grown perpendicular to it in such substrates. He says,

An apical segment of *Stigmaria ficoides* recently has been located among specimens from Pennsylvanian sediments of Iowa, and provides the first indisputable structural evidence for apical organization and development in one of the most enigmatic of all tracheophyte organs. Toward the apex, the specimen tapers to a circular rim. Rootlet scars occur in a helical arrangement from the proximal end of the specimen to the margin of the rim. Within the rim there is a discontinuous groove that surrounds an irregularly concave apex. (p. 1031).

Rothwell and Erwin (1985) describe the well-preserved whole rhizomorph, including apex, as follows:

A rhizomorph of *Paurodendron* with an intact apex recently has been discovered in upper Pennsylvanian sediments of Ohio, and this provides the anatomical evidence necessary to interpret the structure, ontogeny and homologies among lycopphyte rooting organs. The basal meristem of *Paurodendron* is radial and lenticular, and produces an apical plug of parenchymatous tissue similar to a root cap. The plug is surrounded by a furrow associated with radially aligned cells that demonstrate a developmental correspondence to the furrows of *Isoetes*. Based on external structural similarities at the rhizomorph apices of *Paurodendron*, *Stigmaria*, and young *Natherstiana*, and on the anatomical similarities of *Paurodendron* to *Isoetes*, *Stigmaria*, *Chaloneria*, and *Lepidocarpon* embryos, all are interpreted as having a rooting organ that represents a modified shoot system that is fundamentally unlike the primary root system of seed plants. Likewise, the rootlets of rhizomorphic

lycophytes are interpreted as leaves modified for rooting, and that have the equivalent of exogenous origin. As such they are fundamentally unlike the adventitious roots of rhizomatous lycopphytes like *Lycopodium* and *Selaginella*. (p. 86).

Although functionally similar to the root cap of roots in seed plants and many other pteridophytes, the apical plug of *Paurodendron* is not produced by the homologue of a seed plant primary root. This is because the rooting structures of lycopphytes do not originate from the embryonic radical as they do in seed plants. (p. 92).

They also say, "...the rhizomorph appendages are not initially emergent only because of the presence of the [apical] plug tissue. Therefore, their initiation is equivalent to the exogenous origin of leaf primordia." (p. 94).

Note that, because Rothwell and Erwin (1985) detected the comparability of the embryogeny of the small shrubby *Paurodendron* with the germination of *Lepidocarpon*, which is the megaspore complex of the tree *Lepidophloios* (see their Figure 18), one can reason that the structure of the rhizomorph of *Paurodendron* also applies to the tree lycopsids. They say, "From this feature [horizontal vascular strand in center of transition zone], we can interpret the embryogeny of *Paurodendron* to be similar to that of *Lepidocarpon*" (p. 94).

Furthermore, Rothwell and Erwin (1985) reiterate that rhizomorphs are not homologues of seed plant radicle roots or of adventitious roots:

This suspicion [that the rhizomorphic system is a modified shoot system] has been confirmed as the result of the discovery of vascularized embryos of *Lepidocarpon* in which an early dichotomy of the growing tip gives rise to a *Lepidophloios* stem and also to a stigmarian axis.... Bipolar growth is established as the result of the first dichotomy of the shoot wherein one branch bends upward to become the stem and the other bends downward to become the rooting organ. (pp. 94-95).

Rothwell and Pryor (1991) state,

Stigmarian apices (Fig. 6) display all of the diagnostic features of a PTM [primary thickening meristem] in living plants, including sunken apical meristem and young primordia (Rothwell and Erwin, 1985), broad apex where all of the girth of the axis and stele are attained, and cylindrical shape of the axis and stele behind the meristem (Rothwell, 1984). A consistent width of the steles between forks of the stigmarian system and only modest apical decrease in thickness of the wood in some axes are also concordant with the proposal that they result from the activity of a PTM.... We can hypothesize a general scheme by which the known features of *Stigmaria* could have been produced. Because the plant grew from a tiny embryo, the growing apex of *Stigmaria* must have been initially quite small as well. Therefore, most of the basal girth of the rhizomorph and the rhizomorph stele must have been produced by secondary growth. However,

unlike the shoot system, where after each branching the apices were considerably smaller, stigmarian apices probably continued to increase in size after branching. This accounts for the extremely large size of the known apices of *Stigmaria* (Fig. 6). If true, then the ratio of secondary vascular tissue to radially aligned metaxylem would decrease distally, until virtually all of the girth of the axes was achieved at the apex. (p. 1744).

Even though Bateman (1994) assumes the rhizomorphs were shallowly rooted in saturated swamp peat, he does admit, “Not surprisingly, the efficiency of these organs for penetrating well consolidated substrates, anchoring the plant in poorly consolidated substrates, and obtaining some key nutrients from water unsaturated substrates, have all been questioned” (p. 544).

Another observation made by Bateman (1994) but which he does not connect with floating plants is that there is no evidence of soil mycorrhizal fungus associations that would be typical for soil-rooted plants. He says, “The trees in particular seem to be prime candidates for mycorrhizal associations, but mutualistic fungi have not been detected in any of the abundant *in situ* stigmarian rootlets...” (p.544).

Hetherington et al. (2016) statistically analyzed fragments of stigmarian rootlets [rhizomorph appendages] in coal balls as opposed to looking for whole intact rootlet fossils. This provided new and compelling evidence that earlier paleobotanists erred in saying that rootlets could branch no more than once and lacked “root” (surface) hairs. Hetherington et al. still believe stigmarian axes were rooted in swamps, but the analysis they provide make it highly unlikely that rhizomorphs with their appendages could, in fact, grow through any sort of consolidated or semiconsolidated swamp soil. We point out that surface hairs did not necessarily function for mineral absorption in soil; they could have functioned just as easily for mineral absorption in water, increase of mesh strength, or protection of appendages emerging from the water’s surface. See reconstruction, Fig. 4 (our Fig. 1), by Hetherington et al. (2016) to see that the rhizomorph-rootlet architecture of right angle rootlet orientation would be difficult to develop in dense swamp peat. Even though these rootlets are correctly compared to those of *Isoetes*, its structure, probably modified since the Flood, (tiny, highly reduced rhizomorphic axis and stem lacking large air chambers but rootlets that are air-filled, and the rootlets that are much shorter than those of fossil lycopsids and oriented downward to horizontal) allows it to grow in water-saturated mud of shallow, permanent pools.

These data indicate that both sigillarian and nonsigillarian rootlets branched three to four times (Supporting Information). Furthermore, root hairs are present on both sigillarian and nonsigillarian rootlet types (Supporting Information). We conclude that both sigillarian and nonsigillarian rootlets formed similar bifurcating rootlets systems to those found in *Isoetes* today. (p. 3).

We calculated a density of 25,600 terminal rootlets per m of rhizomorph with a surface area 5.5 times larger than unbranched rootlet systems (assuming that living root hairs are present only on the terminal two orders of

branching) (Methods). This model shows a stigmarian system with a densely packed cylinder of interwoven rootlets around the rhizomorph axes (Fig. 4). (pp. 3-4).

We verified the highly branched architecture through quantitative analysis of the numbers and diameters of stigmarian rootlets preserved in coal balls....Such an extensive branched system would have formed a subterranean [*sic*] network with a large surface area available for nutrient uptake and tethering these giant trees in place.

However, because rootlets can extend for over 90 cm from the rhizomorph surface (52–55), this bias means that the morphology of the distal branched regions of the rootlets remained undescribed.

Highly branched rootlets would have contributed to the anchoring of these giant trees. Branched root structures are between twice and seven times more resistant to pull-out compared with unbranched structures (56–58) and the discovery of root hairs would not only have increased the surface area but would have further contributed to anchorage (59). The tree lycophytes would have formed large root plates as individual rhizomorph axes could extend for over 12 m (19) from the trunks of large trees. Given that tree lycopsids have additionally been reported to grow at high densities (up to 1,769 stems per ha (15)) in coal swamp forests (14, 60), root plates would have also interlocked with neighboring stigmarian systems. Highly branched rootlets would have further consolidated these extensive root plates (Fig. 4). It is the ability of root plates to resist movement when the aerial parts of the tree are subjected to lateral force that provides structural support to tall trees (61). We predict that highly branched stigmarian rootlets would have contributed to the anchorage of these giant trees. (p. 4)

The discovery that stigmarian rootlets were highly branched, developed root hairs and share the same branching architecture as extant *Isoetes* rootlets reveals a remarkable conservatism in rootlet architecture between the first giant trees and their only living herbaceous relatives. (pp. 4-5).

13. Propagules of dominant trees were water-dispersed “boats”

Phillips and DiMichele (1992) reiterate the long-held understanding that the megaspore-sporangium-sporophyll complex of the monosporic tree lycopsids functions in water dispersal of these propagules. The spore complex was shaped like a sailboat, so that when the spore complex fell, it floated and blew about by air movements. It was also fertilized and germinated while floating. The genera differ primarily in the width of the sporophyll base supporting the megasporangium and the degree to which the base folded up around the sporangium. Their Figure 6 illustrates the spore complex of *Lepidophloios*:

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 floatation device. (p. 578).

Phillips and DiMichele (1992) do not illustrate *Lepidodendron* spore complexes, but they describe them as:

...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* aquacarps appear to have been suited for aquatic fertilization and dispersal (Phillips, 1979). (p. 576).

Phillips and DiMichele (1992) do not describe the spore complexes of *Diaphorodendron*, including *D. dicentricum*, which is now segregated in the genus *Synchysidendron*, but they illustrate them in their Figure 5. In the legend to the figure, they say, “The megasporangiate cones fragmented into aquacarp units composed of a sporangium with single functional megaspore and associated sporophyll tissues. Fertilization probably was aquatic.” (p. 575). The remaining genera, *Sigillaria* and *Paralycopodites*, produced multiple megaspores per sporangium and released the megaspores directly from the sporangia, i.e., they were free-sporing (see pp. 572-574 and their Figures 3 and 4). However, these plants tended to be smaller statured and their megaspores could have been fertilized and germinated on developing rhizomorph mats of the larger monocarpic species.

APPENDIX B

Psaronius tree ferns -- detailed documentation of observations and interpretations from conventional paleobotanical literature. Comments in square brackets are our insertions. Literature cited in the quotations but not by us are not included in the References list.

1. General structure

The most famous and widely reproduced reconstruction of *Psaronius* comes from the frontispiece of Morgan (1959). Specimens available to her did not show any actual stem base, so the reconstruction is based on extrapolation from the lowest part of the stem she studied and the assumption of rooting in swamp soil. She describes *Psaronius* in this way,

In gross structure (see frontispiece) *Psaronius* was an erect, unbranched stem up to 50 feet high with an apical crown of large compound leaves. The leaves were arranged in vertical rows or in a spiral. As the leaves aged they abscised, leaving large elliptical scars on the surface of the stem. Older parts of the stem toward the base were covered with a thick mantle of adventitious roots, causing the base of the stem to appear much enlarged.

Judging from the structure of its roots, *Psaronius* grew in a

swamp environment along with seed ferns, lepidodendrids, coenopterid ferns, calamites, sphenophylls and other plants typical of the Carboniferous landscape. (p. 1).

The basal portion is a massive structure consisting of a root mantle which surrounds a small stem base approximately 2.3 X 1.5 cm. in diameter at the lowest preserved level....The stem began as a small obconical axis, later becoming encased in a huge mass of roots. By the addition of new cycles [of the stele], each one more internal than the previous one, it increased in complexity. Each stelar cycle, along with the cortex and sclerenchyma sheath, increases in volume at higher levels by addition of primary tissues derived from the apical meristem. (p. 19)

No fronds have yet been found attached to these stems, so it can only be postulated that at the apex of the large whorled forms, two whorls of fully developed fronds may have been retained on the stem at the same time. (p. 21)

2. Increase in diameter of inversely tapered rod-like slender stem

Stidd and Phillips (1968) describe the structure of very young *Psaronius* stems. The youngest and longest specimen bore four leaf petiole bases, a fifth leaf trace and seven adventitious roots. The stem was 4.5 cm long. The base was broken off but the proximal end was only 1.5 mm in diameter with a closed siphonostele only 0.5 mm in diameter. The distal end was 5 mm in diameter with a dicyclic dictyostele 2.5 mm in diameter. The shorter stems were comparable. The authors were primarily concerned with determining how a dicyclic dictyostele in young plants developed ontogenetically from a simple cylindrical siphonostele in the sporeling. The authors speculated that the earliest stem from a germinating spore had a solid protostele which then increased in diameter as the sporeling grew and as the center grew larger it developed pith tissue instead of vascular tissue. The importance of their work is in demonstrating the increase in diameter of the stem and its stele from an early sporeling stage to a young plant stage from wire size to pencil size. See their Figures 1 and 2 (p. 835). In concert with Morgan's (1959) study of distinctly older stems with root mantle and steles increasing from proximal dicyclic dictyosteles to distal polycyclic dictyosteles, this increase in size is understood to depict an inversely tapered rod. Stidd and Phillips (1968) report,

The diameter of the stele [of the longest stem] is 0.5 mm at the base of the simple, closed siphonostele and 2.5 mm at the dicyclic level. Basally the xylem is two to four cells thick or about 0.1 mm in radial thickness (Fig.3) and increases to five or more tracheids at higher levels (Fig.12). (p. 835).

The preserved basal portions of the two stems described by Morgan are about 10 times larger in diameter than the stems in this study. Morgan's specimens were surrounded by a thick mantle of roots, up to 30 cm in radius in *P. blicklei*, indicating that they were the basal portions of quite large plants. The small sizes of the specimens described here, a relatively simple stelar anatomy, attachment of petioles, and the lack of a root mantle suggest that they are basal

portions of relatively young, small sporophytes. (p.837)

Mickle (1984) in his analyses further confirms this, “Analysis of *Psaronius* stem anatomy and morphology suggests that, in general, stems had an open, unidirectional growth mode with a continuously expanding apex and vascular tissue of both cauline and foliar origin” (p. 407). Also, “With a few exceptions, however, the typically expanding vascular structure suggests that the cauline apex in *Psaronius* stems was continuously increasing in size” (p. 417).

Millay (1997) in his review paper reaffirms the same by saying, “*Psaronius* stems from the Bolsovian (ex Westphalian C) to Permian display obconical development of the siphonostelic primary body, and the production of numerous internal cycles of meristeles” (p. 195).

Weiss (2011), a *bona fide* paleontologist in Germany, summarizes his findings on a website available to English speakers:

Any attempt to reconstruct the lowest part of *Psaronius* has to start from the peculiar structure of the tree trunk: Most of it consists of apparently strong aerial roots running down the stem, connected by soft tissue. The stem proper, without the roots, is widest at the top where it bears the fronds but very narrow near the ground. It is as narrow there as it had been in the juvenile stage because there is no subsequent lateral growth. There is no primary root left, hence the whole tree rests on its aerial roots.

3. Some species had air cavities in their stems.

In Morgan (1959) see Figures 29-24 (pp. 86-88); Fig. 57, 58 (p. 97); Fig 61 (p. 98); Figs. 66, 67, 69 (pp. 100-101); Fig. 73 (p. 102). She explains,

One of the more obvious features of *P. blicklei* is the great number of lacunae found in the ground tissue at higher levels of the stem. These are much sparser at lower levels, gradually increasing in number and in size as higher levels. (p. 18).

In *P. blicklei* (figs. 57, 59, 73) large lysigenous lacunae extend vertically through varying vertical distances, depending upon the numbers that have become coalesced throughout the length of the stem. These cavities are found scattered through the ground parenchyma of the stem and petiole bases (fig. 73). They are fewer in number at lower levels of stems of this species (specimen A), but become much more abundant at higher levels and probably increase in number at a particular level as the stem becomes older. They are considered to be of lysigenous origin because there is no evidence of an epithelial layer of secretory cells lining the cavities, and because there is evidence of partially broken-down cell walls within them. (p. 44).

Further evidence that the large cavities in the ground parenchyma of stems of *P. blicklei* were formed during the life of the plant, and are not due simply to disintegration of the plant before or during fossilization, is the internal sclerenchyma present around these cavities which appears in cross-section as finger-like projections between them.

(p.45).

Ehret and Phillips (1977) in their section describing inner roots, note parenthetically that two species are distinguishable by the air spaces in the stem ground tissue, “*P. pertusus*, which has aerenchymatous ground tissue, and *P. blicklei* with its large lacunae, are the only species identified as having inner roots with an aerenchymatous inner cortex” (p. 151).

4. Structure of root mantle

Morgan (1959) describes the root mantle of *Psaronius blicklei* as follows:

All specimens of this group show evidence of a root mantle about the periphery of the stem. Logically, stem fragments with progressively more internal complexity indicate a higher level in the plant and possess fewer and fewer roots at the periphery.... It is obvious that fronds did not extend through an extensive covering of roots, a fact which supports the idea that the upper portions of the stem lacked a very extensive root mantle. That some roots were present between the fronds, while they were still attached to the stem, is supported by the fact that these roots grew down over the leaf scar very soon after the frond dropped away. If these positions of frond abscission were left exposed to the drying conditions of the atmosphere for a great length of time, it is most probable that the outer cortical cells would not have been capable of secondary proliferation which helps interlock the sheath of roots to the stem. (p. 20).

The root mantle consisted of two generally visible layers, the inner root zone (also called bound root zone) and outer root zone (also called free root zone). In her general discussion of several species of *Psaronius*, Morgan (1959) says,

Surrounding the stem except in the more apical portions is a zone of adventitious roots. Roots of the more internal regions of this zone are surrounded by radially aligned parenchyma which proliferated from various parenchyma cells of the stem and roots. (p. 55)

Adventitious roots arise at various points along the length of the peripheral cauline bundles. Figure 57 shows the bulbous base of a root trace departing from a peripheral cauline bundle of *P. blicklei*. The roots grew downward and outward to the periphery of the stem, where, at least for a certain length of the root, they are components of the inner root mantle. While still within the stem, root traces are surrounded by a layer of cortex and sclerenchyma. Roots near their points of origin from the stem have a relatively smaller diameter which gradually increases toward the distal extremity of each root. Roots from more nearly apical regions of a plant are also relatively smaller in diameter at their points of origin than roots arising from more nearly basal portions (figs. 25, 32).... As the roots grew longer they increased in size and parenchyma cells of the cortex assumed the netted appearance [i.e., aerenchyma] often described as characteristic of roots of the free root zone.... At distances removed from their points of origin, roots develop this type of cortex

[i.e. aerenchyma], and at lower levels in their downward course they may or may not become encased in secondary parenchyma. (p. 56).

The nature of the tissue surrounding the more internal roots then seems fairly clear. It was formed by proliferation of various parenchyma cells (although not in the form of elongated hairs) as suggested by Farmer and Hill (1902) and Solms-Laubach (1911) rather than being part of the original stem cortex through which the roots grew (Stenzel, 1906; Sahni, 1935). (p. 57).

As previously suggested in connection with *P. blicklei*, many roots near the apex of the stem begin their course as free roots appressed to the surface of the stem between leaf bases. At lower levels they became enclosed in the proliferating parenchyma cells as did the roots produced at lower levels. These roots continued their downward and outward course through the inner root zone while gradually increasing in diameter, until their outward rate of growth exceeded that of the secondary parenchyma tissue. From this level to the base of the stem (at least until subsequent growth of parenchyma enclosed them) they are considered to be free roots. The mantle of roots about larger stems may exceed 2½ feet in diameter. Thus, by addition of roots from higher levels the circumference of the plant increased as the roots grew out and down over those formed at lower levels. The twofold function of the root mantle is obvious when the structure of this tree fern is considered. The stem itself is an obconical structure which reached heights of 10 meters or more, but at its base may be as small as 2.3 X 1.5 cm. in diameter. This is the smallest stem cross-section observed, but there must have been still smaller portions of these stems. Although some stems at higher levels, in addition to the external sclerenchyma sheath, developed bands of fibers in association with the vascular bundles, many never developed this additional means of support. Obviously, then, the root mantle was one of the main means of support of these plants. (p. 59).

One very essential function of the mantle has been almost entirely overlooked by previous workers. Since at the lowest levels the amount of vascular tissue of the upright stem is very small in comparison with the enormous increase at higher levels, it becomes apparent that in more nearly basal regions this small stele was not mechanically efficient enough to transport the volume of water carried by the vascular cylinders at higher levels, nor by the leaf traces in the huge fronds borne by such plants. The mantle of roots then performs the very necessary function of directly supplying moisture to the vascular tissue of the stem at higher levels. (pp. 59-60).

In Morgan's (1959) taxonomic description of the genus *Psaronius*, we find:

...adventitious roots arising from the peripheral cauline bundles and often from more internal cycles; root traces polyarch; cortex of roots becoming netted in more distal

regions; roots near the stem compacted by a mass of secondary parenchyma tissue proliferated from stem and root cortices, and from parenchyma cells intermixed with fibers in the sclerenchyma zones surrounding the stem and individual roots; free roots generally at the periphery of this region. (pp. (62-63).

Ehret and Phillips (1977) in their detailed analysis of *Psaronius* roots, which updated and corrected Morgan's (1959) work (see their Text Figures 1 and 2), use the term "mantle" to refer to both the inner root zone and outer root zone. They summarize by saying,

Psaronius root system ontogeny in young stems (dicyclic stage) consists only of outer free roots which exhibit some interstitial tissue, jointly generated by outer cortices of root and stem in the area of exit from the stem surface. Later, at that level, inner zone development occurs internal to the initial scattered outer root system, and outer roots are incorporated into a more extensively developed inner root system. Outer roots in some specimens merge with the inner root zone as a result of their own parenchymatous proliferation associated with lateral root development and/or wounding phenomena or remain as a distinctive (or partially surrounded by inner root zone) root zone with some islands or clusters of lateral roots around parent roots. The transition region between inner and outer root systems, as seen in transverse section, may be abrupt with separation by cauline epidermis and scales, gradual with some roots showing outer root anatomy abaxially and inner root anatomy adaxially, or so intermixed with scattered incorporated outer roots or clusters of outer roots with laterals as to lack a clear distinction. Near basal portions, large *Psaronius* trunks have inner and outer root systems (at the dicyclic stem level) that are a meter or more in diameter. At much higher levels of polycyclic stems, but below attached petioles, only an inner root zone is developed, and stages include the presence of cauline scales and epidermis still intact to the outside. Simplified reconstructions of stages in early root system and later root zone developments at the same basal trunk level are illustrated. (p. 148).

Ehret and Phillips (1977) then describe in detail as follows:

Because of their ontogenetic relationships, inner and outer roots are similar in structure. Inner roots (Plate 1, fig. 5) have a polyarch actinostele of 3-6 protoxylem poles and are up to 5 mm in diameter. The compact parenchymatous or aerenchymatous inner cortex is bounded by a layer of sclerenchyma of variable thickness. The sclerenchyma, in turn, is enveloped by a mantle of parenchyma termed interstitial tissue. Outer roots have a greater range of size than do inner roots, being 0.25-20 mm in diameter, and have a greater mean diameter. The polyarch actinostele of 4-9 protoxylem poles is bounded by an aerenchymatous inner cortex (grading outward to compact), followed by a narrow zone of sclerenchyma, then by a parenchymatous outer cortex (Plate 1, fig. 4). (p. 149).

The interstitial tissue is a characteristic feature of the

Psaronius aerial root system. The majority of inner roots produce this tissue at the periphery of the sclerenchyma band, but the quantity, quality, and sites of production are variable. Typically, an inner root will generate the bulk of its interstitial tissue on the abaxial face (Plate 4, fig. 18). (p. 151).

An important addition to the cells of the interstitial tissue is made by the stem. This is particularly evident in specimens exhibiting distinct radial files of roots (Plate 1, fig. 2, 6). The interstitial cauline parenchyma, including that from leaf scars, often cannot be distinguished from the interstitial tissue of inner root origin. (p. 153).

The stem remains active in the establishment of new roots for an extended period of time, even at the base of large plants; in young sporophytes the sparsely produced free roots yield to the growth of inner roots at a time after the fronds have abscised....The bulk of the interstitial tissue of the inner root zone is synthesized by the cauline ground tissue or derived from cells exterior to the sclerenchymatous band of inner roots;... (pp. 157-158).

Millay (1997) provides a concise description:

Another distinctive feature of the stems is the production of a root mantle. Small roots are produced from the outer vascular cycles of the stem, grow through the cortex and epidermis, bend downward, and produce branch roots on the way to the ground. Cell proliferation may occur on the roots or stem, producing a secondary cortical tissue that binds the roots together into a 'mantle' (Plate I, 1). Older portions of stems have a free-root zone outside the root mantle made up of the largest of all fern roots. (p.193).

Weiss (2011) highlights the structure of the free outer roots by saying,

Far-reaching conclusions can be drawn from one feature of the aerial roots: As they get near the ground while growing downward, they develop air-filled tissue, the aerenchyma, thereby largely increasing their cross-section. They become more and more detached from each other, hence their lower parts are called free aerial roots.

5. Roots are filled with air spaces.

See Morgan's (1959) Figures 45, 46, 50, 76, 77, 78 (pp. 92-104). As shown in Fig 77, Most of the cross-sectional volume of the roots is composed of large intercellular air-spaces between the stele and more compact outer cortex. Morgan notes that inner roots contain aerenchyma as do outer free roots, but that the volume of aerenchyma increases with distance away from the point of origin toward the base of the plant. Thus, in outer roots aerenchyma is usually conspicuous but in young inner roots it may be less apparent.

As the roots grew longer they increased in size and parenchyma cells of the cortex assumed the netted appearance [i.e., aerenchyma] often described as characteristic of roots of the free root zone. Study of specimen A, which is surrounded by a massive mantle of well-preserved roots, shows that roots need not necessarily

be free of the secondary parenchyma at levels where the netted cortex is present.

The cortex of a free root is pictured in fig. 77. Large intercellular spaces become sparser near the stele of the root. The cortex is more compact and is composed of smaller cells in this region. Tannin-like remains may be observed widely scattered through the entire cortex (fig. 77). Near the periphery of the root, outside of the netted parenchyma, the cortex is more compact and large intercellular spaces are absent. The cells are much smaller in diameter in this region and grade into a surrounding layer of thick-walled sclerenchyma cells. (p. 56).

Ehret and Phillips (1977) indicate that the inner roots may or may not contain aerenchyma, largely depending on the species, whereas outer roots in all cases typically contain aerenchyma. It is not clear whether they are saying that Morgan (1959) was unduly influenced by having material mostly of *Psaronius blincklei*, claiming aerenchyma in inner roots generally, that Morgan is correct only because *P. blincklei* is the dominant species, or that species have been lumped since Morgan's study. However, Morgan's micrographs appear to uphold her claim of aerenchymatous inner roots in the several species she examined. Ehret and Phillips say,

The compact parenchymatous or aerenchymatous inner cortex [of inner roots] is bounded by a layer of sclerenchyma of variable thickness.... The polyarch actinostele [of the outer roots] of 4-9 protoxylem poles is bounded by an aerenchymatous inner cortex (grading outward to compact), followed by a narrow zone of sclerenchyma, then by a parenchymatous outer cortex (Plate 1, fig. 4). (p. 149).

P. pertusus, which has aerenchymatous ground tissue, and *P. blincklei* with its large lacunae, are the only species identified as having inner roots with an aerenchymatous inner cortex. An aerenchymatous cortex is found in the majority of the inner roots with a 4 mm diameter or more (Plate 1, fig. 5). Although the preservation is often poor, roots situated at higher elevations on the plant are not aerenchymatous (Plate 1, fig. 2). (p. 151).

The following are anatomical characteristics of outer roots: protoxylem poles of the stele are 3-9 in number; the center of the stele is composed of large metaxylem...; an aerenchymatous inner cortex bounds the stele in roots as small as .75 mm diameter; a generally continuous... layer of...sclerenchyma fibers is circumjacent to the inner cortex; an outer cortex of 2-9 cells wide (Plate 1, fig. 4) is exterior to the sclerenchyma ...; an epidermis without evidence of root hairs may be present. (p. 155).

Weiss (2011) appears to concur with Morgan that aerenchyma in inner roots is more or less general among species.

Far-reaching conclusions can be drawn from one feature of the aerial roots: As they get near the ground while growing downward, they develop air-filled tissue, the aerenchyma, thereby largely increasing their cross-section. They become more and more detached from each

other, hence their lower parts are called free aerial roots.

6. Root mantle widely flaring at base of plant.

Ehret and Phillips (1977) in their extensive research of *Psaronius* roots say,

One of the most unusual features of *Psaronius* tree ferns is the extensive aerial root system of the polycyclic forms. The outer roots are the largest of all fern roots, and the inner root system is the only known to be encased in an extensive mantle during part of root system development. If *Psaronius* trees ten meters tall were to maintain a self-supporting habit, the lack of secondary vascular growth by the stem necessitated the exploitation of sclerenchyma and aerial root systems. Root mantles basally attain diameters of up to a meter, thus a large amount of photosynthetic energy went into the synthesis and maintenance of the *Psaronius* root system. (p 149).

Production of free roots preceeds [*sic*] establishment of a mantle of organically fused roots in young sporophytes (STIDD & PHILLIPS 1968).... The initial free roots, if still present, are incorporated into the expanding zone, which does not develop until after frond abscission.... Two small distinct root zones are now evident. Because roots of the inner zone are transformed into outer roots at various intervals, the inner zone becomes lobed, resulting in the engulfing of some free roots with the majority of free roots being pushed outward.... In a later stage of ontogeny, the distinction between outer and inner roots and the exact nature of the so called transition zone, is unclear in many specimens. Clusters of roots actively producing interstitial tissue are found intermixed with predominantly outer free roots. Most of the roots in a cluster are first or second order laterals produced by a central and disfigured mature outer root.... In a final stage of the ontogeny of a *Psaronius* basal root system, twisted and broken outer zone roots, many of them producing secondary tissue by means of lateral roots and proliferating inner cortex cells are encased by a continually expanding inner root zone. The excessive volume of secondary wound tissue from the inner cortex indicates that such outer roots were alive at the time of incorporation.

By the time the tree fern has established an extensive basal root system and buttressing support it is assumed that it attained upwards of 10-15 meters. As initially observed by MORGAN (1959), high aerial roots below frond attachments are not as large as those produced more basipetally. The inner root zone is narrower. MORGAN's contention that free roots are initially produced between petioles has not been confirmed in this study, but is not contradicted. The large number of specimens having a well-established inner zone, but no outer root zone suggests that the majority of roots at this high elevation did not readily become free.

From the numerous stem with root mantle specimens studied, including *in situ* trunks of *Psaronius* in the Friendsville Coal, it is suggested that the excellent

restoration of *Psaronius* by STEWART in MORGAN (1959) should show a more massive and flaring basal root mantle which abruptly diminishes in diameter several feet above the substratum; from that point, the root mantle diameter tapers gradually toward the plant apex. (pp. 160-161).

Rössler (2000) says this concerning size of fossils of intact stem/ bound-root zone plus encasing free-root zone,

Psaronius is considered as having upright, unbranched stems that reach a basal diameter of more than 80 cm (Sterzel, 1887). The largest *Psaronius* specimen known so far (*Psaronius weberi* Sterzel, 1887; MfNC K 620), measures 80 cm in diameter, but the extreme asymmetry of the trunk, interpreted as taphonomic (see Rössler, 1996), may allow basal diameters up to 1.5 m to be predicted. (p. 57).

Rössler (2000) emphasizes symbiotic plants growing in the root mantle, "The massive root mantles protected different developing plants, and they may have improved the possibility of preservation of smaller plants and plant organs in particular" (p. 71).

DiMichele and Phillips (2002), concerning fossils of intact free-root mantle encasing the basal bound-root zone, reiterate,

The largest reported basal diameter is 1 m or more (Willard and Phillips, 1993) from Late Pennsylvanian deposits of Illinois in the USA. In Permian deposits of Chemnitz in Germany, Rössler (1995) estimates stem diameters up to 1.5 m when a correction is made for preservational distortion. The stems of these plants are classified as *Psaronius*. (p. 153).

7. Base of stem and surrounding inner root mantle rotted away while plant grew.

In his analysis of development of *Psaronius* plants (see his Figures 1-6), Mickle (1984) stated,

I suggest that, as the *Psaronius* plant grew, basal portions of the stem and bound root zone decayed. This conclusion is based on specimens in which the stem and bound root zone are completely or partially lacking, the paucity of very basal trunk segments known for the genus, and evidence from living analogs. (p. 407).

Many *Psaronius* specimens from the Shade locality are a hollow cylinder (fig. 1) composed of free-root zone. The position of the stem and bound roots is represented by the central, hollow area. In some specimens, the central cavity may be 13-15 cm in diameter. Other specimens at this locality are partially hollow; the stem and bound root zone are intact for only a portion of the length, with no stem or bound root zone (fig. 4). Invariably, in partially hollow specimens, the stem and bound root zone are intact at the distal end, while the proximal end is hollow (fig. 4) (p. 407).

The large size (up to 50 cm in diameter) of some hollow and partially hollow specimens with thick, well-developed free-root zones indicates that these trunk segments represent basal portions or are at least well removed

from the apex. The absence of stem and bound root zone in hollow specimens suggests that, as apical growth occurred, stem and bound root zone tissues were decaying at some distance proximal to the apex. (pp.407-408).

Additional evidence that the base of a *Psaronius* stem may have decayed as the apex grew comes from the distribution of stem sizes in specimens from the Shade locality and from comparisons with modern analogs.... These data (fig. 6) are consistent with the hypothesis that the stem at the base of the *Psaronius* trunk rotted as the stem continued to grow. Smaller specimens were probably not recovered because many had decayed prior to preservation of the remainder of the trunk. (p. 409).

Mickle (1984) mentions very limited decay of the sporeling stem base in the tree ferns *Angiopteris* and *Cyathea*, “The decay of proximal stem segments in modern [especially rhizomatous] ferns is analogous to basal stem and root mantle decay in *Psaronius*.... Many rhizomatous plants [i.e. non-tree ferns] e.g., *Pteridium aquilinum*, may have decaying proximal segments while the meristem continues to grow”. (pp. 408-409).

Mickle (1984) does consider alternative interpretations: 1) Tightly packed tissues of the inner root zone and stem prevented infiltration of permineralizing solutions. 2) Differential weathering resulted in erosion of stem and inner roots first. However, he emphasizes,

The invariant orientation of partially hollow trunks, lacking bound root zone and stem proximally with these structures distally intact, and closely analogous conditions in modern plants strongly suggest that the basal stem and bound root zone did in fact, decay as the plant grew. (p. 410).

Millay (1997) reiterates by saying,

Mickle (1984b) has shown that the basal portions of large *Psaronius* stems are typically damaged or absent, while more distal portions are well preserved. He suggests an open mode of growth for *Psaronius* in which the older stem portions decay but the apex grows on. (pp. 195-196).

8. A Skirt of free roots became detached from the trunk-inner root mantle

There are sufficient numbers of fossils of free roots (form-genus *Tubiculites*) detached from the stem/bound-root mantle basal to where those have rotted away to support the concept of a skirt of free roots flaring over substrate.

About this free-root skirt Weiss (2011) believes,

The free aerial roots are seen beautifully preserved on cross-sections of the lower part of the large *Psaronius* tree trunks displayed in museums ([reference] 5) but usually they are not found fossilized in the ground. This may be due to the event which supposedly led to the fossilisation of the conspicuous trunks: a volcanic eruption causing a pyroclastic flow moving down the slopes at high speed (typically about 400 km/h) and spreading over level ground, thereby tearing the trees from their base and possibly blowing away their habitat as well, scattering the roots together with the soft ground or mud. So it can be

understood that the big *Psaronius* specimens displayed at the Naturkunde Museum Chemnitz had not been found silicified together with the related parts of the tree.

Luckily, the fossilisation of tree ferns was not always preceded by catastrophic events so that occasionally all parts of the tree, namely the free aerial roots in the ground, the stems with the fused aerial roots, and the foliage, are found in the swamp matter turned into chert.

Numerous chert samples representing a wet habitat with layers of peat and mud silicified while at or near the surface have been found lately in the Lower Permian Döhlen basin. Moults of the aquatic crustacean *Uronectes* and extended microbial layers found among the remains of *Psaronius* / *Scolecopteris* indicate that there was not only wet ground but free water as well. Part of the chert samples contain aerial roots (Figs.1, 2), some of which are preserved in a non-collapsed state.

Weiss's Figure 1 was retrieved April 13, 2016, from http://chertnews.de/pictures/Ps_roots_web.jpg. The legend of Figure 1 reads,

Psaronius “free” aerial roots in the ground, more or less squeezed before silicification, aerenchyma (air-filled tissue) poorly visible here, layered peat consisting of collapsed roots below. Döhlen basin (Lower Permian), type locality of *Scolecopteris*. Width of the picture 9 cm.

9. Structure of *Psaronius*, especially root mantle, better fits model of floating tree

In evaluating the structure of *Psaronius*, Weiss (2011) concludes that the trees actually floated on water or water-saturated mud.

The idea suggests itself that the mass of tangled and branching air-filled free aerial roots would have enough buoyancy in soft mineral mud or even in water or organic mud to support the whole tree. This would be doubtless an advantage or even a precondition for the growth of trees on wobbly ground. Since Nature usually realizes favourable options, it is worthwhile considering the implications of such design. One implication is evident from Fig.3.

Legend for Figure 3 was retrieved April 13, 2016, from http://chertnews.de/pictures/floating_trees_2_web.jpg; it reads, “Fig.3: Advantage of a floating tree in strong winds: Does not get rooted up or broken off.”

Following the legend, Weiss says,

If there were floating trees among the several *Psaronius* species, what could be predicted about their successive growth? The answer is visualized in Fig.4.

The tree sinks in as it grows, with buoyancy increasing such that it keeps equilibrium with the increasing weight. This may explain why the lowermost part of the stem with its tiny centre dating back to the earliest growth stadium is never seen on the conspicuous polished stem cross-sections displayed in museums ([reference] 5): This oldest part of the plant had most probably been dead and gone before the tree became big.

Legend for Figure 4 was retrieved April 13, 2016, from http://chertnews.de/pictures/floating_trees_web.jpg; it reads,

Fig.4: Hypothetical design of floating *Psaronius*: Equilibrium of the growing tree is maintained by successively sinking in, as indicated by the arrow supposed to be fixed to the trunk. Stability against upsetting is brought about by the large raft of air-filled roots.

10. Spores are all microspores

Unlike tree lycopsids with their large, enclosed, boatlike spores, the spores of *Psaronius* were all microspores as in living *Marratiales*. These spores would have been wind-dispersed and need to germinate and be fertilized while resting on something more or less solid. Millay (1997) summarized the information about the spores (see his Plate VII fig. 3-8 and Plate VIII fig 1-6, pp. 204,206), saying,

The oldest fertile marattialean [sporangium-bearing leaf form-species] is *Scolecopteris alta* (Westphalian A-C). The spores in this species are small (average 13.6 μm long), ovoid, monolete, and have a papillate (small warts) exinous ornamentation....Most fossil marattialean ferns have oval to spherical spores (11-130 μm in diameter) with a smooth exine, and a coating of sculptine that constitutes the ornamentation. (p. 207).

11. Sporelings free living, similar to extant *Marratiales*

Steur (2016) cites work of Weiss (2001) that documents a fossil of a likely *Psaronius* sporeling having only three small leaves, saying,

Latest news! Tiny club-shaped objects with well preserved tissue have been found together with *Scolecopteris* / *Psaronius*. They resemble the mm-size first leaves of some extant fern and thus have been assumed to be very young plants of *Psaronius* emerging from a gametophyte.

The accompanying small image of the sporeling was retrieved April 14, 2016, from <http://steurh.home.xs4all.nl/engpsar/epsaron.html>

The small image also provides a link to a secondary page, <https://steurh.home.xs4all.nl/engpsar/ekiem.html> -- with two enlarged images, and legend, which says,

Photo and drawing of tiny objects assumed to be the first leaves of a young *Psaronius*-plant.

Click the photo to see one of them enlarged.

Coll. and photo H.-J. Weiss. Width of the photo 6 mm.

Weiss, H.-J., 2001. Keimpflanze des Baumfarns *Scolecopteris/Psaronius* aus dem Rotliegend (Unter-Perm)

Photo of fossil of sporeling on the secondary page was retrieved April 14, 2016, from <https://steurh.home.xs4all.nl/Psaronius/psakiem1.jpg>. Drawing of sporeling was retrieved April 14, 2016, from <https://steurh.home.xs4all.nl/Psaronius/recokiem.jpg>. On this secondary web page, the photo of the sporeling fossil is further linked to a tertiary page (retrieved April 14, 2016 from <https://steurh.home.xs4all.nl/engpsar/ekiemdt.html>) with an enlargement image and legend. The legend of the fossil's photo on the tertiary page reads, "Alleged leaf of a young *Psaronius*-plant with clearly seen tissue structure." Enlargement image retrieved April 14, 2016, from <https://steurh.home.xs4all.nl/Psaronius/psakiem2.jpg>.

12. Rapid preservation of *Psaronius*

Rössler (2000) notes that in connection with the rapid preservation of symbiotic relationships of plants and animals living in or on *Psaronius* trunks and roots:

All examples of interactions mentioned above are interpreted as having happened on living tree ferns. The orientation of the climbers/epiphytes and their dense interaction with the host plant allows us to conclude there was rapid preservation, and to exclude the possibility that the interactions could have resulted during taphonomic processes. (p. 71).