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SEM STUDIES ON VESSELS IN FERNS. 18. MONTANE CHEILANTHOID FERNS (PTERIDACEAE) OF NORTH AMERICA

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ABSTRACT

Xylem of roots and rhizomes of five species of four genera of tribe Cheilantheae (Pteridaceae; recently recognized by some as a segregate family, Cheilanthaceae) has been studied by means of scanning electron microscopy (SEM). All of these species occur in habitats (cliffs, talus) of mountains of North America that are seasonally dry in summer and cold in winter. The vessels prove diverse, indicating that different perforation plate modifications are represented in the cheilanthoid ferns of these habitats, rather than different degrees of the same kind of modification. The modifications include wide perforations alternating with narrow perforations (especially prominent in *Bommeria*); discontinuous perforation plates (*Cheilanthes*, *Pellaea*); and narrow, slitlike perforations (*Cheilanthes*). The discontinuous perforation plates are newly reported for ferns. The exceptionally prominent perforations of *Bommeria* vessels may be correlated with greater laminar surface and higher transpiration during wet periods in that genus; the other genera have small laminae with probable low transpiration rates even during moist periods.

Key words: Cheilanthaceae, ecological anatomy, intermittent perforation plates, pit dimorphism, Pteridaceae, vessel evolution, xeromorphic ferns, xylem.

INTRODUCTION

When we began SEM studies on vessels in ferns, we investigated genera in which vessels were believed or suspected to have perforation plates with perforations fewer and larger than pits on lateral walls of the same vessels. This pattern parallels perforation plate specialization in angiosperms, in which the number of bars per perforation plate is fewer in woods of more specialized members of a given phylad (Frost 1930; Cheadle 1942). Fewer bars per perforation plate correlate with habitats that offer marked fluctuation in moisture availability; a perforation plate with fewer bars would offer less resistance and promote more rapid conductive rates during periods of greater water availability (Carlquist 1975). Perforation plates with fewer bars were observed in our studies in some ferns of habitats with periods of marked dryness or cold or both: *Woodsia* (Carlquist et al. 1997; Schneider and Carlquist 1998a; Carlquist and Schneider 1998), *Pteridium* (Carlquist and Schneider 1997a), and *Astroblepis* (Carlquist and Schneider 1997b).

As our studies on fern vessels progressed, we found that other fern genera show little modification in bar number of perforation plates (with respect to the secondary wall framework) as compared with lateral wall pitting. For example, *Dicranopteris* (Gleicheniaceae) shows perforation plates much like lateral walls except for absence of pit membranes (Schneider and Carlquist 1998b). In some instances, we have observed perforation plates in which wide perforations alternate with

narrow ones, as in *Phlebodium* (Schneider and Carlquist 1997), although the dimorphism was not pronounced in that genus. We have concluded that modifications of perforation plates are to be expected not with respect to phylogenetic position, but rather with relation to habitats with extremes of moisture and cold. Temperatures below freezing result in minimized moisture availability, just as drought during summer heat does. Therefore, we have elected to study a group of ferns from montane habitats of North America (mostly arid areas of the southwestern United States) that experience such climatic regimes. We wanted to determine whether these ferns all show modifications of perforation plates, and whether these modifications are similar to each other or represent a variety of morphological manifestations. Ferns of Cheilanthaceae are often found in habitats with marked fluctuation in moisture availability, and therefore we selected five cheilanthoid species from such habitats as material for examining these questions. *Astroblepis* is a cheilanthoid fern, and has perforation plates modified so that more rapid conduction during periods of greater water availability can likely be accommodated (Carlquist and Schneider, 1997b). Because *Astroblepis* shows some perforation plate specialization, investigations of other cheilanthoid ferns seemed a logical step, and we therefore collected material of the cheilanthoid ferns studied in the present paper.

Geographical ranges and basic ecological information for the five species studied may be found in the

Flora of North America (Editorial Committee 1993). We follow taxonomy for the five species in the Flora of North America (Editorial Committee, 1993) for *Cheilanthes* (Michael D. Windham, Eric W. Rabe), *Bommeria* (Christopher H. Haufler), and *Pellaea* (Michael D. Windham). All of the species studied can be termed epipetric in that they grow either on talus or in crevices among rocks. The habitats of these species feature prolonged periods during which the soil is dry or frozen, interrupted by relatively brief moist periods.

MATERIAL AND METHODS

The sources for our material are as follows: *Bommeria hispida* (Kuhn) Underw., University of California, Berkeley, Botanic Garden 92.0103, grown from material collected by Sean Hogan; *Cheilanthes bonariensis* (Willd.) Proctor [= *Notholaena aurea* (Poir.) Desv.], University of California, Berkeley, Botanic Garden 91.1233, grown from material collected by Bonnie Brunkow at Leach Botanic Garden, Portland, Oregon; *Cheilanthes californica* (Hook.) Mett. [= *Aspidotis californica* (Hook.) Nutt. ex Copel.], summit of Glendora Mountain Road just west of Mt. Baldy Village, Los Angeles Co., California, collected by S. Carlquist 29 September 1997; *C. tomentosa* Link, cultivated at the University of California, Santa Barbara; *Pellaea mucronata* (D. C. Eaton) D. C. Eaton, summit of Glendora Mountain Road 2 km west of Mt. Baldy Village, Los Angeles Co., California, collected by S. Carlquist, 29 September 1997. The above materials are derived both from plants in cultivation as well as naturally occurring plants. Some may wonder whether the greater moisture availability would alter vessel morphology. If such modifications were possible, one would expect, among the species in the present study as well as in our earlier studies, that perforation plates altered for greater rates of conduction would be present in the species studied on the basis of cultivated material. That is not the case, however. Likewise, the ferns in our earlier studies did not show xylem morphology related to conductive capabilities to bear any relationship to whether the plants were cultivated or wild-occurring.

Material was preserved in 50% aqueous ethanol. Portions of roots and rhizomes for each species studied were macerated with Jeffrey's Solution (Johansen 1940); macerations were stored in 50% ethanol. Macerations were spread onto aluminum stubs, air-dried, sputter-coated, and examined with a Bausch and Lomb Nanolab SEM.

Porosities in pit membranes are not, in our opinion, the result of preparation methods. We know of no demonstration that porose pit membranes such as we figure are artifacts created by maceration techniques. In our earlier studies, we employed sections as well as

macerations (Carlquist and Schneider 1997a; Carlquist et al. 1997), and with SEM, the sections revealed pit membrane patterns identical to those in the macerations. No evidence has been presented that in ferns, porosities of the types we discussed are induced by air drying. A detailed rationale for our interpretations of porosities in pit membranes will be presented in a summary paper that will conclude this series. We believe that each paper in our series on fern xylem should not contain a detailed discussion of the effect of preparation methods, and further information will be presented in our summary paper.

RESULTS

Roots of *Bommeria hispida* are extremely slender and fibrous, and we were unable to recover tracheary elements from them by means of macerations. Our data on this species are therefore confined to rhizomes. The range of perforation plate types is shown in Fig. 1, in which the central tracheary element has a scalariform perforation plate, but the elements at left and right have much-widened elliptical perforations that lack pit membranes, whereas pit membranes are present on all intervening pits. The spacing of these elliptical perforations makes application of the term "perforation plate" difficult, but there seems little doubt that these wide elliptical perforations on an element facet serve, collectively, as a perforation plate. In Fig. 2, the nature of these wide elliptical perforations is shown: they are the result of dimorphism in pits, with pit membranes apparently intact in the narrower pits between the perforations. Additional details of this pit dimorphism are shown in Fig. 3: pits adjacent to the wide perforations may contain pores or holes in the pit membranes. As with vessels of many other ferns we have studied, the tracheary elements of *Bommeria hispida* may have, on some facets, pit membranes that contain porosities of various sizes (Fig. 4, 5), ranging in diameter from the (axial) width of a pit to holes so small they are at the limit of the resolution of our equipment.

Cheilanthes californica (Fig. 6–9) shows a range of types of tracheary elements. Few tracheary elements from roots were obtained, but one we are illustrating (Fig. 6) suffices to show a scalariform perforation plate common in ferns. The rhizome tracheary elements (Fig. 7) have some scalariform perforation plates, but also some tracheary elements have dimorphic pits, the wider of which we consider perforations (Fig. 7). Porose pit membranes are common on some facets of tracheary elements (Fig. 8, 9); these may be regarded as potential perforation plates that have lost pit membranes to a degree much less than is typical of most perforation plates. The facet shown in Fig. 9 illustrates dimorphism in pits, with pit membranes absent or

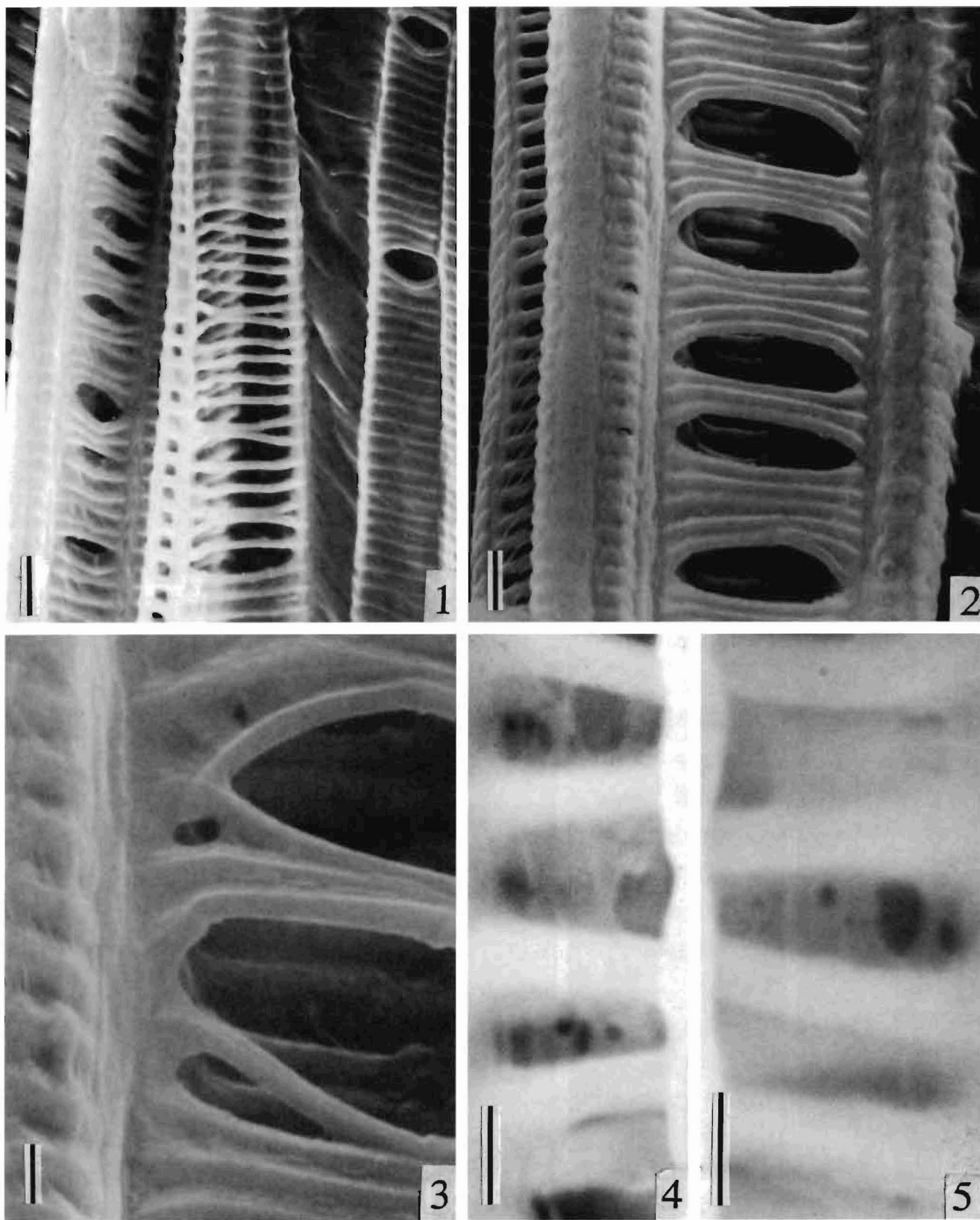


Fig. 1-5. Tracheary elements of rhizome of *Bommeria hispida*.—1. Scalariform perforation plate, center; at right and left, vessels that have large perforations interspersed among pits.—2. Vessel portion showing pit dimorphism: large perforations separated by narrow pits (scalariform perforation plate at extreme left, above).—3. Two large perforations from a vessel, adjacent to which are pits the membranes of which contain pores.—4. Several porose pit membranes from tracheary element facet.—5. Tracheary element facet in which one of the pit membranes contains porosities. (Scale bars in Fig. 1-2 = 5 μm ; in Fig. 3-5 = 2 μm).

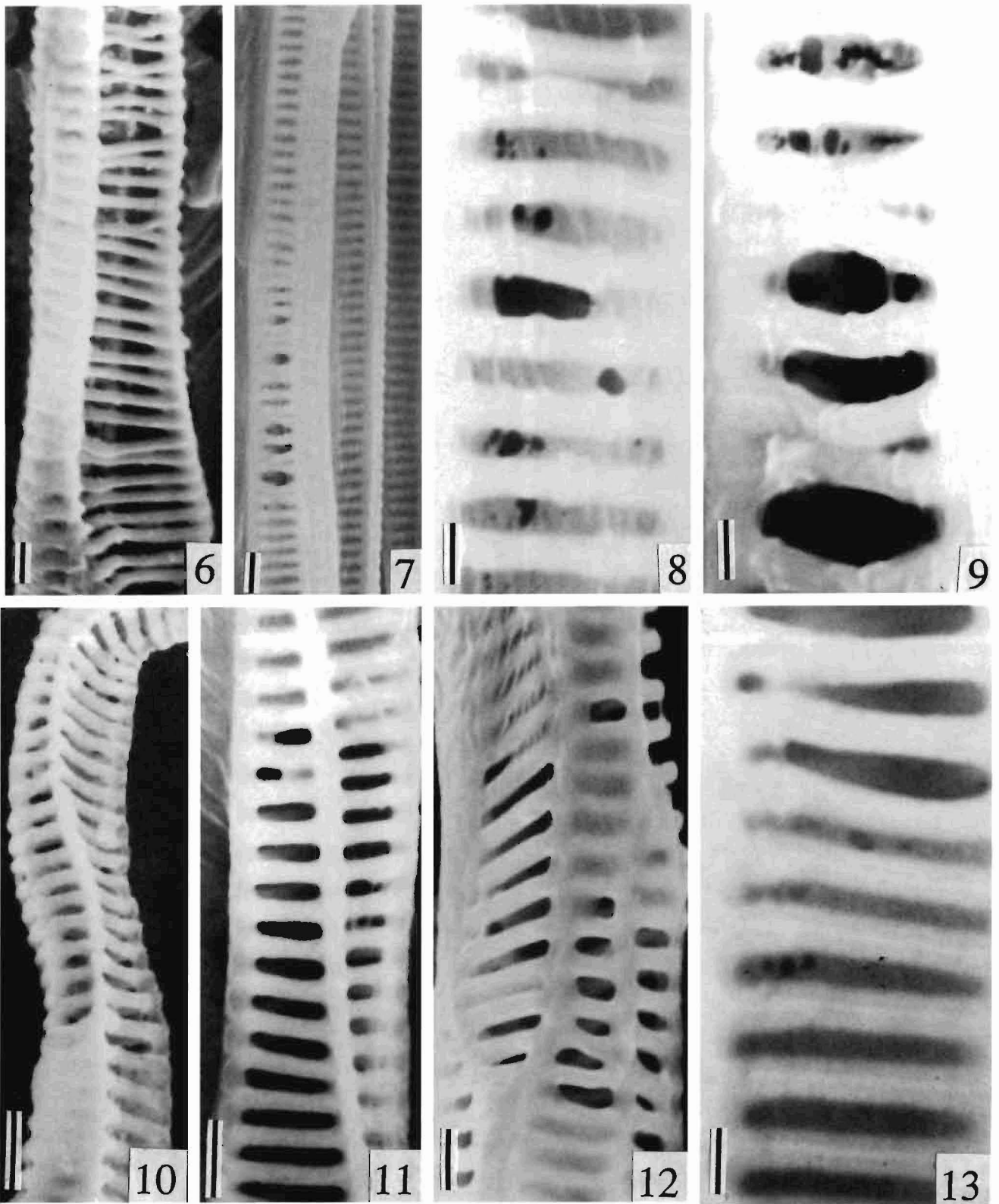


Fig. 6-13. Tracheary elements of *Cheilanthes californica* (6-9) and *C. tomentosa* (10-13).—6. Scalariform perforation plate on end wall of root tracheary element.—7. Wide perforations in rhizome tracheary element at left; no perforations on tracheary elements, center and at right.—8. Pit membranes with porosities of various sizes, rhizome tracheary element.—9. Rhizome tracheary element facet with porose pits (above), dimorphism in width of pits, below; the wider ones are perforations.—10. Scalariform perforation plates on two facets of tip of tracheary element.—11-13. Rhizome tracheary elements.—11. Two facets with scalariform perforation plates.—12. Facets on an element with intermittent perforation plates: groups of perforations separated by pits.—13. Facet with pit membranes that are porose to various degrees. (Scale bars in Fig. 6, 7, 10-12 = 5 μ m; bars in Fig. 8, 9, 13 = 2 μ m).

nearly so in the wider pits (which therefore can be called perforations).

Cheilanthes tomentosa (Fig. 10–13) possesses well-defined scalariform perforation plates in roots (Fig. 10). In rhizomes, the perforation plates are scalariform, but of various lengths: that at left in Fig. 11 is longer. The other perforation plate in Fig. 11 and several of those in Fig. 12 are shorter, incorporating five or six perforations, in places, isolated from the next group of perforations by pits with intact pit membranes. We do not believe that this configuration represents an artifact, because we characteristically observed it in this species, and saw no torn pit membranes in the openings that we are regarding as perforations. As with other species examined in this paper, some facets of rhizome tracheary elements possess pit membranes with small but definite porosities (Fig. 13).

In *Cheilanthes bonariensis* (Fig. 14–20), few root tracheary elements were observable in our preparations. The one illustrated (Fig. 14) shows large perforations, although limited in number to three per facet. In the rhizome, many facets did not bear perforation plates (Fig. 15), but we are unable to say whether these are tracheids or not because the tracheary elements are quite long (and therefore frequently broken into segments) and not all facets are observable. Inconspicuous perforation plates were present on some tracheary elements (Fig. 16, 17). In the narrow slitlike perforations of some tracheary elements, porose pit membrane remnants were present to various degrees (Fig. 18). Porosities are more dramatically seen in the pit membrane remnants where the perforations are wider (Fig. 19, 20).

Roots of *Pellaea mucronata* (Fig. 21–23) have scalariform perforation plates (Fig. 21), some of the discontinuous type noted above for *Cheilanthes bonariensis*. The tracheary element of *Pellaea mucronata* in Fig. 21 is particularly interesting in that what appear to be nearly intact pit membranes at low power prove, when enlarged (Fig. 22), to be porosities of various sizes. Porose pit membranes in roots of this species are also seen in Fig. 23. The perforations in roots of *Pellaea mucronata* are not larger than lateral wall pits on tracheary elements of this species.

Rhizome tracheary elements of *Pellaea mucronata* (Fig. 24–29) clearly show scalariform perforation plates. The longest ones (two in Fig. 24; one in Fig. 26) are on end walls (tips of elements not shown in these figures, but visible in the preparations). A shorter scalariform perforation plate is shown in Fig. 25. In other tracheary elements, discontinuous perforation plates are present (Fig. 27–29). One or two perforations, separated from other perforations by pits with intact membranes, are shown in Fig. 27–29. Such perforations can occur on more than one of the adjacent facets of a single tracheary element (Fig. 27, 28). Ob-

servation at high magnification shows that a few of the pit membrane remnants bear pores (Fig. 28, bottom center) or are strandlike (Fig. 29). In no instance in *Pellaea mucronata* were the perforations larger than the lateral wall pits.

DISCUSSION AND CONCLUSIONS

The material of *Cheilanthes californica* and *Pellaea mucronata* came from the same locality: about 1800 m. on a ridge below Mt. San Antonio, California. At this locality, snow falls in winter, yet summers are hot and dry, and summer thundershowers rarely occur at this elevation. This locality is clearly xeric and highly seasonal, but the vessel elements of these two species do not show end-wall modifications that might promote more rapid conductive rates (fewer bars per perforation plates, larger perforations) which one finds in the xeric ferns *Astrolepis*, *Pteridium*, and *Woodsia* (for references, see Introduction). One must remember that xeric regimens are not merely those that feature long periods without precipitation; periods of freezing of soil moisture, as likely happens in *Pteridium* localities, may be equally significant. The vessels of *Cheilanthes californica* and *Pellaea mucronata* are comparable in potential rapidity of conduction to those of ferns of mesic habitats, such as Marattiaceae (Carlquist and Schneider 1999) or Cyatheaceae (Carlquist and Schneider 2000). However, one must take into account factors other than habitat. In all of the ferns studied here except *Bommeria hispida*, the leaves are subdivided into small, coriaceous segments with thick epidermis. The laminae of *Bommeria hispida* curl and present a smaller surface during drier periods, but at times when peak transpiration would occur (when more moisture is available), the laminae are relatively broad and nearly flat. Transpiration is, therefore, likely minimal for all of these species during the dry season although somewhat greater during wet seasons. A reading for diffusive resistance, when obtained for these species, may prove to be high, and add to the very moderate laminar surfaces presented by leaves in most of the species. In addition, during the dry season, many of the leaves on the plants of these species have died, so that the transpiration is minimal compared to what occurs during the moister seasons of the year. Limited laminar area and high diffusive resistance would limit transpirational rates even during the wet season and thereby might provide less selective value for vessels capable of rapid conductive rates. High transpiration during brief wet periods might be expected to provide selective pressure for vessels with more specialized perforation plates, although other mechanisms would be effective also. The probable low rates of transpiration during dry periods would not be expected to relate to morphology of xylem elements;

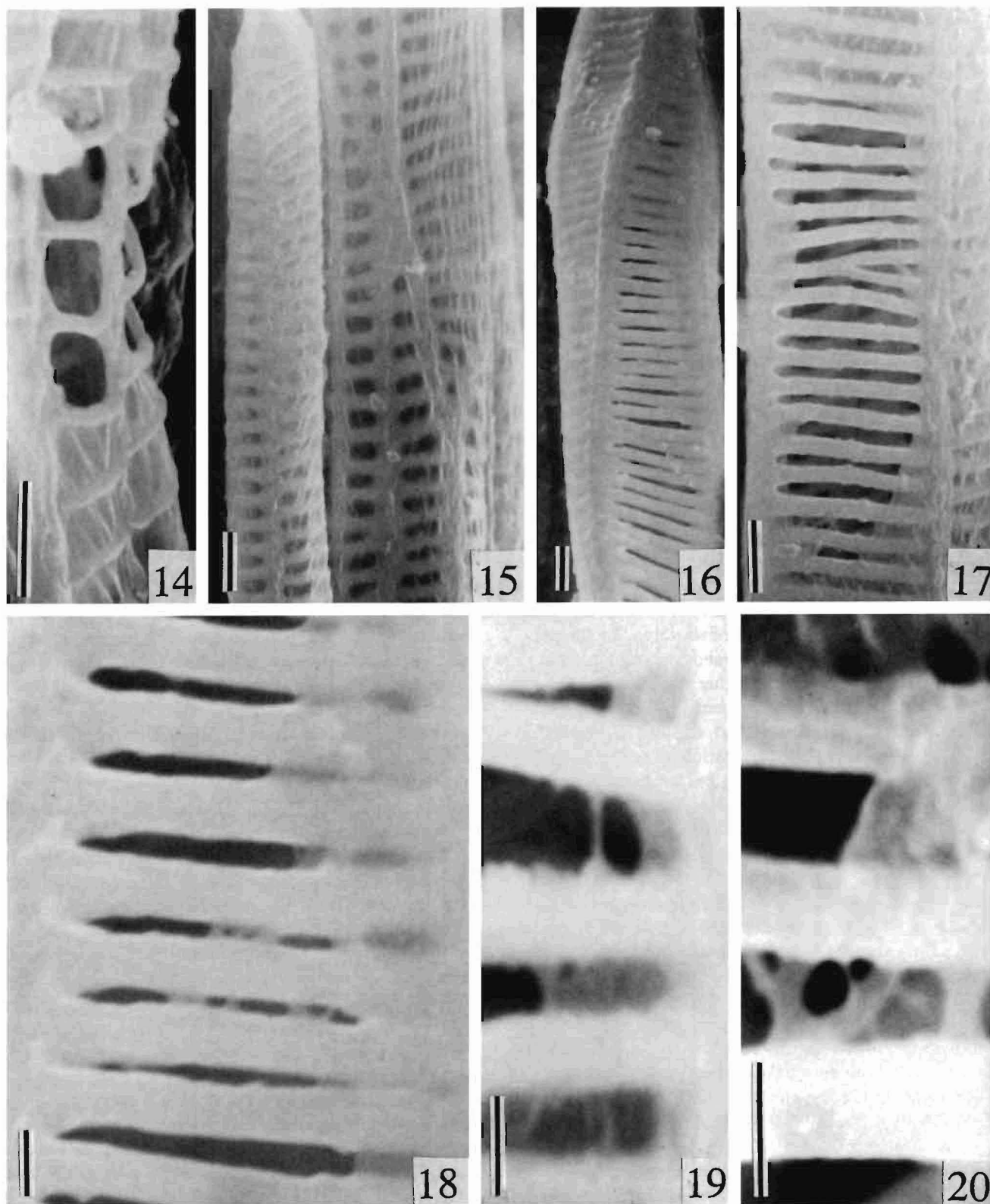


Fig. 14–20. Tracheary elements from root (Fig. 14) and rhizome (Fig. 15–20) of *Cheilanthes bonariensis*.—14. Group of several wide perforations.—15. Adjacent tracheary elements; pits but no perforations visible.—16. Tracheary element tip with facet containing narrow slitlike pits.—17. Moderately narrow perforations of a perforation plate.—18. Several narrow slitlike pits or perforations in which pit membranes are porose or vestigial.—19–20. Pits to show various sizes of pores in pit membranes of incipient perforation plates. (Scale bars in Fig. 14–17 = 5 μ m; bars in Fig. 18–20 = 2 μ m).

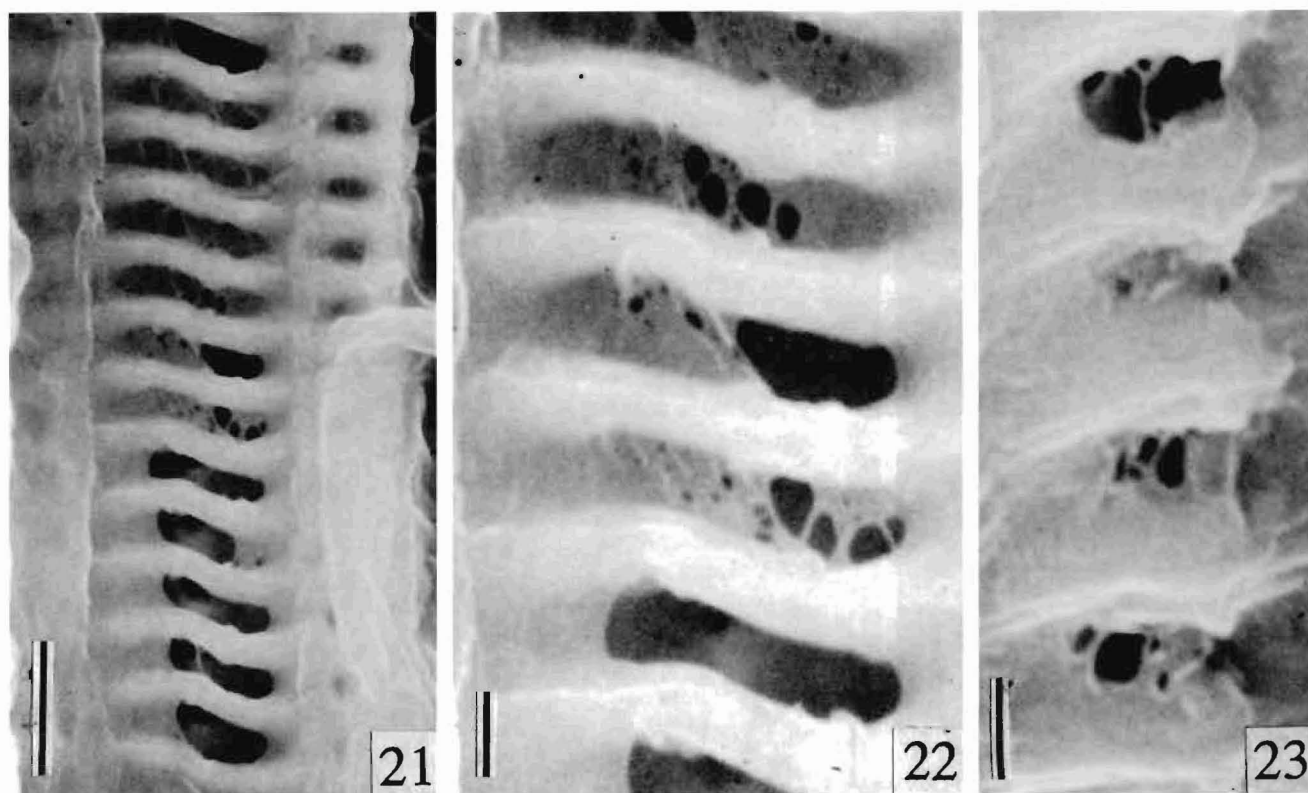


Fig. 21–23. Tracheary elements of *Pellaea mucronata* roots.—21. Perforation plate with incomplete absence of membranes in some perforations.—22. Enlarged portion of the perforations shown in Fig. 21, to show the presence of numerous porosities.—23. Facet with oval perforations, each of which bears porosities of various sizes. (Scale bar in Fig. 21 = 5 μm ; bars in Fig. 22–23 = 2 μm).

other foliar strategies (limited laminar area, cuticular thickness, dying of leaves during the dry season) would be of overriding importance.

In *Bommeria hispida*, the leaflets are more broadly webbed by the lamina, and the leaves are less coriaceous than those of the other species studied here. Of the ferns in this study, *Bommeria hispida* would be expected to exhibit the greatest adaptation to more rapid conduction by the xylem during a moist season. This hypothesis is, in fact, fulfilled if one credits not only the prominent scalariform perforation plates in this species, but also the large perforations that are related to what may be considered pit dimorphism. A group of large perforations near each other on the end wall of a vessel could well be equivalent in conductive capability to a scalariform perforation plate with few bars and large perforations in an angiosperm. The figures of Bierhorst (1960) for tracheary elements of an *Asplenium viride* Huds. rachis are suggestive of pit dimorphism, but he does not call attention in the text to that feature of his drawing.

The distinctive vessels of *Bommeria* mentioned above induce us to stress that the modifications in end-wall perforation plates that one sees in *Astrolepis*, *Pteridium*, and *Woodsia*, which do remind one of specializations in angiosperm perforation plates, should not be expected in all ferns of such habitats. Rather,

alternative xylem structures may potentially increase rapidity of conduction just as well as a simplified scalariform end-wall perforation plate. As one example of this, we may mention the perforation plates on lateral walls that we described for *Pteridium* (Carlquist and Schneider 1997a). Perforation plates on lateral walls of fern vessels may be much more widespread than we at present imagine. Fern vessel elements are often very long, and differentiating under the electron microscope between a lateral wall and an end wall is often not possible. Because vessels are disposed in fasciculate strands in ferns, the end wall of one vessel may interface with the lateral wall of an adjacent vessel. A perforation plate could be terminal in one vessel element yet lateral in the other. Such nesting of vessel elements does not occur in angiosperms, in which vessels are in vertical series and do not have multiple end-wall perforation plates, which are common in ferns. The positive effect upon conduction of the presence of lateral-wall perforation plates and multiple end-wall perforation plates are intriguing topics for future studies. Certainly one can hypothesize that presence of lateral perforation plates converts a strand of vessels from a series of independent units to a kind of multiple vessel. Multiple end-wall perforation plates on a single vessel element of a fern also has this effect. Because vessels have been defined in terms of a vertical connection

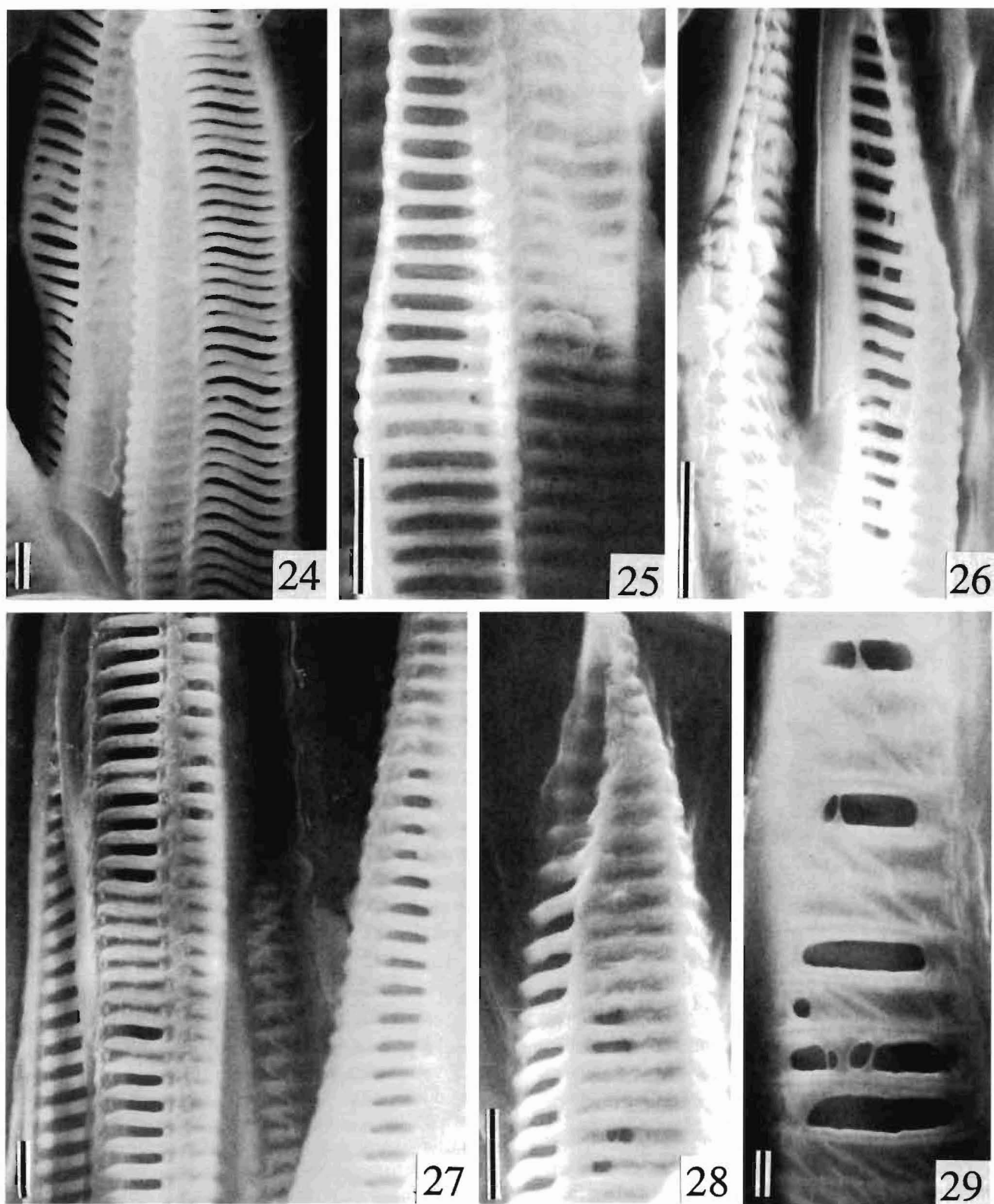


Fig. 24–29. Tracheary elements from rhizome of *Pellaea mucronata*.—24. Two adjacent tracheary elements, each with a scalariform perforation plate.—25. Perforation plate in facet, upper left.—26. End wall bearing well-defined perforation plate.—27. Adjacent tracheary elements from maceration; the element left of center contains intermittent perforation plates.—28. Tracheary element tip with perforation plate on facet at left; there are pores in pit membranes, center bottom of the other facet.—29. Facet with intermittent perforations in some of which strandlike pit membrane remnants are present. (Scale bars in Fig. 24–28 = 5 μ m; bar in Fig. 29 = 2 μ m).

between a vessel element and the element above it and the one below it, we do not even have a terminology for a strand of vessels in which perforation plates occur both on end walls (often on several such end walls per tracheary element) and on lateral walls.

We have called attention to "intermittent perforation plates," in which a few pits intervene between groups of adjacent perforations on a single vessel facet. These are well illustrated by *Pellaea mucronata* (Fig. 27–29), but the perforation dimorphism in *Bommeria hispida* (Fig. 1–3) may also represent a form of intermittent perforation plate. The term "intermittent perforation plate" is presented as a new concept here, one which invites further investigation. Within a single vascular strand, we need to know the comparative distribution of normal and of intermittent perforation plates. Likewise, we need to know the effect upon conduction of perforation plates that occur in variable modes such as this. There is no known equivalent to intermittent perforation plates in angiosperms other than, in unusual instances, double perforation plates (a pair of perforation plates, well separated from each other, at one end of a vessel element).

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