Reports

Sieve Cells in Phloem of a Middle Devonian Progymnosperm

Abstract. *Phloem tissue from a Middle Devonian member of the Aneurophytales (Progymnospermopsida) is described. This may be the oldest firm evidence of conducting elements of the phloem, extending our knowledge of this tissue back some 35 million years. The discovery indicates a close phylogenetic relation between progymnosperms and gymnosperms and provides a basis for investigating patterns of specialization in the phloem of these groups of plants.*

One of the most important events in the history of plants was the evolution of vascular tissues, the xylem and phloem. These tissues provided plants with a means of escape from what, up to that time, had been largely an aquatic existence by giving them both internal support (cells of the xylem have thick, lignified walls) and a system for transporting solutes and water throughout the plant (xylem conducts water, phloem transports solutes). The importance of this evolutionary event is illustrated by the rapid diversification of land plants after the first appearance of vascular tissues approximately 400 million years ago.

Because of its thick-walled cells, xylem is generally well preserved in the fossil record, and much paleobotanical research has focused on its organization, development, and histological characteristics. In contrast, the phloem, being composed primarily of delicate, thin-walled cells, is rarely well preserved in fossil plants. In living plants the conducting elements of the phloem, or sieve elements, can be recognized by the presence of small perforations, or sieve pores, in the cell walls. The pores are aggregated into well-defined regions called sieve areas. Because these definitive characteristics of sieve elements are rarely preserved in fossil plants, identification of phloem is most often based on the relative position of the putative phloem in the axis, with the assumption that the topographical relations that are generally true in living plants were true in the past as well (*1*). As one looks at plants farther and farther removed from the present, this assumption may lose its validity because (i) the phylogenetic hypotheses on which this expectation is based may become weaker, (ii) the organisms being compared may be only distantly related, and (iii) the patterns of development among the organisms being compared may be different (*2*).

A group of plants in which topographic relations have been used to identify phloem is the Progymnospermopsida, a class of Paleozoic pteridophytes that includes three orders: Aneurophytales, Protopityales, and Archaeopteridales. Several investigators (*3, 4*) have labeled as secondary phloem tissue that is produced by a bifacial cambium and that is located immediately external to the secondary xylem. Proof of conducting elements in this tissue has not been established heretofore; consequently, this identification has remained tentative. It is, however, important to students of seed plant evolution to know with certainty the nature of this putative secondary phloem because progymnosperms (or at least some part of the group) are regarded as ancestral to seed plants (*5*). Part of the evidence used to support this phylogenetic hypothesis is the conclusion (*3*) that progymnosperms shared with seed plants the characteristic of a bifacial vascular cambium; that is, a vascular cambium that produced both secondary xylem and secondary phloem. According to Scheckler and Banks (*6*), "the early evolution of secondary phloem in Aneurophytales and its presence in Archaeopteridales . . . and Protopityales . . . is perhaps the strongest evidence for the gymnospermous affinity of the progymnosperms . . . . It is noteworthy that cambial activity does not produce any secondary phloem in woody ferns, lycopods, and calamites" (*7*). However, because the evidence of secondary phloem used in support of this phylogenetic hypothesis is largely based on the assumption of topographical homology with seed plants and therefore on a priori acceptance of the phylogenetic hypothesis, this argument is not compelling (*8*). Independent confirmation of the nature of this secondary phloem is essential.

Included in a group of specimens collected from the Millboro Shale (Middle Devonian, probably upper Eifelian) of southwestern Virginia (*9*) and identified as members of the Aneurophytales of the Progymnospermopsida is one of particular interest because it contains an extensive region of well-preserved secondary phloem enclosing the secondary xylem (Fig. 1A). This tissue is closely comparable in organization and histological complexity to that described for other aneurophytes [for example, *Triloboxylon arnoldii*, *Triloboxylon ashlandicum*, *Tetraxylopteris schmidtii*, and *Proteokalon petryi* (*3*)] and some modern gymnosperms (*10*). Transverse and longitudinal sections (*11*) through this region show a complex tissue composed of elongate thick-walled fibers, isodiametric to slightly elongate parenchyma cells, isodiametric sclereids, and elongate thin-walled cells that we believe are the conducting elements of the secondary phloem (Fig. 1, A and B). These conducting cells exceed 0.3 mm in length, are 15 to 25 μm in diameter, appear to taper gradually, and have well-defined elliptical to rectangular regions of dark brown spots on their walls (Fig. 1, B to D). The spotted regions are distributed evenly on the cell walls and are approximately 3.8 to 7.5 μm long and 15 to 25 μm wide; the individual spots are approximately 0.6 μm in diameter. We interpret the regions as being sieve areas and the spots as being sieve pores. The measurements fall within the range observed for homologous structures in extant gymnosperms. The cells conform to the definition of sieve cells (*10*).

This discovery is important for several reasons. First, although others have reported sieve elements in Paleozoic plants (*2, 12–15*), this appears to be the oldest firm evidence (*16*), extending our knowledge of phloem back some 35 million years from the Lower Carboniferous (lower Visean) (*12*) to the Middle Devonian. Second, it provides evidence to support prior interpretations of similar tissues as secondary phloem by students of progymnosperms. Consequently, the presence of a bifacial vascular cambium in progymnosperms strengthens the case for their evolutionary relation with gymnosperms. Third, this discovery provides an opportunity to make meaningful comparisons between the phloem of progymnosperms, other pteridophytes, and seed plants occurring later in time and to supplement our knowledge of phylogenetic trends in specialization of the phloem as inferred from living plants (*17*).

The sieve elements in our material resemble closely those proposed for *Calamopitys*, *Medullosa pandurata*, *Callistophyton poroxyloides*, and *Heterangium tiliaeoides*, all Paleozoic pterido-

sperms (primitive gymnosperms) (*12, 14*). There are also similarities between the sieve elements in our material and those of some modern pteridophytes (*17*). However, because our phloem is of secondary origin and that of almost all other pteridophytes is not, we are inclined to regard these similarities as the result of the retention of primitive characteristics and not as indicative of any close phylogenetic relation. Finally, we note again the complex nature of the secondary phloem in our specimen and other aneurophytalean progymnosperms (*3*). This is in sharp contrast to the secondary phloem of *Archaeopteris/Callixylon* (*4*), a supposedly more advanced progymnosperm, and that of Paleozoic pteridosperms in general (*12–14*), which apparently is composed primarily of parenchyma cells and sieve elements. Among gymnosperms, more complex secondary phloem appears again in the fossil record in the Mesozoic (*18*) and is present in some modern taxa (*10*). This new information may cause us to reformulate our hypotheses concerning the relations of specific gymnospermous groups to the progymnosperms and to each other. For example, similarities in phloem tissue might suggest that all Paleozoic pteridosperms are derived from some member of the Archaeopteridales and not from aneurophytes. However, the validity of this suggestion and of others that might be made can be determined only by a complete phylogenetic analysis.

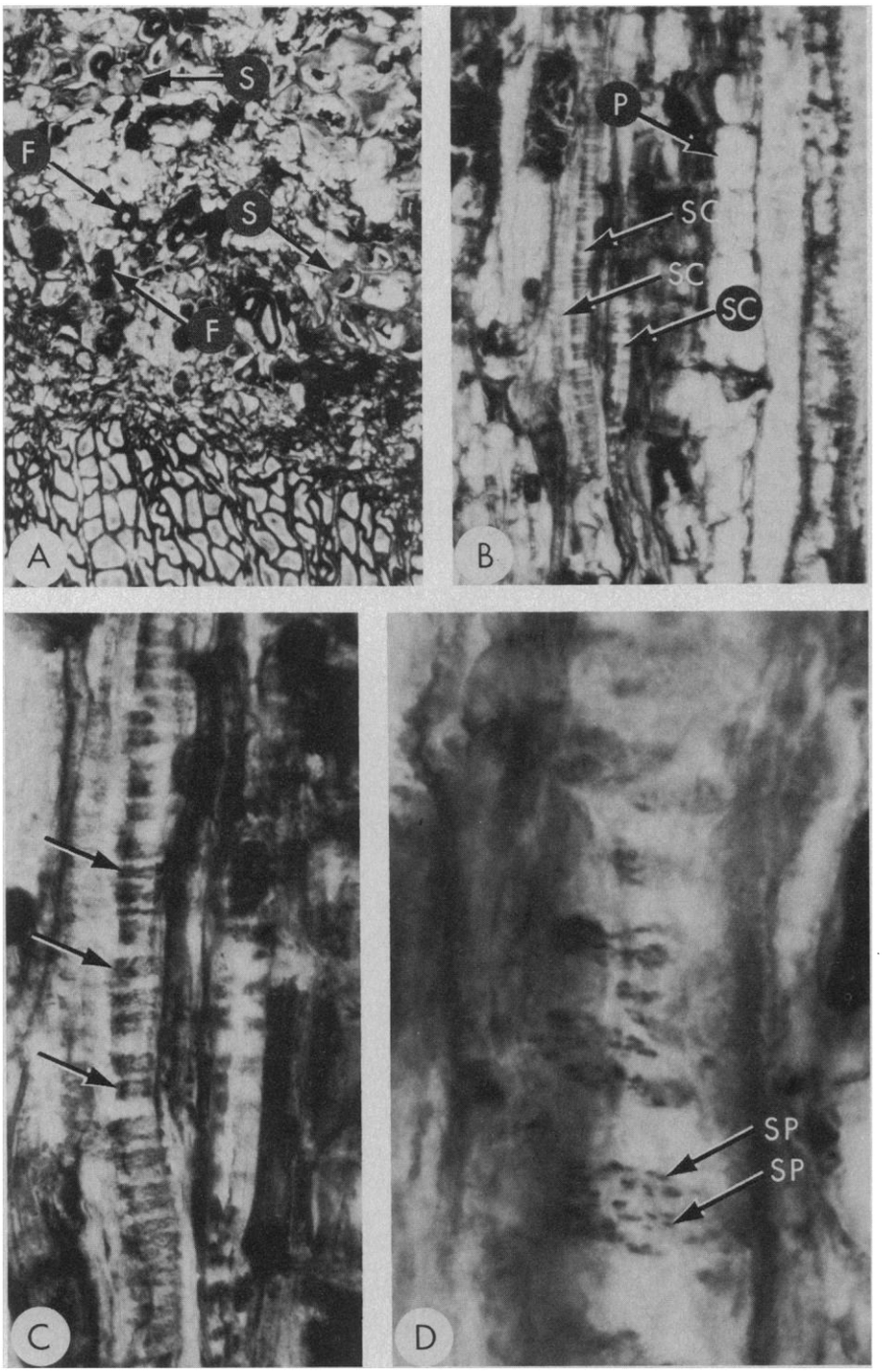

Fig. 1. Secondary xylem and phloem of an aneurophytalean progymnosperm. (A) Transverse section of axis with secondary xylem at bottom and secondary phloem at top. Arrows indicate fibers (F) and sclereids (S) in the phloem (×90). (B) Longitudinal section through the secondary phloem. Arrows indicate sieve cells (SC) and parenchyma (P) (×200). (C) Sieve cells in (B) at higher magnification. Arrows indicate sieve areas (×510). (D) Sieve cell showing sieve pores (SP) (×1680).

Aneurophytalean progymnosperms provide us with a great deal of information about the evolution of anatomical features in vascular plants. We now know that only 30 to 35 million years after the first appearance of vascular plants, a bifacial vascular cambium existed in aneurophytes. This feature provided these plants with a method of growth that allowed them to attain large size and that has persisted to the present in their presumed descendants, the seed plants. However, whether the bifacial vascular cambium first evolved in aneurophytes and precisely when it evolved are questions that await studies of plants that existed before Middle Devonian times.

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References and Notes

1. Generally, in the stems of extant plants, phloem is located immediately adjacent to and exterior to the xylem.
2. For an example of problems in the interpretation of phloem tissue that may in part be attributable to the use of a positional criterion, see the work of D. H. Scott [*Studies in Fossil Botany* (Black, London, ed. 1, 1900); *ibid.*, vol. 1, *Pteridophyta* (Black, London, ed. 2, 1908); *ibid.* (Black, London, ed. 3, 1920)], Y. Lemoigne [*Bull. Soc. Bot. Fr.* **109**, 5 (1962); *Ann. Sci. Nat. Bot. Biol. Veg.* **7**, 445 (1966)], and D. A. Eggert and N. Y. Kanemoto [*Bot. Gaz. (Chicago)* **138**, 102 (1977)] on the lycopsid genus *Lepidodendron*.
3. C. B. Beck, *Am. J. Bot.* **44**, 350 (1957); S. E. Scheckler and H. P. Banks, *ibid.* **58**, 737 (1971); *ibid.*, p. 874; W. E. Stein, Jr., and C. B. Beck, *Contrib. Mus. Paleontol. Univ. Mich.* **26**, 257 (1983).
4. C. A. Arnold, *Bot. Gaz. (Chicago)* **90**, 427 (1930); C. B. Beck, in *Paleobotany, Paleoecology, and Evolution*, K. J. Niklas, Ed. (Praeger, New York, 1981), vol. 1, pp. 193–230; Y. Lemoigne, A. Iurina, N. Snigirevskaya, *Palaeontogr. Abt. B Palaeophytol.* **186**, 81 (1983).
5. C. B. Beck, *Brittonia* **12**, 351 (1960); in *Paleobotany, Paleoecology, and Evolution*, K. J. Niklas, Ed. (Praeger, New York, 1981), vol. 1, pp. 193–230; G. W. Rothwell, *Rev. Palaeobot. Palynol.* **37**, 7 (1982).
6. S. E. Scheckler and H. P. Banks, *Am. J. Bot.* **58**, 749 (1971).
7. For more recent information on calamitalean phloem, see M. L. Wilson and D. A. Eggert, *Bot. Gaz. (Chicago)* **135**, 319 (1974).
8. There is, however, much additional evidence

supporting this phylogenetic hypothesis (*5, 6*).
9. For detailed stratigraphic information, see W. E. Stein, Jr., D. C. Wight, and C. B. Beck, *Can. J. Bot.* **61**, 1283 (1983).
10. K. Esau, *The Phloem* (Borntraeger, Berlin, 1969).
11. Techniques used in preparing this specimen are detailed in W. E. Stein, D. C. Wight, and C. B. Beck, *Rev. Palaeobot. Palynol.* **36**, 185 (1982).
12. J. Galtier and C. Hébant, *C. R. Acad. Sci. Ser. D* **267**, 2257 (1973).
13. J. W. Hall, *Am. Midl. Nat.* **47**, 763 (1952); G. W. Rothwell, *Palaeontogr. Abt. B Palaeophytol.* **151**, 171 (1975).
14. T. Delevoryas and J. Morgan, *ibid.* **96**, 12 (1954); W. N. Stewart, *Am. J. Bot.* **38**, 709 (1951); W. C. Williamson and D. H. Scott, *Philos. Trans. R. Soc. London Ser. B* **186**, 703 (1895).
15. W. N. Stewart, *Trans. Ill. State Acad. Sci.* **33**, 54 (1940); *Am. J. Bot.* **34**, 315 (1947); E. L. Smoot and T. N. Taylor, *Science* **202**, 1081 (1978); E. L. Smoot, *Am. J. Bot.* **66**, 511 (1979); K. B. Pigg and G. W. Rothwell, *Bot. Gaz. (Chicago)* **144**, 132 (1983).
16. D. F. Satterthwait and J. W. Schopf [*Am. J. Bot.* **59**, 373 (1972)] describe cells that they consider to be conducting elements of the phloem in *Rhynia major*, a fossil plant from the Lower Devonian of Scotland. However, their data, although suggestive, are, we believe, insufficient for a positive determination.
17. K. Esau, V. I. Cheadle, E. F. Gifford, *Am. J. Bot.* **40**, 9 (1953).
18. C. G. K. Ramanujam and W. N. Stewart, *ibid.* **56**, 101 (1969).
19. Supported by NSF grant BSR-8113542 to C. B. B. We thank W. H. Wagner, T. Johns, and M. A. Cichan for helpful suggestions concerning the manuscript.

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Rayleigh-Benard Convection in an Electrochemical Redox Cell

Abstract. *Damped voltage oscillations occur when current steps are applied to a cell consisting of a thin layer of Fe^{III}/Fe^{II} electrolyte sandwiched between horizontal, parallel, platinized platinum electrodes. The upper electrode must be the anode, and the magnitude of the current must be larger than a threshold value. The oscillations signal the onset of convection in the fluid. The experiment provides a new method for investigating transient convection processes.*

We report here what we believe are previously unobserved phenomena in a simple, well-studied electrochemical system, the ferrous-ferric redox cell. We used horizontal, platinized platinum electrodes, 5.1 cm^2 in area, spaced a distance, d, 0.94 to 3 mm apart (*1*). The electrolyte was 0.05*M* $FeCl_2$, 0.05*M* $FeCl_3$, and 1*M* HCl in water (*2*). Steps of constant current, i, were applied, and the voltage, $V(t)$, was measured as a function of time.

When the top electrode was negative or when it was positive and i was small, $V(t)$ exhibited the monotonic transients that one expects (*3*) for diffusion-controlled kinetics (the dashed curve in Fig. 1). Interesting effects (the solid curve in Fig. 1) occurred only when the top electrode was positive and i was larger than a threshold value, i_c. Then $V(t)$ followed the diffusion transient at first but suddenly fell away, executed a series of damped oscillations, and came to a steady value less than that with the cathode up. When i was turned off, $V(t)$ rapidly reversed sign and then decayed slowly.

The oscillation period increased with decreasing i and became infinitely long as i approached i_c, which made it difficult to determine i_c precisely by observing whether oscillations occurred or not with a given i (a graphical method is described later). The oscillations decayed with a time constant close to the rise time of the cathode-up curve, independent of i and proportional to d^2. In a few experiments the potentials of the platinum electrodes were measured with respect to a Ag/AgCl electrode. They were opposite in sign and equal in magnitude (to ≃0.5 mV) at all times, even during the oscillations.

Convection in the fluid was observed when 0.79-μm latex polystyrene spheres were added and they were viewed with scattered light, with the observer looking through a telescope in a direction parallel to the electrodes (*4*). The spheres moved continuously when the anode was up and $i > i_c$, otherwise not at all. Those moving in planes normal to the line of sight, thus staying in focus, were seen to execute square-shaped, closed orbits. Their orbital periods were close to the period of the voltage oscillation that had occurred when i was first applied. When i was turned off, the particles executed half an orbit more and then came to rest.

These phenomena manifest Rayleigh-Benard convection (*5–7*), a process that occurs in nature when a fluid is heated from below. It customarily is induced in laboratory experiments in the same way. The following arguments suggest that in our experiment, as in those of a few earlier investigators (*8, 9*), the density gradients that drive convection result from composition gradients rather than temperature gradients in the fluid.

In either case, a density difference, Δρ, is created between the top and bottom of the fluid. If Δρ exceeds a critical threshold value, convection occurs. Theory shows that the threshold is determined solely by the value of the Rayleigh number

$$Ra = g\Delta\rho d^3/\mu D \quad (1)$$

Here g is the acceleration of gravity, μ is the viscosity, and D is the diffusion constant with which density gradients are dissipated by diffusion processes in the fluid (for example, for thermally induced convection D is the thermal diffusivity). Convection begins when Ra exceeds a critical value, Ra_c, calculable at the outset; for our boundary conditions, $Ra_c = 1707.76$. Testing our observations against this prediction, we conclude that convection in our experiments cannot be thermally driven. All thermoelectric effects that are possible (*10*) would produce small values of Δρ and $Ra << Ra_c$.

To perform the same test assuming that convection is composition-driven, we must first deduce values of Δρ and D to be inserted in Eq. 1 in that case. Several features of the electrochemistry simplify this analysis. Reactions at the platinized electrodes are fast. Overall kinetics are limited by transport of Fe^{II} and Fe^{III}. Because the electric field in the electrolyte is negligible (*11*), the transport of these ions occurs by diffusion (if there is no convection) or by diffusion plus convection. We determined (*12*) the diffusion constants of Fe^{II} and Fe^{III} and found them to be the same within experimental error, $D = (6.2 \pm 0.5) \times 10^{-10}$ m^2/sec at 25°C (*13*). The equality of the diffusion constants means that double-diffusion effects (*7*) do not appear.

It also simplifies the way in which electrolysis affects composition and hence Δρ. A fraction of the $FeCl_2$ immediately adjacent to the anode is replaced

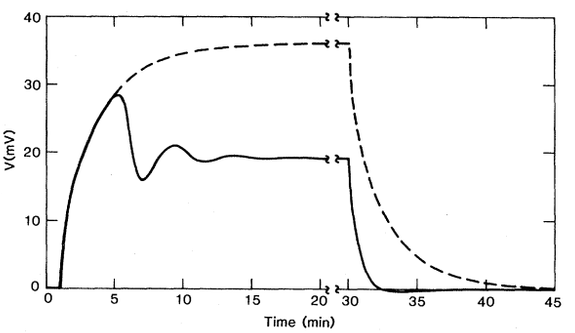

Fig. 1. Voltage plotted as a function of time. A current of 1 mA was applied at 1 minute and removed at 30 minutes; d = 1 mm. The dashed curve was obtained with the cathode up, the solid curve with the anode up.