The Parichnos Problem and the Function of Aerenchyma in the Lycopsida

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Abstract

The term *parichnos,* coined in 1891, has been used since then with more or less precision to describe a morphological or anatomical feature in several taxa of fossilized lycopsids. The parichnos is a tissue system found surrounding or accompanying the (vascular) leaf traces on their paths from the stele to the leaves. By analogy, the term has also been applied to features of some extant lycopsids. Associated with the minor, semantic issue of precisely defining the term, there is the problem of fully understanding the underlying feature that it describes, and a substantive debate about the function of that anatomical or morphological feature. In this article, I review the history of the term and of the associated problem of interpreting the nature and function of the parichnos system. This examination illustrates the constraints that morphological terminology can place on theories of plant function and in turn how accepted ideas about plant function affect the interpretation of observed morphology.

Keywords

parichnos, arborescent lycopsids, aerenchyma, leaf trace

Introduction

Parichnos is a morphological term originally applied to a feature of the fossil species *Lepidodendron harcourtii,* Witham by Bertrand (1891). Within 10 years, the term was used in a sense other than originally intended, and since then it has been extensively and variously employed, often without careful definition.

In this article, I begin by examining the history of the term itself: What did it mean originally? How has it been used in practice? How is it and how should it be defined now? Then I review some of the available observations made of the feature described by the term and espouse a particular interpretation of the anatomy and function of the parichnos system. In conclusion, I advocate a redefinition of the term parichnos on a functional basis, as I used it in a prior publication (Green 2010). In that paper, I argued that the parichnos system is important because it provides a clue to the physiology of the arborescent lycopsids: many of them seem to have concentrated sedimentary and respired CO_2 in internal gas spaces and transported CO_2 and O_2 in the parichnos system. This theory is restated in more detail in the “Discussion” section, but it should be borne in mind from the outset that the function of the parichnos system is of biological, not merely historical, interest. The history is also interesting in its own right as an example of the way in which anatomical and morphological nomenclature is tied not only to our interpretations of observed features in a plant or fossil, but also to larger-scale ecological and physiological preconceptions of how plants work.

History

Specimens of *Lepidodendron* and related genera were illustrated multiple times in the late 18th century and early 19th century (Andrews 1980), and descriptions of fossils now known by the generic name *Lepidodendron* appeared before Sternberg’s *Flora der Vorwelt* (Sternberg 1820–1838), which is taken as the starting point for formal paleobotanical nomenclature. Taking Sternberg’s descriptions as a general summary of prior

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work, however, it is easy to identify the feature that has subsequently come to be referred to as (external) parichnos: "glandulae" (or "little glands"), which appear in Sternberg's description of the genus *Lepidodendron* as well as many lycopsid species descriptions. These "little glands" appear as short lines or dots on the leaf cushions of bark compression/impression fossils of the arborescent lycopsids—typically as sunken pits in the case of compressions and external casts and raised dots in the case of external molds. Sometimes three are mentioned (e.g., *L. aculeatum*, which is "glandulis tribus horizontaliter notato" [marked horizontally with three little glands]); in other cases, two are mentioned ("glandula una in utroque latere" [one little gland on each side]; Sternberg 1820–1838, 4[1825]:X). It is not entirely clear when or whether the ligule scar or vascular bundle abscission scar was included in Sternberg's enumeration of "glandulae," or whether he distinguished between marks found on the leaf abscission scar and those on the leaf cushion. Current observations indicate that some species show as many as six marks on each leaf cushion: vascular strand, ligule scar, two intrafoliar parichnos, and two infrafoliar parichnos.

In the middle of the 19th century, the technique of mounting thin sections of permineralized peat that preserve histological detail became widespread (Witham 1831; Andrews 1980), and it became possible to examine the internal anatomy of permineralized fossils properly. It then quickly became clear that what looked superficially like glands in the bark of compression fossils were actually longitudinal features, the central one in the leaf abscission scar always showing a vascular strand, identifiable by the spiral secondary thickenings of tracheids. This vascular leaf trace was flanked by two other marks, and there were (in some cases) additional marks on the leaf cushion outside of the leaf abscission scar.

It took until the end of the 19th century before the geometry of these features was worked out. In 1891, Bertrand published a monograph on one of the earliest taxa to be known in anatomical detail, *Lepidodendron harcourtii*, originally described by Witham (1832) and now considered a species of *Lepidophloios* (DiMichele 1979). In his reexamination of *L. harcourtii*, Bertrand coined the term "parichnos" (from παρα, "next to," and ίχνοσ, "trace") to describe "un arc plus ou moins épais d'un tissue trés special" ([an arc more-or-less-dense of a very special tissue accompanying the leaf trace]; Bertrand 1891:84). As described by Bertrand, the parichnos is bounded by a kind of sheath ("une sorte de gaîne"), elsewhere referred to as a protective sheath or Casparian strip ("gaîne protectrice" or "gaîne casparyenne"; Bertrand 1891:153). The parichnos becomes thicker as it approaches the "suberized zone" (periderm or so-called secondary cortex), and when it crosses this zone, its thickness is often double the thickness of the vascular bundle in the leaf trace ("la partie libéro-ligneuse") at the same level.

Bertrand added a footnote during printing stating that he was in agreement with Hovelacque (1892) that "le parichnos est directement en rapport avec le deux glandes latérales que accompagnent la trace foliaire dans la fronde" ([the parichnos is directly in connection with the two lateral glands that accompany the leaf trace into the leaf]; Bertrand 1891:84). Another footnote describes the parichnos as the secretory arc ("son arc sécréteur") of the leaf trace (Bertrand 1891:85).

In the paragraphs initially describing the parichnos, no mention is made of a laticifer, but a feature labeled laticifer is prominently shown in the accompanying illustration (redrawn as Figure 1 here).

It seems highly unlikely that the dark region labeled as a laticifer represents any sort of secretory tissue, much less a latex canal; it might be associated with the vascular bundle (possibly representing sclerenchymatous fibers), though that cannot be determined from the original illustration. The cell labeled as parichnos does look like a parenchyma cell, but the drawing of the surrounding cells does not clearly distinguish cell lumens from intercellular spaces. Therefore, I have added the letter "a" to identify regions that I interpret as aerenchymatous intercellular lacunae.

The protective sheath described by Bertrand is also not easily recognized in his figures (Bertrand added dots to identify the cells that composed it, reproduced in Figure 1), and there was contemporary doubt as to his identification of a coherent endodermis: "after examining this sheath in various stages of development. I do not find the characteristic marking of the radial walls [for an endodermis or Casparian strip], nor is the sheath itself in any way clearly defined as regards arrangement of cells" (Bower 1893:338).

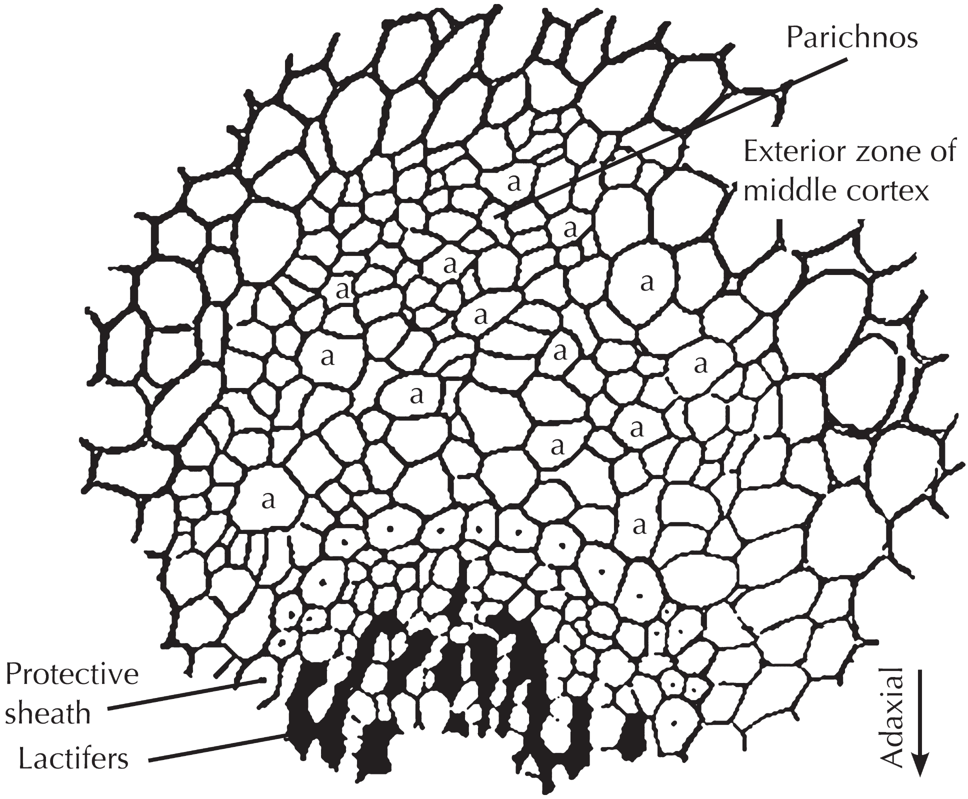

FIGURE 1. Original illustration of the parichnos, redrawn from Bertrand (1891, fig. 21). Labels are from the original illustration with the exception of the areas marked with an "a," which I added to identify regions that I interpret as possible intercellular lacunae—the original did not distinguish between cell lumina and intercellular spaces. The dots marking cells making up the "protective sheath" were present in the original and were needed because the cells they identify are not otherwise visibly distinct from the surrounding parenchyma cells. Overall, the tissue including the cell labeled parichnos in this illustration seems to correspond to what Hovelacque (1892) called "latticework cells" and Weiss (1907) called aerenchyma. Magnification approximately ×55.

Bertrand also confirms in the text that the parichnos is made up of parenchyma cells, which are very uneven ("trés inégales"); however, no distinction is made between cell lumens and intercellular spaces. In all figures, the parichnos is labeled "*t.ac.*," presumably standing for the phrase "Tissu qui ACcompagne la trace foliaire."

All of Bertrand's figures include the note "after the preparation by M. Hovelacque." Contemporaneously, Hovelacque (1892) published a more detailed and better-drawn series of figures illustrating serial sections showing rather more clearly the equivalent anatomy of the leaf trace of *Lepidodendron selaginoïdes*.

Both monographs identify an abaxial lacuna ("lacune postérieure") separate from the parichnos and any laticifer. Hovelacque shows no laticifers but instead labels a series of lacunae visible at different levels that seem to match what Bertrand identifies as laticifers or lacunae, including an abaxial lacuna in the phloem ("lacune postérieure dans le liber") and latticework cells ("cellules grillagées"; Hovelacque 1892: 75).

These authors' recurrent use of terms like laticifer, gland, fiber and particularly the word "liber" (which can refer either to the phloem in general or specifically to phloem bast fibers) is confusing because such cell types are rarely positively identifiable in fossil material (Seward 1902). Even tracheids are difficult to identify in transverse section alone. A phloem cell can be difficult to identify even in fresh material without specific staining techniques unless sieve plates happen to be visible. Heavy reliance on expected patterns (e.g., collateral vascular bundles) seems to account for a huge proportion of the anatomical description by Bertrand (1891) and to a lesser extent by Hovelacque (1892).

The convincing results of these two monographs can be summarized as follows: the parichnos consists of a system of cells accompanying the leaf trace from the middle cortex (middle region of the primary cortex) out to the leaf bases (and into the leaf before leaf abscission). It is associated with greater or lesser intercellular spaces at different levels in the two species studied. Hovelacque seems to have avoided any speculation as to function. Bertrand mentions only gummy material (“matière gommeuse”; Bertrand 1891:143), and he admits that “Je ne puis rien spécifier sur la nature du contenu des éléments laticifères” ([I can specify nothing on the nature of the contents of the laticiferous elements]; Bertrand 1891:142).

Potonié (1893), probably working independently, as he does not cite Bertrand (1891) or Hovelacque (1892), discussed the same tissues, both internal and external, in *Lepidodendron* and *Lepidophloios.* He used the term “marks” (“Male”) for the external features and clarified the fact that the internal parichnos tissue communicates both with the two marks flanking the leaf trace in the leaf abscission scar (what comes to be called intrafoliar parichnos) and (where it is present) with the pit or pits on the leaf cushion under the leaf abscission scar (infrafoliar parichnos). In addition to not citing the work of Bertrand or Hovelacque, Potonié did not use the term parichnos. He called the (internal) parichnos strands transpiration strands (“Transpirations-Stränge”) and referred to the external marks on the leaf cushion as transpiration openings (“Transpirations-Oeffnungen”), comparing them explicitly to lenticels.

Bower (1893) also discusses and illustrates the lacunae or trabecular aerenchyma found in the reproductive structure of *Lepidostrobus brownii*, drawing extensive parallels with the aerenchyma found in the extant genus *Selaginella*, and pointing out that lacuna found in fossil specimens “may have been due to the existence of lacunae in the living plant, or they may owe their origin to imperfect preservation after death of tissues present in the living state; or both of these factors may combine to produce that discontinuity of tissues which is so frequently found in such specimens” (Bower 1893:329).

Less than a decade after Bertrand’s original definition of parichnos as an internal parenchymatous tissue, Scott’s comprehensive book *Studies in Fossil Botany* used the term to refer explicitly to Sternberg’s external glandulae: “two lateral prints on the leaf scar, called the parichnos” (Scott 1900:138). He also did not speculate about the function of the connected tissue system but accepted the geometry as described by Bertrand and Hovelacque.

> The parichnos-strands die out in the leaf itself, and seem to lose themselves in the mesophyll. The function of the whole arrangement is quite uncertain. We can only say that the parichnos-tissue kept up communication between the delicate parenchyma of the inner cortex and the assimilating mesophyll of the leaves. (Scott 1900:145)

The subsequent editions of Scott’s book in 1908 and again in 1920 altered the paragraph above to include the sentence, “The function may probably have been to facilitate respiration” (Scott 1908:157), showing that the interpretation of the parichnos by Potonié (1893) as gas canals had become widely accepted.

The acceptance of this and the exchange of “respiration” for “transpiration” as an assumed function was due predominantly to an analytic review by Weiss (1907)—to which a citation was added in Scott’s *Studies in Fossil Botany* (1908)—which pulled together the anatomical results discussed previously as well as the results of Hill (1904, 1906), Weiss (1903), and so forth. Weiss (1907) still clearly represents the best summary of anatomical data on the parichnos available, so full discussion of it is postponed to the following section. Seward (1910) also relied heavily on the description of the parichnos system by Weiss (1907). He also used the terms intrafoliar and infrafoliar parichnos for the external features and labeled the internal canals parichnos.

Little new substantive work focused on the parichnos system seems to have been attempted since then, and when anatomy has been examined in detail for taxonomic or other reasons (e.g., DiMichele 1979, 1980, 1981, 1985), it has tended to confirm the geometry described by Weiss (1907).

Contemporary textbooks differ in their exact use of the term parichnos, one, for instance, defining it as “two channels of loosely arranged parenchyma tissue, termed parichnos” (Taylor 1981:131) and stating (without any supplementary detail) that “parichnos is a system of aerating tissues within the stem” (Taylor et al. 2009:282). Stewart and Rothwell (1993), on the other hand, restrict the term parichnos to the external scars, labeling parichnos and infrafoliar parichnos marks on diagrams of a *Lepidodendron* leaf cushion but referring to “branched channels filled with aerenchyma. ... that terminate on the surface of the leaf cushion in the form of the parichnos scars. These may have functioned as a means of gas exchange in much the same way as lenticels in the bark of arborescent seed plants” (Stewart and Rothwell 1993:130). So there remains a slight semantic ambiguity as to whether the term should be used to describe the external feature or the internal canal or both. Current use in general seems to associate the term parichnos with both the internal and external features extending from the leaf cushion adaxially and basipetally as far as the middle cortex.

Anatomy

Weiss (1907) provides a full analysis of the three-dimensional morphology of the parichnos system connecting the middle cortex (a rectangular toroid) to the spongy mesophyll in the leaf (via the two strands of intrafoliar parichnos) and to the atmosphere (via the infrafoliar parichnos, in species where it is present). Weiss uses the term parichnos to refer to the whole tissue system and points out that “all this tissue to which the parichnos strand joins up is aërenchymatous” (Weiss 1907:12). He also takes some care to distinguish between intercellular spaces and cell lumens, a distinction not explicitly made in the figures by Bertrand (1891): “the large white areas of this tissue are not cell cavities, but round intercellular spaces lying between small slightly irregular, or sometimes even rectangular cells” (Weiss 1907:12).

In addition, Weiss observes that *Stigmaria* (the rooting organ genus associated with the arborescent lycopsids) also shows an aerenchymatous connection between the middle cortex in the stigmarian root or rhizophore and the aerenchyma in the stigmarian appendage or rootlet. He uses the term “parichnos” (in quotation marks) to describe the aerenchymatous tissue in *Stigmaria*, and he remarks on the similarity between root aerenchyma and the parichnos in stem and leaf. He also points out that the interconnection of the aerenchymatous tissue system must run from the stigmarian root all the way up to the leaves via the middle cortex.

Despite Weiss’s careful summary, aspects of the anatomy and particularly of the ontogeny and variation of the tissues constituting the parichnos system remain far from clear: for instance, it is not yet clear whether there is (ever) a direct aerenchymatous connection between the stigmarian rootlet and the stigmarian root. Routine publication of photographic plates to document plant anatomy began in the 20th century, the first example identifying parichnos apparently provided by Weiss (1903). Publication of photographs still requires some selectivity, so conclusions based on extensive examination of fossil material can still be difficult to document in publications.

In this article, we can only provide illustrations of a few slides (Figures 2 and 3) showing several views of *Lepidodendron harcourtii*, now *Lepidophloios harcourtii* (Witham) DiMichele (DiMichele 1979), and *Lepidodendron selaginoides*, now *Diaphorodendron vasculare* (Sternberg) DiMichele (DiMichele 1985). All slides were collected and prepared by James Lomax (Howell 2005) in the 19th century, and the contemporary names are used here rather than the current taxonomy. A full, specimen-based anatomical treatment of the parichnos system would not be a trivial undertaking. It would require access to a substantial volume of material, preferably including figured specimens from some of the 19th-century monographs discussed previously as well as new material for serial sectioning either by grinding rock sections, as was done in the past, or using acetate peels. Alternatively, the development of high resolution X-ray computer tomography (DeVore et al. 2006) might provide the best method for future investigations.

Two additional sources of uncertainty when examining this material should be kept in mind: First, serial sections of individuals at different developmental stages drawn from the same population, such as are available when studying modern plants, are seldom or never available for fossils. Second, a whole adult, permineralized

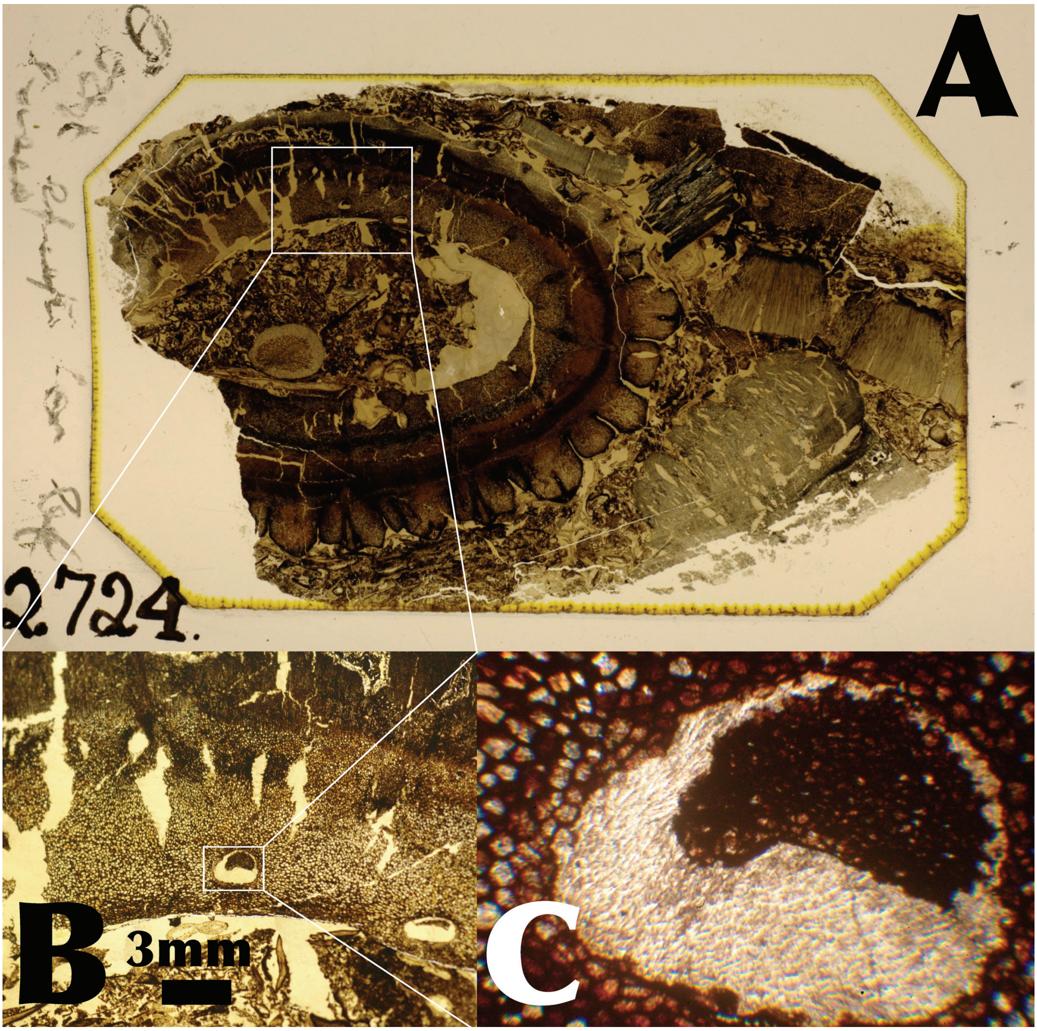

FIGURE 2. Transverse section of *Lepidodendron harcourtii* [=*Lepidophloios harcourtii* (Witham) DiMichele] axis. Lomax slide 2724, Harvard Botanical Museum, labeled "Dulesgate, England, Carboniferous." **A,** Transverse section of small axis showing preserved stele and periderm. The primary cortex area is empty or secondarily filled in with other macerated plant tissues and stigmarian rootlets penetrating the peat. Leaf cushions are clearly visible on the lower right quadrant of the axis. **B,** Magnified region of A showing leaf trace in the periderm. **C,** Magnified region of B showing kidney-shaped cross section of what I interpret as the vascular strand, suspended in an oval lacuna, the parichnos. Note the absence of any thickening of the cell walls or ruptured cells bordering the lacuna, suggesting a constitutive trabecular aerenchymatous canal rather than merely decomposition of infilling parenchyma.

arborescent lycopsid has never been found, so we must piece together our knowledge of the whole plant from specimens whose exact taxonomic identification cannot be known with certainty. These sources of morphological variation—ontogeny and intraspecific variation (or intrageneric variation when the specimen cannot be identified to species)—are impossible to disentangle fully.

With the material available in published form, and examination of a relatively small collection of original specimens, I nevertheless feel some confidence in two general conclusions. First, the parichnos provides a clear connection between the middle cortex and the spongy mesophyll in the leaves via the intrafoliar external parichnos and with the atmosphere via the infrafoliar external parichnos (in species where it is present). Second, the diffuse

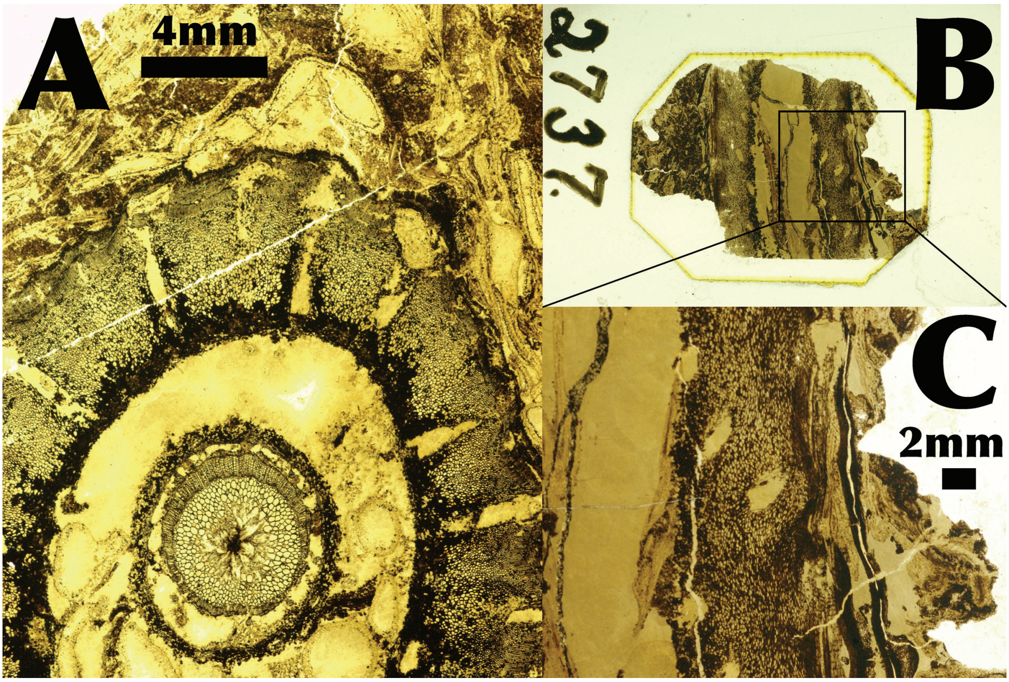

FIGURE 3. Sections of *Lepidodendron selaginoides* [=*Diaphorodendron vasculare* (Sternberg) DiMichele]. **A,** Transverse section of axis showing stele and cortical tissues; radial lacunae represent parichnos in the periderm with the vascular strands of leaf traces not visible. Again, the middle cortex has been secondarily infilled by stigmarian rootlets. Lomax slide 7903, Harvard Botanical Museum. **B,** Longitudinal section of a similar axis showing the parichnos lacunae as ovals angling away from the stele in the periderm. In this case, small black dots in each lacuna may represent the vascular leaf traces. Lomax slide 2737, Harvard Botanical Museum, labeled "Halifax Hard Bed." **C,** Magnified region of B, showing possible vascular leaf traces as small dark areas in each of the two central lacunae. The longest dimension (major axis) of the leaf trace lacunae is approximately 2.5 mm.

parenchymatous or aerenchymatous tissue making up the parichnos system shows its greatest development of intercellular space in the middle cortex and surrounding the vascular bundle, often forming an empty canal but, in some places, resembling undifferentiated ground parenchyma.

As pointed out by Bower (1893) and Hill (1906), it is not clear to what extent development and taphonomy play roles in the progressive creation of lacunae via schizogeny or other developmental processes, compared with the preferential decay of delicate tissues. However, the position of the most fully degraded or least well-preserved tissue is homologous not only across fossil arborescent lycopsids, but also in extant members of Lycopsida. It is more certain that the equivalent tissues in the stigmarian root/rootlet—also positionally homologous—constitutively form empty, gas-filled canals in which the rootlet vascular bundle is supported only by parenchymatous trabeculae.

Interpretation

The difficulties of inferring anatomy are immensely magnified when we attempt to assign a conclusive function to the parichnos system. I will begin by attempting to eliminate the unconvincing explanations that have been put forward, beginning with Bertrand's "lactifer." This is an identification that we can probably reject out of hand as latex canals seem to be anatomically as well as biochemically distinctive and found only in certain restricted groups, though for understandable reasons, this was not recognized at the time Bertrand was writing (Mahlberg 1993; Hagel et al. 2008). Resin ducts might be less anatomically distinctive but also appear in restricted plant groups, so there is a low a priori likelihood of finding them in a group like the lycopsids, none of whose modern representatives show any evidence of their presence (Langenheim 2003). Both resin and latex seem to be relatively specific and comparatively rare defensive responses to herbivory, containing alkaloids, terpenoids and other toxins.

The production of proteinaceous and polysaccharide mucilage is more common—perhaps even ubiquitous—across vascular plants and has been observed specifically in lycopsids (e.g., by Bruce 1976). As Potonié (1893) and Weiss (1907) pointed out, however, the parichnos is unlikely to represent a secretory system of any description because it has a connection to the atmosphere either directly or via foliar spongy mesophyll, which requires a free gas path to the atmosphere if gas exchange is to take place through stomata. At its proximal end, the parichnos connects to aerenchymatous primary cortex—the least likely tissue to be attacked or to be worth protecting from herbivores. In addition, secretory ducts in modern plants show some degree of wall thickening or cellular differentiation in the epithelial cells lining the ducts, while aerenchymatous lacunae are typically bordered by cells that are not differentiated from other ground parenchyma cells. Although a comprehensive survey of this propensity is outside the scope of this article, it makes sense that the contents of any secretory system must be produced by epithelial cells, while aerenchyma can form via rexigeny, schizogeny or lysigeny. Only lysigeny requires programmed cell death; the other modes of aerenchyma formation can involve only differential growth (Drew et al. 2000).

The final contribution provided by Weiss (1907) consists of introducing respiration as a functional explanation for the parichnos system. As he points out, the explanation offered by Potonié (1893), that the parichnos system was implicated in transpiration (presumably acting to reduce water loss), would require a connection between the atmosphere and the xylem, not gas spaces connecting the interior of the stem with photosynthetic tissue or the atmosphere. Weiss's conclusion, therefore, was that the parichnos acted as respiratory tissue, like the pneumatophors of mangroves, "such as *Avicennia*, where we also get a transition from somewhat stellate cells to a tissue of smaller and more rectangular cells surrounding large intercellular spaces" (Weiss 1907:12). This is accurate, but only half of the story.

Respiration as Weiss envisioned it involved the net adaxial and basipetal transport, and respiratory consumption of O_2, a concept reasonably well understood at the time. The reciprocal process of photosynthesis, however, was less clearly comprehended: in fact, the term *photosynthesis* was not coined until around the same time by Barnes (1893). Before it came into general usage, the term *assimilation* was used to describe CO_2 consumption by plants, and the assimilation of carbon was not differentiated from that of nitrogen or, for that matter, from the catabolic assimilation of carbon compounds by heterotrophs (Gest 2002).

A full functional explanation of the parichnos system was not suggested, to the best of my knowledge, until recently: "the parichnos would appear to be an internal system of gas exchange associated with photosynthesis, corresponding more to recycling of CO_2 and O_2 than to external diffusion balances" (Phillips and DiMichele 1992:568). Even then, it was not explored in any detail until the connection was made to physiological measurements of carbon recycling recently observed in wetland plants related to the extinct arborescent lycopsids (Keeley et al. 1984; Green 2010).

Discussion

To summarize, the term parichnos was coined to describe a distinctive tissue observed in anatomically preserved, permineralized fossil material whose three-dimensional structure could be determined. It soon became clear that this tissue was distally connected to external features that had originally been described as glands, so the term was generalized and used to refer to the entire tissue system, at least from the leaf base to the cortical aerenchyma. This system was observed to extend distally all the way out to the atmosphere via infrafoliar parichnos, where it is present, or via the spongy mesophyll and stomatal openings in the leaves, where infrafoliar parichnos is absent. Proximally, the parichnos system extends all the way down to the buried, rooting rhizophore (stigmarian root). The term parichnos has not generally been used to refer to the whole system nor applied outside the lycopsids. It has also long been recognized to be a gas-exchange system, and its respiratory function recognized.

In a recent paper (Green 2010), I articulated the theory that basipetal O_2 transport (for respiration) and acropetal CO_2 transport (for photosynthesis) would both take place in any aerenchyma system connecting buried and photosynthetic organs. Therefore, I extended the term parichnos to describe such connected aerenchyma systems. Plants with such a feature include many species of the extant genus *Isoëtes* (a close relative of the arborescent lycopsids) as well as many other wetland or aquatic plants across vascular plants (Keeley 1998). This circumscription excludes pneumatophores and aerenchyma localized in roots whose sole function seems to be basipetal O_2 transport to allow root respiration in anoxic sediments. Acropetal CO_2 transport leading to fixation of sedimentary and respired carbon, however, constitutes a carbon-concentrating mechanism, which would have been particularly valuable in the low-CO_2, high-O_2 atmosphere of the late Paleozoic. Therefore, I described plants with a parichnos system that fix sedimentary carbon as having a previously uncharacterized photosynthetic pathway, called LPP for lycopsid photosynthetic pathway or (in original conception) for Lagadan photosynthetic pathway, after Jonathan Swift's satirical Grand Academy of Lagado where Lemuel Gulliver encountered a researcher who had "been eight years upon a project for extracting sunbeams out of cucumbers, which were to be put in phials hermetically sealed, and let out to warm the air in raw inclement summers" (Gulliver 1726, 2:63).

According to Gest (1988), this was a specific reference to the work of Stephen Hales, whose seminal work on *Vegetable Staticks* (published in 1727, but read earlier to the Royal Society) argued that "it is very probable, that the air freely enters plants, not only with the principal fund of nourishment by the roots, but also thro' the surface of their trunks and leaves, especially at night, when they are changed from a perspiring to a strongly imbibing state" (Hales 1727:153).

Hales's theories of plant perspiration and imbibition, though necessarily ignorant of the biochemistry of O_2 and CO_2 respiration and fixation, might well have suggested a more nearly correct interpretation of the parichnos system had detailed knowledge of the anatomy of the arborescent lycopsids been available in his day. In the early 18th century, however, there was still remaining debate as to whether fossils in fact even represented formerly living organisms. Similarly, if we were working out the anatomy of the arborescent lycopsids for the first time today, we might have been more open to a consideration of the complexity and physiological variety found among plants. However, description of the anatomy of the arborescent lycopsids was attained in the late 19th century, either too early or, ironically, too late for the function of the parichnos system to have been immediately apparent.

Acknowledgments

Most of the late Leo Hickey's paleobotanical investigations concerned flowering plants, but his instinct for approaching the plant or ecosystem as a real biological entity pertained even in the Paleozoic. My interest in the parichnos system stems from a conversation with him and Erika Edwards during a paleobotany class that he taught in 2001. Hickey's thorough, scholarly and occasionally lighthearted approach to botanical terminology in its historical context inspired this article. Thanks to Bill DiMichele, Andy Knoll, Suzanne Costanza, Katy Black and an anonymous reviewer for helpful suggestions, corrections and comments on the manuscript.

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