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SEM STUDIES ON VESSELS IN FERNS
7. *MICROGRAMMA NITIDA*

EDWARD L. SCHNEIDER*
SHERWIN CARLQUIST*

RESUMEN

Con el empleo de la microscopía electrónica de barrido (MEB), hemos intentado establecer si existen vasos en las raíces y en los rizomas de *Microgramma nitida*, helecho epifítico de México tropical. Los vasos de los rizomas son más anchos que los de las raíces; probablemente no existen traqueidas. Los elementos vasculares tienen algunas placas o caras terminales; cada una es una placa perforada. Las perforaciones son más grandes que las punteaduras de las paredes laterales. En algunas placas perforadas hay perforaciones anchas y estrechas alternadas. Los vasos de *Microgramma* se adaptan a un flujo rápido, como es de esperar en una planta epifítica. Sin embargo, no se conocen los elementos traqueales de muchos helechos, por lo que las correlaciones entre estructura y función son tentativas.

Palabras clave: *Microgramma*, Polypodiaceae, anatomía ecológica vegetal, elementos traqueales, evolución de vasos, xilema primario, epífita, helechos leptosporangiados.

ABSTRACT

Using scanning electron microscopy (SEM), we show that vessels occur in roots and stems of *Microgramma nitida*, an epiphyte of tropical Mexico. The vessel elements of rhizomes are wider than vessel elements of roots; tracheids are apparently lacking. Vessel elements have several facets at their ends; each can be a perforation plate. Perforations are larger than the pits of lateral walls. Alternating wide and narrow perforations occur in some perforation plates. The vessels of *Microgramma* are suited to rapid flow, as expected in an epiphyte, Nevertheless, tracheary elements of most ferns are unknown, so correlations between structure and function are tentative.

*Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105, U.S.A.

Key words: *Microgramma*, Polypodiaceae, ecological plant anatomy, tracheary elements, vessel evolution, primary xylem, epiphyte, leptosporangiate ferns.

INTRODUCTION

In a series of papers, we have studied vessels in a wide range of ferns (Carlquist *et al.*, 1997; Carlquist and Schneider, 1997a, 1997b; Schneider and Carlquist, 1997; Carlquist and Schneider, in press; Schneider and Carlquist, in press). We have selected these ferns for study on the basis that they likely had vessels. In the case of *Pteridium* (Carlquist and Schneider, 1997a), vessels had already been reported and photographed with light microscopy (e.g., Bliss, 1939). Vessels had been suspected in *Woodsia* on the basis of light microscopy (White, 1962), so we studied that genus (Carlquist et al., 1997; Carlquist and Schneider, in press; Schneider and Carlquist, in press) and confirmed vessel presence. *Woodsia* occupies exposed habitats with winter cold and summer drought. We believe that presence of vessels in *Woodsia* may correspond to these habitats, because vessel distribution in vascular plants is closely related to habitats in which water availability fluctuates more markedly (Carlquist, 1975). Vessels likely permit rapid conduction of water during brief wet periods in plants of these regions.

In pursuing our explorations of vessel presence in ferns, we have sought other species that live in highly seasonal habitats. For example, *Phlebodium* is a terrestrial or moderately climbing fern that can grow in dry tropical sites (Schneider and Carlquist, 1997), and the species of *Polystichum* we studied (Schneider and Carlquist, 1997) survives freezing temperatures in winter. *Astrolepis* (Carlquist and Schneider, 1997b) occurs in dry temperate areas that could be described as arid scrub. We selected *Microgramma nitida* (J. Sm.) A. R. Sm. because it is a tropical epiphyte with elongate rhizomes. Epiphytes experience prolonged periods of drought even in rain forests, so that vessel presence could be expected. The genus *Microgramma* C. Presl (Polypodiaceae) consists of about 24 species in the New World from tropical Mexico to Argentina (Moran, 1995). All have elongate rhizomes and are epiphytic or occupy similarly exposed sites on rocks (Tryon and Tryon, 1982). *Microgramma nitida* is characteristic of tropical wet Mexican forests from the state of Veracruz to the state of Tabasco.

MATERIALS AND METHODS

Our material of *Microgramma nitida* comes from cultivation. It was grown at the University of California Botanic Garden, Berkeley (accession number 79.0314) from a plant collected 3 km SE of Villahermosa, Tabasco, Mexico, by F. Dortort.

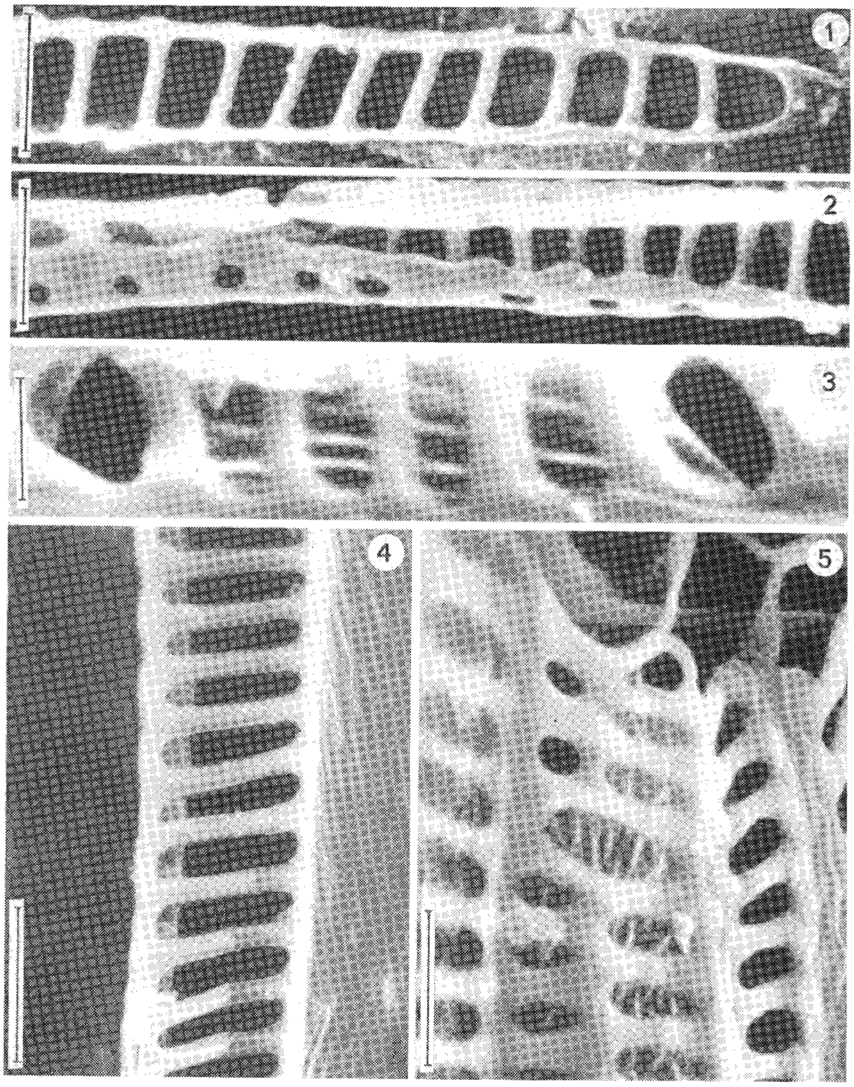
Roots and rhizomes were preserved in 50% aqueous ethanol. Although we did attempt sections, the presence of inner cortex cells with massive hard phlobaphene (oxidized tannin) deposits produced excessive cell fracturing. Therefore, we relied, as in earlier papers, primarily on macerations, which when compared to sections have proved to be accurate indicators of vessel presence and of the nature of perforations (see Carlquist and Schneider, 1997a). Macerations were prepared with Jeffrey's Fluid (Johansen, 1940). After storage in 50% ethanol, cells were spread onto the surfaces of aluminum stubs, dried, sputter-coated, and examined with a Bausch and Lomb Nanolab SEM. Roots are very slender and contain fibers that complicate the maceration process, whereas macerated rhizomes provided tracheary elements rather easily.

RESULTS

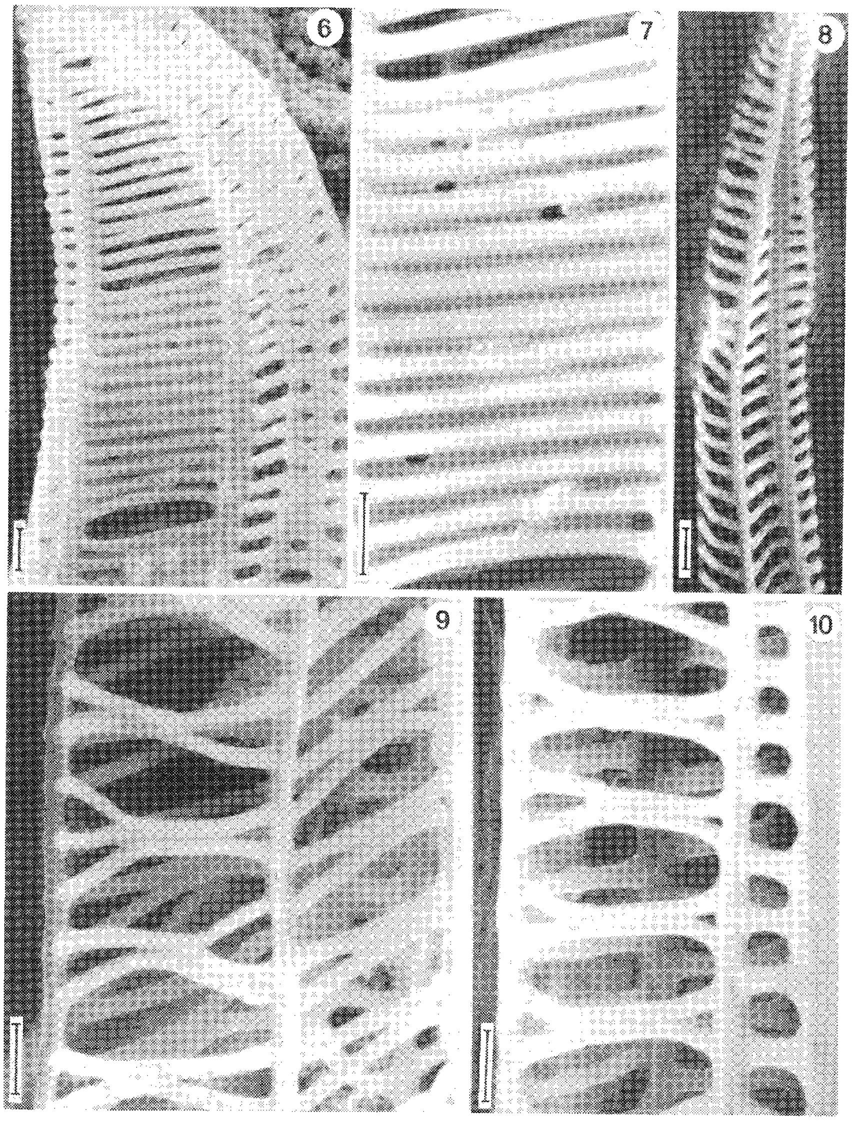
Tracheary elements of roots (Figs. 1-4) are very slender, corresponding to the slenderness of the roots. End walls have perforation plates, so vessels clearly are present (Figs. 1, 2, 4). Perforation plate bars are slender and are separated from each other by typical scalariform perforations (Fig. 4) or by wide perforations that lack pit membrane remnants (Figs. 1, 2). Perhaps because the vessel elements are so narrow, lateral wall pits are not scalariform, but are circular to oval (Fig. 2, left, bottom; Fig. 3). Pits on some lateral walls are widely spaced from each other (Fig. 2, bottom). Striations were observed in pit membranes of lateral wall pits (Fig. 3).

Rhizomes have vessels that are generally wider than those of roots (Figs. 5-7, Figs. 9-10); some are moderately narrow (Fig. 8), but still usually wider than those of roots. Lateral wall pits are scalariform to oval or circular; the latter types are found on narrow wall facets. Striations occur in pit membranes of at least some of the lateral wall pits (Fig. 5). Perforation plates are mostly clear of pit membrane remnants (Fig. 5, top; Figs. 8-10). However, the perforation plate shown in figure 6 has a portion (below) that consists of membranes intact except for small pores where lysis has occurred; these pores are shown, enlarged, in figure 7.

Several unusual features characterize perforation plates in rhizomes of *Microgramma nitida*. Vessels terminate in more than one facet where they interface with adjacent cells, and several of these terminal facets can be perforation plates. The traditional concept of perforation plates, based on those of dicotyledons and monocotyledons, depicts a single end-wall, with a single perforation plate on each end of the vessel. Multiple perforation plates at ends of vessel elements can be found in a number of ferns. We saw this commonly in *Polystichum* (Schneider and Carlquist, 1997), for example. Wide and narrow perforations alternate in some perforation plates of *Microgramma nitida* (Fig. 5, 9, 10). The pairs of bars adjacent to narrow perforations may be fused in their central portions. No tracheids were observed in either roots or rhizomes, but in macerations studied with SEM, one cannot see the entirety of a tracheary element, and therefore one cannot be sure if a tracheary element is entirely lacking in perforations.



Figs. 1-5. Vessels of roots (1-4) and rhizome (5) of *Microgramma nitida*. 1. Portion of perforation plate of a slender vessel element; perforations are wide, bars narrow. 2. Perforation plate (above, right) and lateral wall pitting (below and at left) of vessel element to show marked difference between perforation plate and lateral wall pitting. 3. Lateral wall pitting of a slender vessel element showing axial primary wall striations in pit membranes; absence of membranes in pits at extreme right and left is likely an artifact. 4.Scalariform perforation plate, with narrow perforations. 5. Lateral wall pitting from rhizome vessel; at top, large openings of an atypical perforation plate. Scale bars at upper left = 5 µm except for Fig. 3, in which bar = 2 µm.



Figs. 6-10. Perforation plates of rhizome vessels of *Microgramma nitida*. 6. Facets of diverse width —all likely perforation plates— of a wide vessel element. 7. Enlargement of portion of perforation plate in Fig. 6 to show presence of small pores in pit membrane remnants. 8. Tip of slender vessel element; the three facets shown are likely perforation plates. 9. Portions of perforation plates in which wide and narrow perforations alternate, so that adjacent bars are fused. 10. Portions of perforation plates showing circular perforations in narrow facet at right; in left, alternating wide and narrow perforations with fusions between bars. Scale bars at upper left in all figures = 5 μm.

CONCLUSIONS

Microgramma has clearly defined vessels. In roots more than in rhizomes, perforation plates differ in thickness and spacing of secondary wall material. Several end wall facets of vessels are converted into perforations plates in rhizomes, in which vessels are wider than they are in roots. With a few exceptions, perforation plates lack pit membrane remnants. All of the features cited in this paragraph tend to provide ease of water passage from one vessel element into the next. Thus, vessels appear suited to enhanced conduction during peak periods of water availability that undoubtedly occur in an epiphyte such as *Microgramma nitida*.

Although we imply a correlation between the probable enhancement of conduction by vessels in roots and rhizomes and the habit and ecology of *Microgramma*, this correlation must be tempered by the incompleteness of our knowledge of vessels in ferns. Thus far, we have selected for study ferns that experience prolonged periods of drought or cold. All of the ferns we have studied to date (see Introduction) possess vessels. In addition, vessels occur in *Marsilea* (White, 1961). Some ferns may have evolved vessels in less extreme environments. Our knowledge of vessel distribution in ferns, both systematically and ecologically, is as yet quite incomplete, so conclusions must be tentative. Only studies with SEM, which has been applied to fern vessels relatively recently, can reliably indicate vessel presence, because presence or absence of pit membranes in end walls of tracheary elements cannot be determined by means of light microscopy.

The presence of alternating wide and narrow perforations in some perforation plates of *Microgramma nitida* is curious. We have, however, reported this condition (in a somewhat less extreme form) in another genus of Polypodiaceae, *Phlebodium* (Schneider and Carlquist, 1997). Alternating width of perforations potentially provides excellent conduction through the wide perforations. The altered conformation of secondary walls between the narrow and wide perforations may confer greater strength to these walls —the diagonal direction of bars suggests bracing elements used in construction.

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