

## Perforation plate pit membrane remnants in vessels of Sarraceniaceae: possible indicators of relationship and ecology

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SCHNEIDER, E. AND S. CARLQUIST (Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105). Perforation plate remnants in vessels of Sarraceniaceae: possible indicators of relationships and ecology. *J. Torrey Bot. Soc.* 131: 1-7. 2004.—All three genera of Sarraceniaceae possess pit membrane remnants in perforations: the abundance of pit membrane remnants parallels the number of bars per perforation plate: most in *Heliophora*, fewer in *Sarracenia*, fewest in *Darlingtonia*. *Heliophora* perforation plates were reported earlier, so *Darlingtonia* (monotypic) and two species of *Sarracenia* are considered here. The majority of perforations lack extensive pit membrane remnants, but occasional meshwork-like remnants can be seen at the lateral ends of a number of perforations. Perforations intermediate in size and morphology between perforations and lateral wall pits (pit membranes nearly intact, but containing numerous pores) often occur at upper and lower ends of perforation plates. Pit membrane remnants of this type have been reported in scalariform perforation plates of families thought to be closely related to Sarraceniaceae (Clethraceae, Cyrillaceae, Ericaceae). Species of all four families in which pit membranes are present occur in highly mesic or bog habitats.

Key words: Clethraceae, Cyrillaceae, ecological wood anatomy, Ericaceae, Ericales, primitive woods, systematic wood anatomy, Theales, vessel elements.

The family Sarraceniaceae, according to a recent global molecular phylogeny of angiosperms (Soltis et al. 2000), falls in Ericales, and lies on a clade that includes Actinidiaceae, Clethraceae, Cyrillaceae, and Ericaceae. Goldberg (1986) has presented, in tabular form, the ordinal location of all dicotyledon families according to twelve leading phylogenists. Of these, only Thorne (1983) places Sarraceniaceae in Theales, an order that now falls within Ericales (Soltis et al. 2000). The unusual tubular insect-catching leaves undoubtedly seemed an aberrant feature for any existing order and thus distracted phylogenists from allying Sarraceniaceae with families now thought to be closely related.

Using scanning electron microscopy (SEM), we have been studying woods of the clade that includes the families named above, because Clethraceae, Cyrillaceae, and Ericaceae have been reported to have pit membrane remnants in scalariform perforation plates (Ohtani and Ishida 1978, Carlquist 1992a, Carlquist and Schneider in press, Schneider and Carlquist 2003). In Sarraceniaceae, *Heliophora* was reported to have

extensive pit membrane remnants (Carlquist 1992a), despite the presence of relatively wide perforations in perforation plates. Some might have concluded that pit membrane remnants are to be expected if perforations are numerous and narrow, but the data of Carlquist (1992a) on such families as Bruniaceae do not agree with that idea. Because all of the families listed in the review of Carlquist (1992a) have numerous wood features traditionally thought to be primitive, presence of pit membrane remnants in perforation plates can be interpreted as a primitive feature. In order to examine that hypothesis, we are studying Ericales as a potential case of retention of primitive wood features in an order. Another small order, Berberidopsidales (Carlquist, 2003) seems to exemplify this tendency also.

Thus far, all of the instances of pit membrane remnants occur in dicotyledons of highly mesic habitats, just as scalariform perforation plates do (Carlquist 1975), although "mesic" must be defined in terms of water availability, not rainfall amounts. Some long scalariform perforation plates lack any perceptible pit membrane remnants (Carlquist 1992a). Sarraceniaceae as a whole characteristically grow in bogs where standing water occurs throughout the year or in

<sup>1</sup> Dr. Holly Forbes of the University of California Botanical Garden, Berkeley, kindly provided the material of *Darlingtonia* and *Sarracenia* for study.

materials and methods. Rhizomatous stems, with attached roots, were available, preserved in 50% aqueous ethanol. Roots of the two genera were judged too slender to be sectioned readily for SEM examination. The portions of stems selected were the oldest for each species provided that the portions lacked rot or other signs of necrosis. Radial sections were cut on a sliding microtome, dried between clean glass slides, sputter coated, and mounted on aluminum stubs for examination by means of SEM. A Hitachi S2600N SEM was employed. Other methods were not attempted because freshly cut thick sections should, in our opinion, provide the least disturbance to pit membrane remnants. The sections contained large areas of starch-filled pith and cortical parenchyma, but strips of secondary xylem sufficiently wide for sectioning were also present. Axial xylem is formed in sinuous strips, and therefore, relatively few perforation plates were ideally displayed, but a sufficient number were oriented well and permitted us to determine the presence or absence of pit membrane remnants. We believe that artifacts other than obvious tears in the pit membranes were few. However, where threads of pit membrane material were relatively coarse, light impregnation of the membrane by the living plant during the process of membrane lysis seems possible. Degree of presence or absence of pit membrane remnants in perforation plates is not related to degree of maturation, because we took our samples from the oldest (prior to decay) stem portions, in which cambial activity had not occurred for several years (as indicated by presence of incremental additions to the stem as seen in gross aspect).

The collection data for the species studied are as follows: *Darlingtonia californica* Torr., University of California Botanic Garden, Berkeley, cultivation number 86.1690; *Sarracenia minor* Sweet, North Carolina Botanical Garden cultivation number 1985-0928; and *S. alabamensis* F. W. Case and R. B. Case subsp. *wherryi* F. W. Case and R. B. Case, North Carolina Botanical Garden cultivation number 1985-0962.

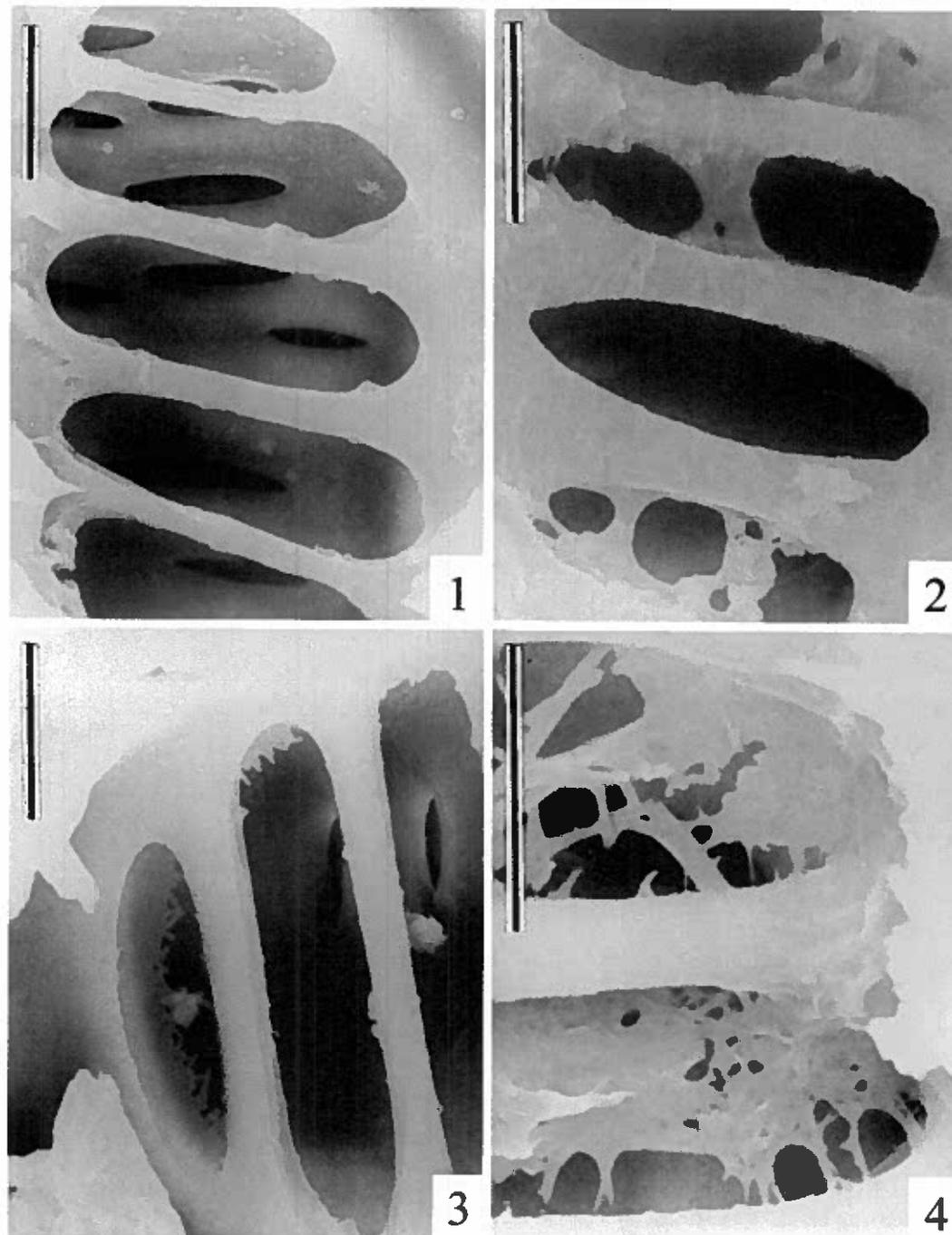
**PERFORATION PLATE OBSERVATIONS.** *Darlingtonia californica* has relatively few bars per perforation plate (Fig. 1); DeBuhr (1977) reports an average of 5.4. Bars are bordered. The majority of these plates are clear, and have only the most

of stem perforation in a perforation plate may contain more extensive remnants (Fig. 3), partially traversing the perforation. A shredlike remnant is present at the lateral end of one perforation (Fig. 3, top center). An unusual perforation plate is shown in Fig. 4: here, sheetlike remnants perforated by holes of various sizes, distributed nonrandomly, were found (note holes separated by threads at bottom of perforation, Fig. 4, below).

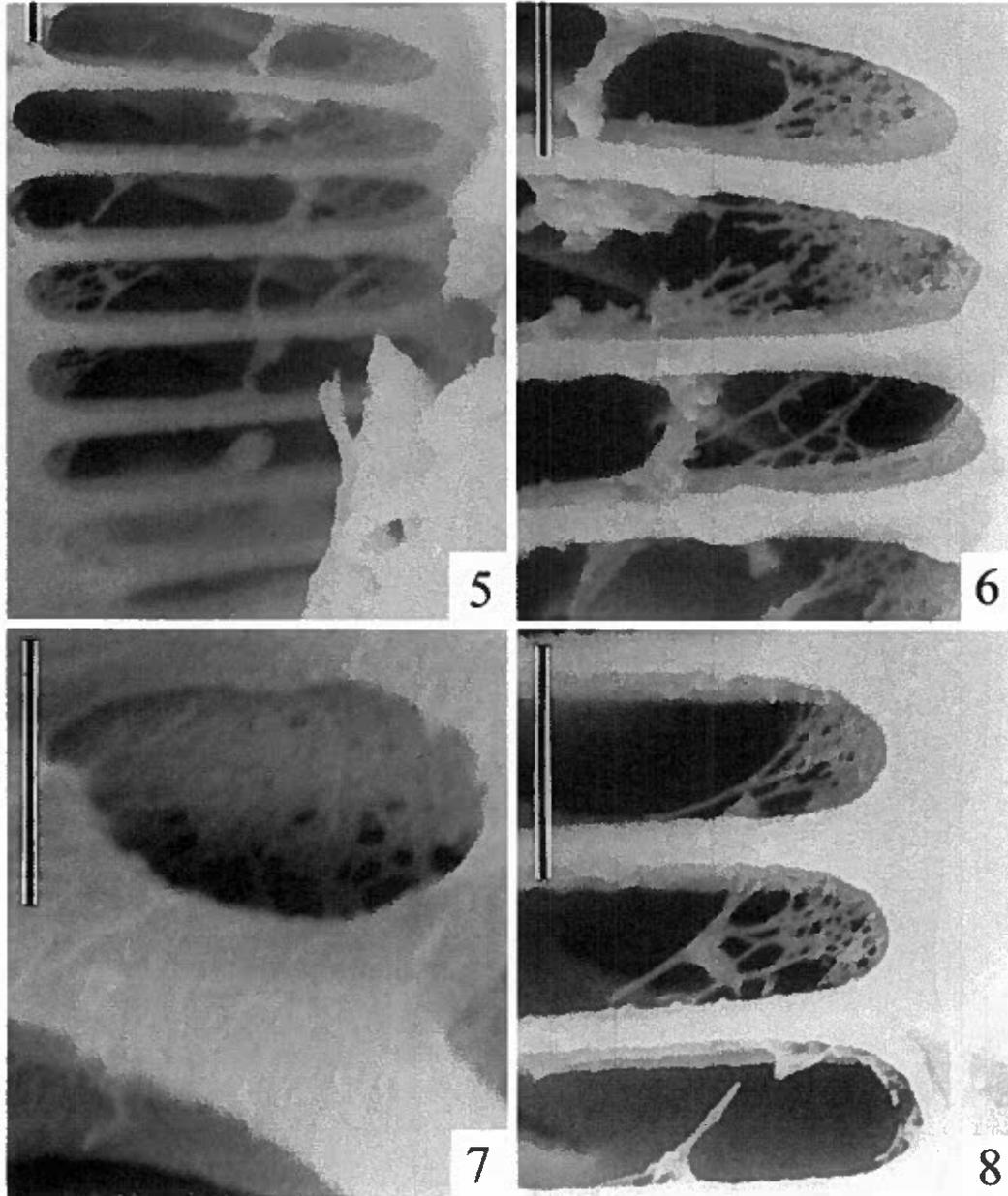
In *Sarracenia alabamensis*, bars per perforation plate are more numerous than in *Darlingtonia*, and they are not spaced so widely apart (Fig. 5). Bars are bordered. DeBuhr (1977) reports the mean number of bars per plate from 8.5 to 10.1 in the species of *Sarracenia* he studied. Strandlike remnants between bars may be seen in a few plates of *S. alabamensis* (Fig. 5), although most perforation plates contain few remnants of pit membranes. Such remnants are, however, well shown in Fig. 6 and Fig. 8; in these instances, they occur in the lateral ends of perforations and are weblike in appearance. The transition between perforations and lateral wall pits is shown in Fig. 7, in which a pit membrane is intact, but perforated by small pores.

Although most perforations in *S. minor* (Figs. 9-12) retain few pit membrane remnants, the plate portion of Fig. 9 has band-like remnants of pit membranes interconnecting some bars. The transition between pits and perforations at the upper and lower ends of perforation plates is illustrated in Figs. 10 and 12. At right in Fig. 10 is a lateral wall pit with intact membrane; to the left of that pit is a transitional pit in which a porous membrane is present; this could be termed either a perforation or a lateral wall pit. A similar situation is illustrated in Fig. 12: below is a lateral wall pit (the small tear in the pit membrane is an artifact), whereas the transitional pit/perforation, in which the pit membrane contains holes of various sizes, is above. At the ends of some perforations, networklike pit membrane remnants are present. The remnant figured in Fig. 11 has rather coarse threads, suggesting inhibition of lysis in the thinner portions of the membrane or else accretion onto the network of a secondary compound.

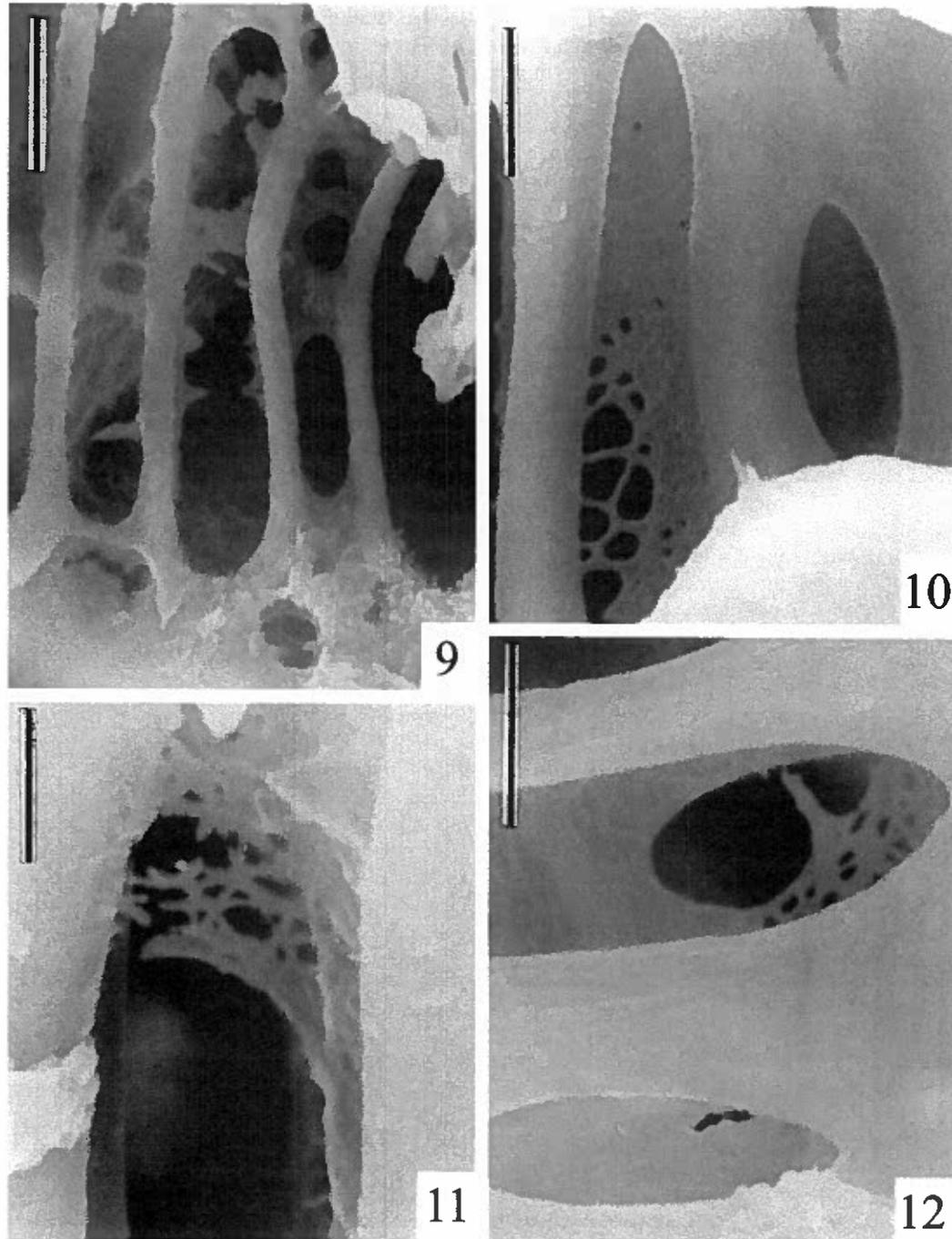
**Conclusions. SYSTEMATICS.** The microfibrillar webs figured by Ohtani and Ishida (1978) for *Enkianthus* and *Pieris* (Ericaceae), as well as the



Figs. 1-4. SEM photographs of perforation plates from vessels as seen in radial sections of *Darlingtonia californica* rhizomes (bars oriented horizontally except in Fig. 3). Fig. 1. A perforation plate (upper and lower tips not shown), illustrating almost complete absence of pit membrane remnants (which occur merely as irregular



Figs. 5-8. SEM photographs of perforation plate portions from radial sections of rhizome of *Sarracenia alabamensis* (bars oriented horizontally). Fig. 5. Entire perforation plate (except as obscured by contaminant, lower right) to show strandlike and weblike pit membrane remnants in most perforations (pit membranes nearly intact in top two perforations). Fig. 6. Lateral ends of perforations from the plate shown in Fig. 5; weblike and strandlike pit membrane remnants are common. Fig. 7. Perforation at tip of a perforation plate, transitional to lateral wall pitting; pit membrane is intact, but perforated by holes of various sizes. Fig. 8. Lateral ends of perforations, showing strandlike and weblike pit membrane remnants. Scale bars in Figs. 5, 6, and 8 = 5  $\mu\text{m}$ ; bar in Fig. 7 = 2  $\mu\text{m}$ .



Figs. 9–12. SEM photographs of perforation plate portions from radial sections of *Sarracenia minor* rhizomes (bars oriented vertically except in Fig. 12). Fig. 9. Bandlike pit membrane remnants interconnecting bars of perforation plate. Fig. 10. Transition region between perforation plate and lateral wall pitting; perforation at left has a series of holes of various sizes (left) in the lateral wall through the pit membrane. Fig. 11. A series of holes of various sizes in the lateral wall. Fig. 12. A large oval perforation plate with a smaller one below it.

Sarraceniaceae. The axially-oriented threads in several Clethraceae are distinctive; however, taken as a whole, these families all seem to possess a similar level of retention of pit membrane remnants. There is a similar level of primitive wood features in these families: they have scalariform perforation plates (some simple in some genera of Ericaceae), tracheids rather than fiber-tracheids or libriform fibers as imperforate tracheary elements (except for several genera of Ericaceae), diffuse axial parenchyma, and heterogeneous rays (Metcalf and Chalk 1950; DeBuhr 1977). Thus, the occurrence of pit membrane remnants in perforations of vessels of the four ericalean families cited above is consistent with the idea that pit membrane remnants represent a primitive feature in dicotyledons (Carlquist 1992a) and thus the presence of pit membrane remnants would be a symplesiomorphy in the clade that includes these families.

Within Sarraceniaceae, *Heliophora* clearly has more extensive pit membrane remnants (Carlquist 1992a), corresponding to the greater number of bars per perforation plates in that genus compared with *Darlingtonia* and *Sarracenia* (DeBuhr 1977), and tending to confirm that greater abundance of pit membrane remnants is a primitive feature. There is no perceptible difference between *Darlingtonia* and *Sarracenia* in presence of pit membrane remnants in perforation plates based on our material, nor is our survey sufficient to indicate any differences among species reliably.

**ECOLOGY.** Extensive presence of pit membrane remnants would form an impedence to conduction, and would therefore not be expected in highly seasonal climates where water availability in soil fluctuates markedly. The ecology of the species in which pit membrane remnants have been reported (Carlquist 1992a) supports this interpretation. Presence of numerous bars per perforation plate could conceivably be considered a mechanism for removing air bubbles from the conductive stream following thawing of ice in vessels (Zimmermann 1983), and pit membrane remnants would form an even greater impedence to passage of air bubbles from one vessel element to the next. However, species with numerous bars per perforation plate and species with extensive pit membrane remnants do not occur in areas where freezing is common.

species included in Carlquist (1992a) could also be cited. Thus, presence of pit membrane remnants and presence of numerous bars per perforation plates are best regarded as vestigial features retained in phylads that have had an unbroken occupancy of mesic areas. The preference of Sarraceniaceae for bogs and other areas with a water table very close to the ground surface is certainly exemplary of occupancy of a wet habitat. The fact that pit membranes are most extensive in *Heliophora* but present to the smallest extent in *Darlingtonia* may correlated with a more constant availability of water in the Guayana Highland tepui bogs where *Heliophora* grows. Although no ecological observations are available for moisture fluctuation in *Darlingtonia* habitats, some of them are in small montane streams in northern California (S. Carlquist, personal observation) that may dry somewhat during warm summer months. No Sarraceniaceae grow in habitats that lack some degree of moisture throughout the year, however. Presence of pit membrane remnants would constitute an impedence to conduction during periods of more rapid transpiration, and would therefore not be expected in species in which moisture fluctuates markedly. This would be especially true if moisture is available for only a short period of the year, when very rapid conduction would be expected. One can hypothesize that Clethraceae, Cyrillaceae, and Sarraceniaceae have had an unbroken history of occupancy of mesic or bog habitats that are relatively constant in water availability throughout the year. Relatively constant, moderate transpiration of plants in such habitats would lessen selection against higher impedence in perforation plates.

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