

## Vestigial pit membrane remnants in perforation plates and helical thickenings in vessels of Ericaceae

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Perforation plates from 15 species of 10 genera with scalariform perforation plates, representing three subfamilies of woody Ericaceae (Rhododendroideae, Arbutoideae, Vaccinioideae) were studied with scanning electron microscopy (SEM). In most of them, pit membrane remnants were present, but these remnants were less extensive than in the ericalean families Clethraceae, Cyrillaceae, and Sarraceniaceae. Pit membrane remnants in perforations of vessels of Ericaceae are characteristically found at lateral ends of the perforations and in perforations (which may alternatively be called pits) transitional to lateral wall pitting. Pit membrane remnants were most extensive in *Enkianthus*. Phylogenetic and physiological factors for vestigial membrane presence in the perforations are discussed. Helical thickenings on vessel walls as seen with SEM are figured and described for *Leucothoe* and *Pieris*, and their significance is assessed.

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### Introduction

A survey by Carlquist (1992) on presence of pit membrane remnants included Ericaceae, on the basis of work by Ohtani and Ishida (1978). Other families that are now included in Ericales (Soltis et al. 2000; APGII 2003) were listed in the survey of Carlquist (1992). Studies devoted to exploring the range of expressions in pit membrane presence in vessels have been done on Clethraceae (Carlquist & Schneider 2004), Cyrillaceae (Schneider & Carlquist 2003), and Sarraceniaceae (Schneider & Carlquist 2004). Viewed against the background of those three studies, the Ericaceae first selected for the present study proved to have relatively vestigial pit mem-

branes. This circumstance induced us to sample more widely among woody Ericaceae with scalariform perforation plates. The possibility that this minimal level of pit membrane presence characterizes a relatively large family – the first family in which such a condition has been reported – has induced us to consider phylogenetic and physiological explanations for the conditions observed. Our sampling has, we believe, given us something approaching the full range of degree of membrane presence in perforations of Ericaceae. We are attempting to expand data on the phenomenon of persistent membranes in perforation plates of some families is advanced by this survey. Hopefully, a broader data base will clarify the significance of this phenomenon.

In the course of our study of vessels by means of SEM, we observed helical thickenings in two genera. Helical thickenings occur in vessels of certain Ericaceae: *Andrachne*, *Arbutus*, *Arctostaphylos* (some species), *Menziesia*, and *Rhododendron* (some species) according to Solereder (1908) and Schweingruber (1990). Our studies add two genera to this list, and we discuss variations in helical sculpturing in vessels as visible with SEM.

## Material and methods

Fresh materials of *Enkianthus* (two species), *Gaultheria erecta*, *Pieris japonica*, *Rhododendron occidentale*, and *Vaccinium ovatum* were available. These specimens were fixed in 50% aqueous ethanol. All other materials studied were available in dried form, either from xylarium or herbarium materials, and were boiled in water and stored in 50% aqueous ethanol. Once in alcohol, radial sections of wood samples were prepared with a sliding microtome. Sections were dried between clean glass slides, mounted on aluminum stubs, sputter-coated with gold, and examined with a Hitachi 2600N scanning electron microscope.

The collections studied are as follows: *Enkianthus campanulatus* Nichols, cult. Washington Park Arboretum (Seattle); *E. cernuus* Makino, cult. Washington Park Arboretum (Seattle); *Gaultheria erecta* Vent., cult. University of California Botanic Garden, Berkeley (90.02644, seed collected at km 63 on Route 2, inside Cartago Province near border of San Jose Province, Costa Rica), M. Grantham & J. Parsons 0440-90 (UC); *G. shallon* Pursh, near summit of Mt. Tranquillon, Santa Barbara Co., California, Clifton Smith 3531 (SBG); *Ledum glandulosum* Nutt., Pt. Reyes, Marin Co., California, A.D.E. Elmer 4944 (SBG); *Leiophyllum buxifolium* (Berg.) Ell., Atsion, Burlington Co. New Jersey, W. L. Dres and J. E. Cruise 5952 (SBG); *Leucothoe axillaris* (Lam.) D. Don, cult. University of California Botanic Garden, Berkeley (86.0647, seed collected in deciduous woodland along Indian Creek, Transylvania Co., North Carolina); *Pernettya prostrata* (Cav.) DC., cult. University of California Botanic Garden, Berkeley (90.2275, seed collected on summit rim of Vulcan Irazu, 3400 m, Cartago Prov., Costa Rica), M. Grantham & J. Parsons 0197-90 (UC); *Phyllodoce breweri* (Gray) Heller, Piute Lake, Piute Pass Trail, 3750 m, W of Bishop, Inyo Co., California, K. K. Muller 997 (SBG); *Pieris japonica* D. Don ex G. Don, cult. Washington Park Arboretum (Seattle); *R. moullainense* Hook., Thailand, Abbe 9290, Usw-36293; *R. occidentale* A. Gray, cult. Santa Barbara

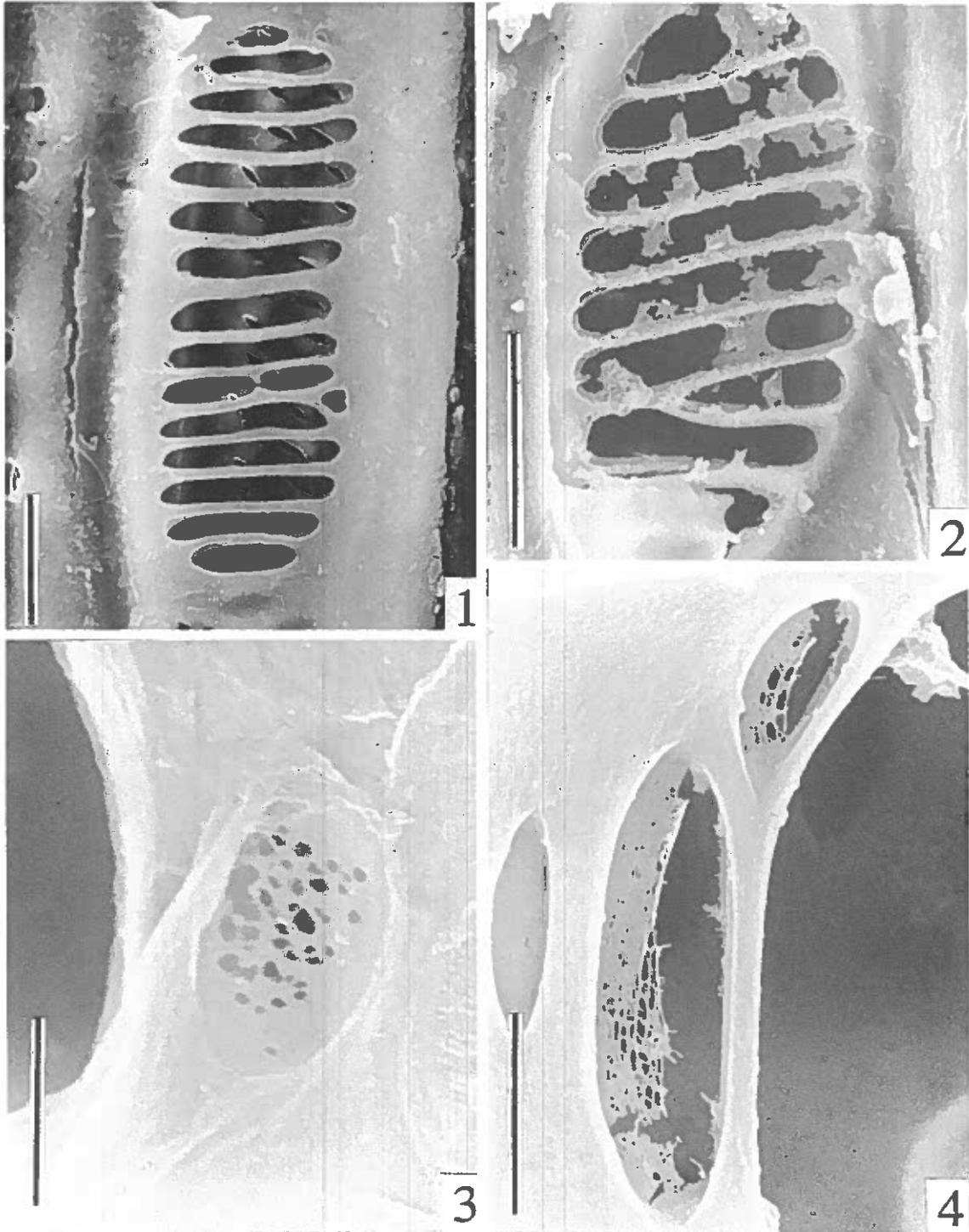
Botanic Garden; *R. sumatranum* Merrill, Indonesia, Boeeca 11356, Usw-29265; *Vaccinium ovatum* Pursh, cult. Santa Barbara Botanic Garden; *V. uliginosum* L., Crater Springs area, Crater Lake National Park, Klamath Co., Oregon, M. Piehl 27 July 1956 (SBG). We did not study *Cassiope* sections once we had determined that material of the species we selected had simple perforation plates (some *Cassiope* species do have scalariform perforation plates), and likewise, all Ericaceae reported to have simple perforation plates were omitted from this study. Although small pit membrane remnants can occur on simple perforation plates (e.g., *Knightia* of the Proteaceae, Meylan and Butterfield 1978), simple perforation plates lack any such remnants so frequently that search for this phenomenon in species with simple perforation plates is not considered practical at present.

The illustrations are arranged as nearly as practicable in systematic groupings. The genera studied fall into the three subfamilies as follows (classification from Melchior 1964): subfamily Rhododendroideae (*Ledum*, *Leiophyllum*, *Rhododendron* in tribe Rhododendroideae; *Phyllodoce* in Phyllococeae); subfamily Arbutioideae (*Gaultheria* and *Pernettya* in tribe Gaultherieae; *Enkianthus*, *Leucothoe*, and *Pieris* in tribe Andromedeae); and subfamily Vaccinioideae (*Vaccinium* in tribe Vaccinieae). No species of the subfamily Ericoideae are included in this study on account of the simple perforation plates of that subfamily.

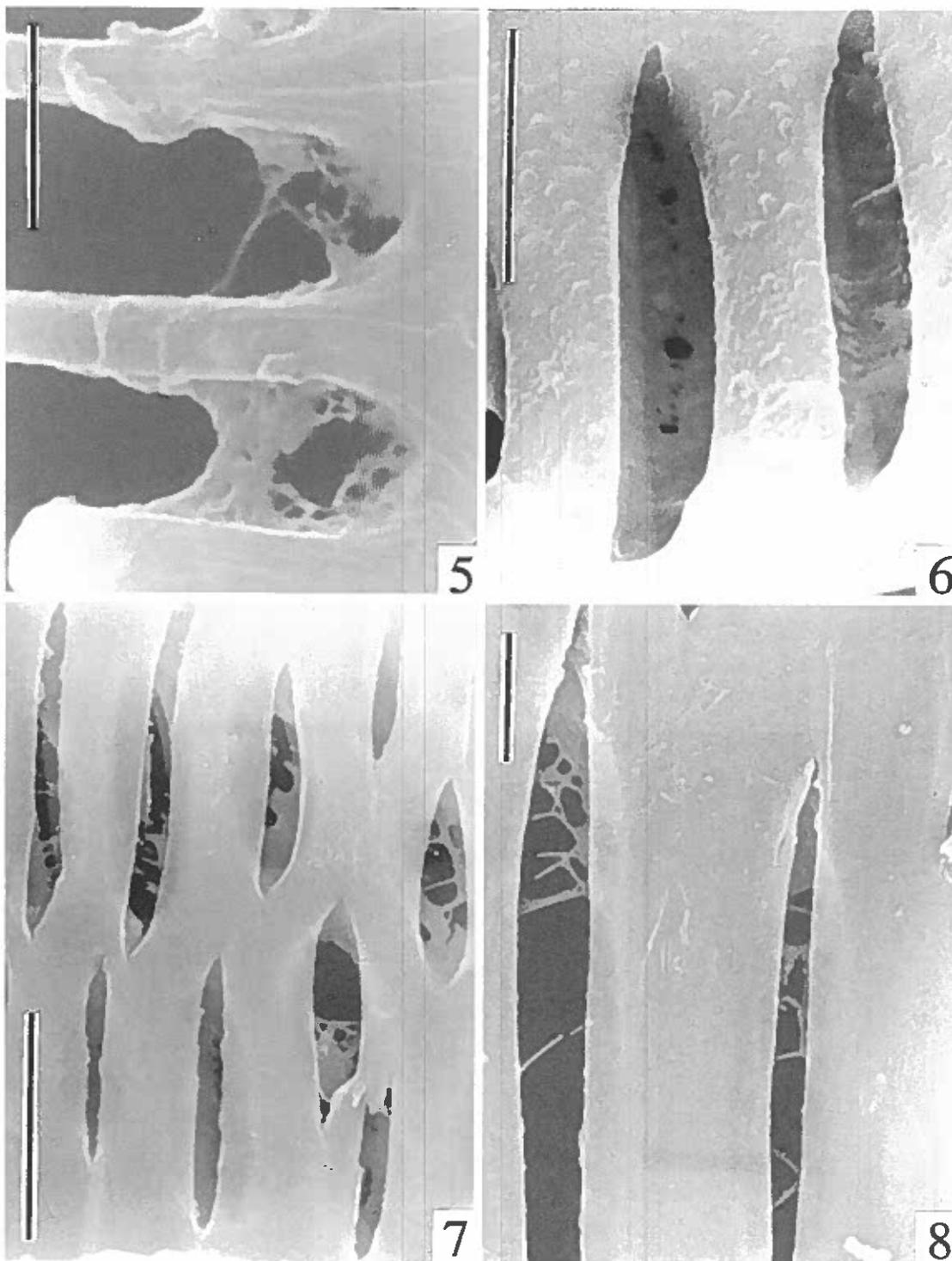
## Results

*Rhododendron* has scalariform perforation plates, such as that shown for *R. sumatranum* in Fig. 1 (there is a slight tendency in the plate shown for the plate to subdivide into two halves). In *R. sumatranum*, we did not observe any appreciable pit membrane remnants in perforations. In *R. moullainense* (Fig. 2), on the contrary, flakelike pit membrane remnants were observed. Because we did not see flakelike pit membrane remnants elsewhere in Ericaceae, we believe that these remnants may be, at least in part, artifacts in which preservation of pit membrane remnants has been aided by natural impregnation of the pit membranes with small amounts of secondary compounds. Possibly the flakelike configuration is a natural expression, and consequently we report it so that future studies can assess such manifestations.

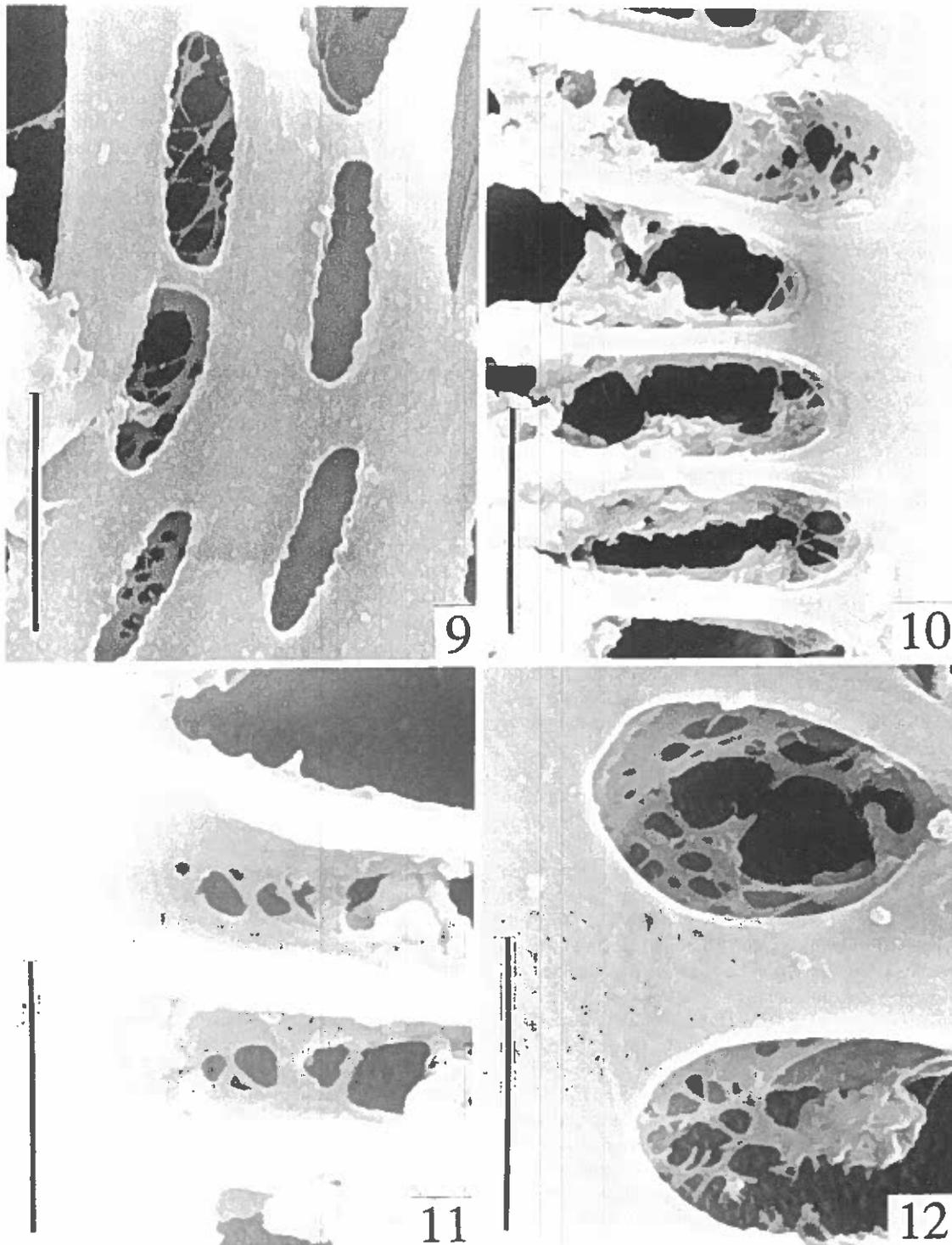
In *Rhododendron occidentale*, pit membranes bearing pores of various sizes were seen in pits (which alternatively may be considered incomplete perforations) at the upper and lower ends of



Figs 1-4. Perforation plates of *Rhododendron*. – Fig. 1. *R. sumatranum*, entire perforation plate, showing absence of pit membrane remnants. – Fig. 2. *R. moulmainense*, perforation plate with flakelike pit membrane remnants that may be atypical in shape of portions of preserved pit membranes because of deposition of secondary compounds. – Figs 3-4. *R. occidentale*, portions of perforation plates transitional to lateral wall pitting. – Fig. 3. Pit at end of perforation plate, showing circular pores. – Fig. 4. Pits at end of perforation plate, showing porose membranes; the large tears are artifacts. – Fig. 1, 2, bar = 20  $\mu$ m; Fig. 3, bar = 2  $\mu$ m; Fig. 5, bar = 5  $\mu$ m.



Figs 5-8. Portions of perforation plates of Ericaceae. – Fig. 5. *Ledum glandulosum*, lateral ends of perforations, showing pit membrane remnants. – Fig. 6. *Leiophyllum buxifolium*, transition between perforation plate and lateral wall pitting; a median line of circular holes is present in the pit (perforation), left of center. – Figs 7-8. *Pernettya prostrata*, narrowly elliptical perforations characteristic of this species. – Fig. 7. Perforations containing various degrees of pit membrane presence. – Fig. 8. Threadlike pit membrane remnants in two perforations. – Figs 5, 8, bars = 2  $\mu$ m; Figs 6, 7, bars = 5  $\mu$ m.



Figs 9-12. Portions of perforation plates of *Enkianthus campanulatus*. – Fig. 9. Transition between lateral wall pitting (right) and perforation plate (left), showing various degrees of pit membrane retention in three pits (perforations) in transitional zone. – Fig. 10. Lateral ends of perforations, showing netlike pit membrane remnants; areas at left overlaid with deposits of unknown material. – Fig. 11. Holes in median position of membrane remnants in lateral ends of two perforations. – Fig. 12. Pores of various sizes and shapes in membrane remnants at ends of two lateral ends of perforations. – Fig. 9, bar = 5  $\mu$ m; Figs 10-12, bars = 2  $\mu$ m.

perforation plates (Figs 3, 4). The transitional status of these pits is indicated by their position (intermediate between perforations with few pit membrane remnants and lateral wall pits, which have intact pit membranes) and their size (larger than lateral wall pits, smaller than other perforations). The pores are circular (Fig. 3) to oval (Fig. 4). The pit membrane in Fig. 3 is interpreted as nearly free of artifacts, whereas the two perforations bearing porose pit membranes in Fig. 4 show prominent tears, which are clearly artifacts; the pores, however are considered a natural phenomenon (note the lack of pores in the pit at left, Fig. 4). Porose pit membranes were observed in pits transitional between lateral wall pitting and perforations in *Phyllodoce breweri* (not illustrated).

In *Ledum glandulosum* (Fig. 5), another type of occurrence of pit membrane remnants observed in a number of Ericaceae is represented. Threadlike or porose sheetlike pit membranes are located at lateral ends of perforations, but the central portions of perforations are clear; two perforation ends are illustrated in Fig. 5. *Leiophyllum buxifolium* (Fig. 6) has perforations mostly clear of pit membrane remnants, but in the zone of transition between perforation plate and lateral wall pitting, porose pit membranes were observed in several vessels. The pit membrane at right in Fig. 6 is intact, but there is a series of small circular pores in the median area of the pit membrane in the perforation at left.

*Pernettya prostrata* (Figs 7, 8) has narrow, slitlike perforations; they are arranged in scalariform fashion (Fig. 8) or in dispositions intermediate between scalariform and multiperforate (Fig. 7). Pit membrane remnants seem retained to a greater extent in narrower perforations than in wider ones. Pit membrane remnants take the form of threads (Fig. 8) or of holes of various sizes in laminar portions of pit membrane (Figs 7, 8). The only other species of gaultherioid Arbutioideae illustrated here is *Gaultheria erecta* (Fig. 23). Pores, which may show artifact formation in their elongate shape, occur in two pits observed in the central portion of a perforation plate which otherwise consisted of typical elongate perforations (Fig. 23, right and left). Threadlike and porose sheetlike remnants were observed in the larger perforations in this species (Fig. 23, right). No pit membrane remnants were observed in our material of *Gaultheria shallon*.

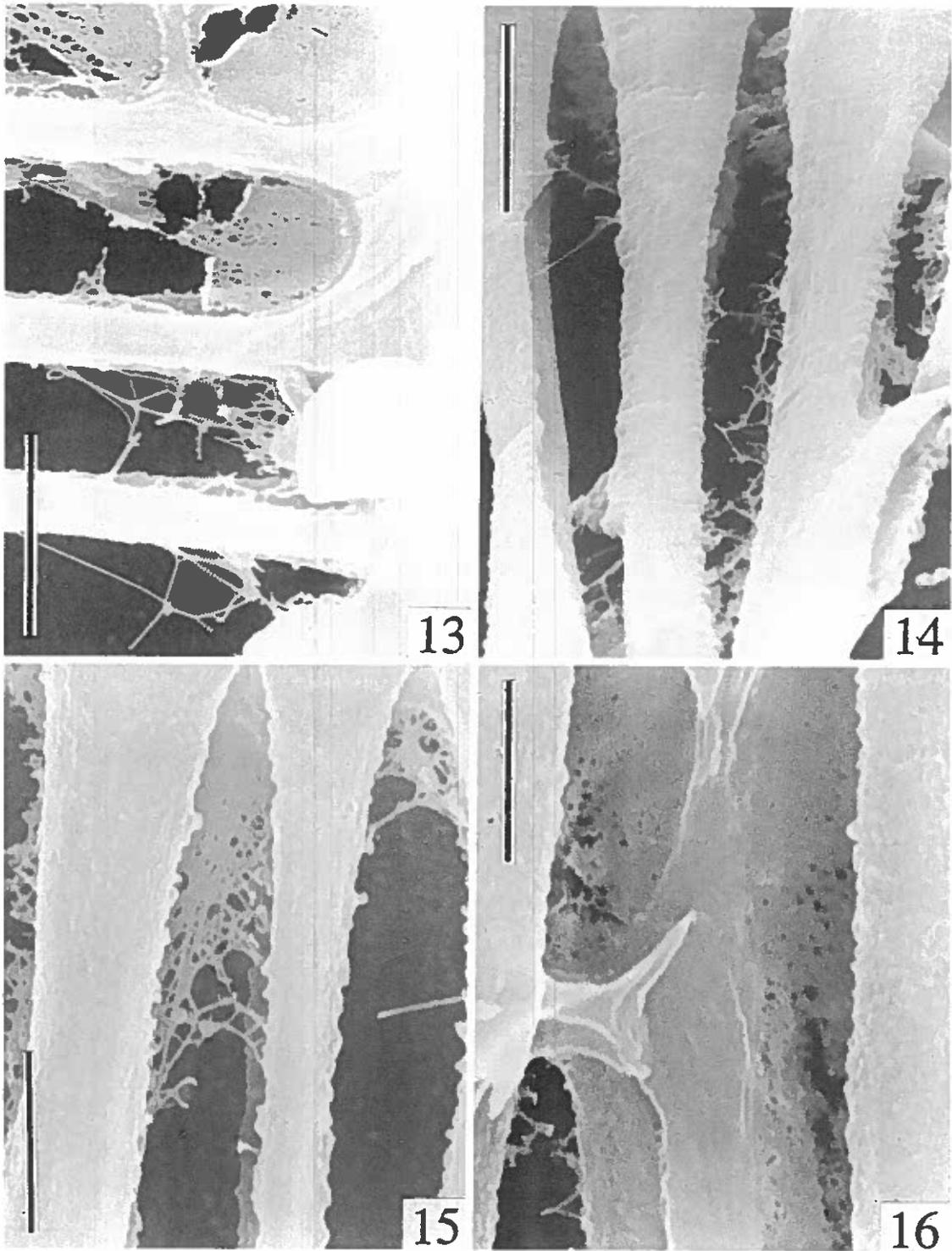
Of all Ericaceae studied here, pit membrane remnants in perforations were most abundantly represented in *Enkianthus*, of the subfamily Arbutioideae, tribe Andromedeae. Pit membrane remnants were cited for *Enkianthus* perforation plates by Ohtani and Ishida (1978), but only a few

were figured by those authors. *Enkianthus campanulatus* (Figs 9-12) shows both modes of pit membrane occurrence we have cited as characteristic in Ericaceae. Pit membrane retention occurs in pits (perforations) transitional between lateral wall pits (Fig. 9, right) and typical perforations (Fig. 9, extreme left). The pit membrane remnants in Fig. 9 range between porose sheets of primary wall and threadlike vestiges. Pit membrane retention also occurs in lateral ends of perforations (Figs 10-12). One may note that tears (Fig. 10, bottom), and accretion of unidentified deposits (Fig. 10, left) obscure this pattern to some extent, but it is so abundantly evident in our material that such artifacts are insignificant in determining the presence of pit membranes in the specimen as a whole. Holes can occur in median portions of pit membranes at lateral ends of perforations (Fig. 11). Alternatively, intricate weblike patterns are formed by pit membrane remnants in this species (Fig. 12).

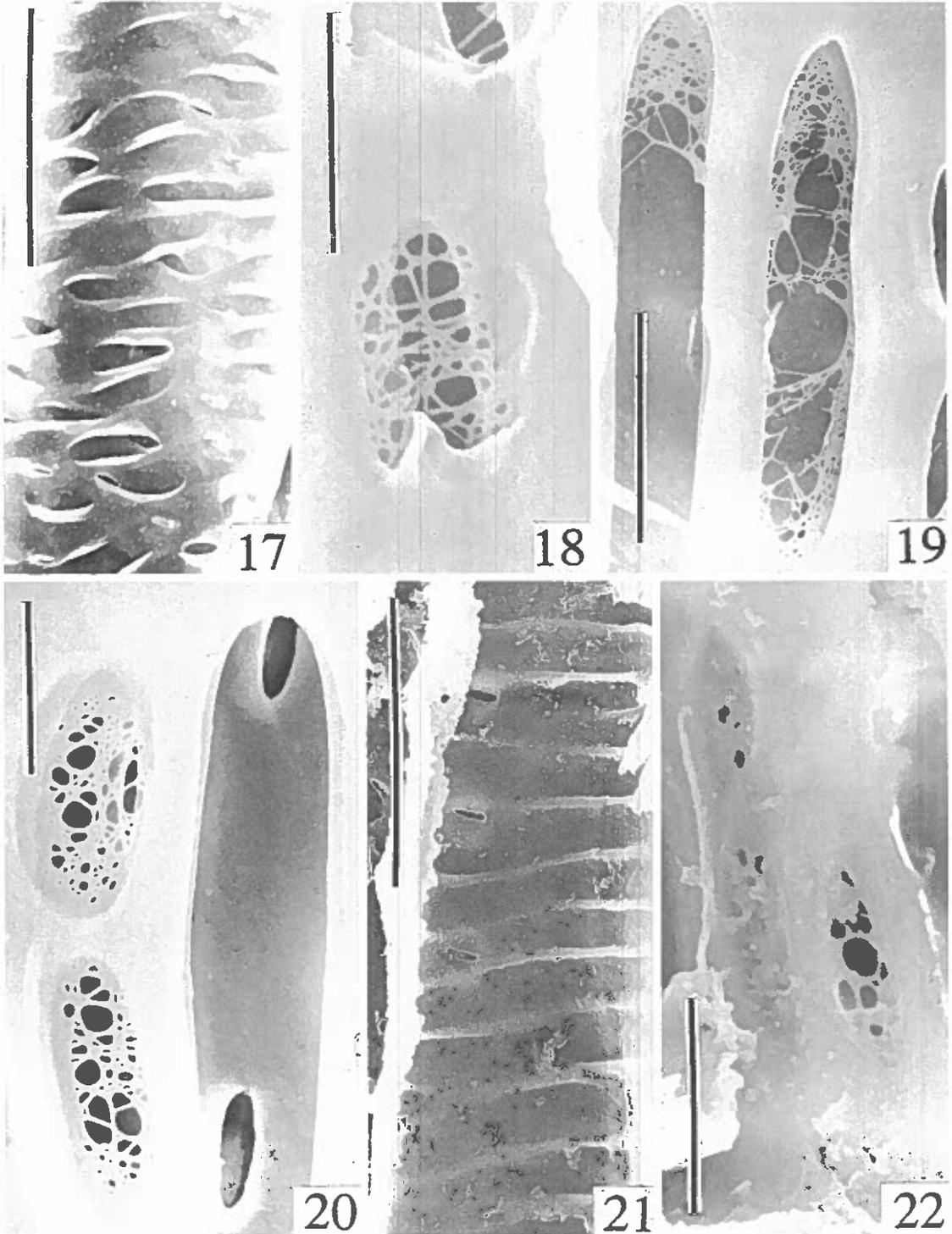
*Enkianthus cernuus* (Figs 13-16) has maximal pit membrane retention in perforations: few if any perforations can be said to be entirely free of such remnants. The range of appearances in the membrane remnants is wide in the examples shown here: distinctive threads but also sheets with small pores (Fig. 13; a few tears in the sheetlike portions); predominantly threadlike and strandlike remnants (Fig. 14); threads intergrading into porose sheets of pit membrane material (Fig. 15); and pit membranes that are essentially intact (aside from some tears) but which contain pores of various sizes (Fig. 16, right; upper left).

*Leucothoe axillaris*, another andromedoid species of Arbutioideae, possesses pit membrane remnants abundantly (Figs 18-20), although some perforations contain no apparent remnants (Fig. 20, right). Smaller pits transitional between perforation plates and lateral wall pitting (Fig. 18; Fig. 20, left) contain intricate webs composed of threads that seem resistant to breakage. Larger perforations contain pit membranes more abundantly at lateral ends (Fig. 19), and these threads seem more delicate, if only because they extend across wider gaps than do those of the smaller pits, and are therefore more subject to breakage (possibly due to accelerating voltage of the electron beam). In another andromedoid species, *Pieris japonica* (Fig. 22) we observed pit membranes with holes of various sizes in the zones transitional between lateral wall pitting and perforation plates.

Within tribe Vaccinioideae, the two species of *Vaccinium* we studied both possess pit membrane remnants, although the two species differ appreciably in the nature of these remnants. In *V. uliginosum* (Fig. 24), the specimen we studied had



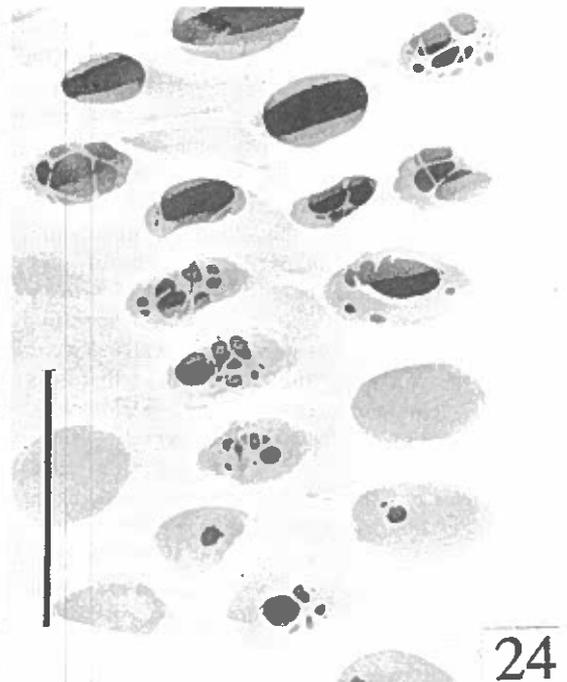
Figs 13-16. Portions of perforation plates of *Enkianthus cernuus*. – Fig. 13. Lateral ends of perforations, showing threads (below) and perforate sheets of pit membranes (above). – Fig. 14. Portions of several perforations, showing chiefly threadlike pit membrane remnants. – Fig. 15. Lateral ends of two perforations, showing that pit membrane remnants are confined to the ends of the perforations. – Fig. 16. Area of pits (perforations) transitional between lateral wall pitting and perforations; pit membranes (above) contain small circular pores. – Figs 12-16, bars = 2  $\mu$ m.



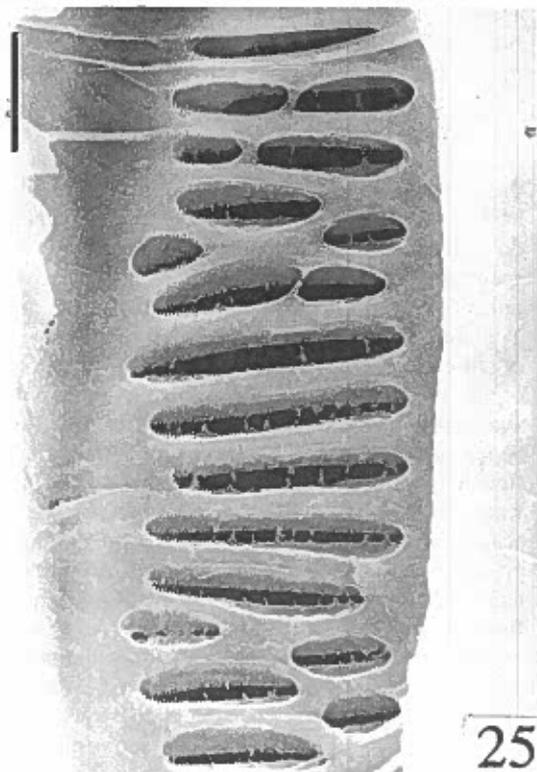
Figs 17-22. Details of vessel structure of Ericaceae as seen with SEM. – Figs 17-20. *Leucothoe axillaris*. – Fig. 17. Lateral wall of vessel, showing paired ridges, some adjacent to pit apertures, some not. – Fig. 18. Pit (perforation) from transition between perforation plate and lateral wall pitting; pit membrane remnants in the form of fine threads. – Fig. 19. Two perforations; membrane remnants more extensive in perforation at right, confined to lateral end of perforation at left. – Fig. 20. Perforation (right) devoid of pit membrane and pits (perforations) in transition zone (left), showing holes separated by coarse threads. – Figs 21-22. *Pieris japonica*. – Fig. 21. Lateral wall of vessel; helical thickenings are relatively low. – Fig. 22. Transition between perforation plate (right) and lateral wall pitting; two pits (perforations) have membranes containing pores of various sizes. – Figs 17, 21, bar = 20  $\mu$ m; Figs 18, 19, 20, 22, bars = 5  $\mu$ m.



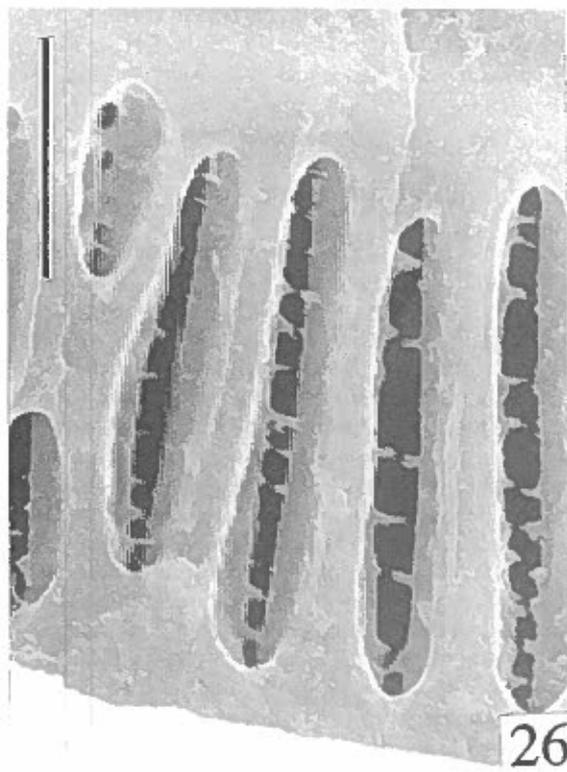
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Figs 23-26. Perforation plates of Ericaceae as seen with SEM. — Fig. 23. *Gaultheria erecta*. Pit membranes retained in smaller perforations, center. — Fig. 24. *Vaccinium uliginosum*. Transition between a multiperforate perforation plate (top) and later wall pitting (below). — Figs 25-26. *Vaccinium ovatum*. — Fig. 25. About  $\frac{1}{4}$  of a perforation plate, to show axially-oriented threadlike pit membrane remnants. — Fig. 26. Central portion of a perforation plate, to show nature of the threadlike pit membrane remnants. — Figs 23-25, bars = 5  $\mu$ m.

multiperforate perforation plates almost exclusively, and the perforations of these bore intact pit membranes, porose pit membranes, pit membranes traversed by threads, or pit membranes with no visible membrane remnants. Our material of *V. ovatum* (Fig. 25) had nearly typical scalariform perforation plates (Fig. 25), and in each of the perforations of such plates, threadlike pit membrane remnants are scattered along the length of the perforations. To be sure, these threads have broken in places, an artifact likely due to handling (Fig. 26).

Helical thickenings on vessel walls were conveniently observed at the same time that we studied pit membrane remnants in perforations plates, and are mentioned in the present study because helical thickenings have not, to our knowledge, been reported in the genera in which we observed them. In *Leucothoe axillaris*, the helical thickenings (Fig. 17) take a form that is difficult to define: short parenthesis-shaped ridges occur in pairs near pits, but many such pairs do not appear to be associated with pits; they fade into the wall in various ways, and some of the ridges do not occur in pairs. In *Pieris japonica*, helical thickenings are present (Fig. 21), but they are rather widely spaced, not prominent, and fade into the wall surface at various points.

## Discussion and conclusions

Our materials of Ericaceae showed that pit membrane remnants are widespread in most Ericaceae with scalariform perforation plates. These remnants, however, are not as extensive as they are in other families of Ericales. In three families placed in Ericales by recent authors (APG II 2003; Soltis et al. 2000), Clethraceae (Carlquist & Schneider 2004), Cyrillaceae (Schneider & Carlquist 2003), and Sarraceniaceae (Schneider & Carlquist 2004), pit membrane remnants can occur in more than a quarter, often more than half, of the area formed by perforations of numerous perforation plates. In Ericaceae, pit membrane remnants are minimal in most perforation plates. Where present in Ericaceae, these remnants tend to be confined to (1) the lateral ends of perforations; and/or to (2) one or several pits (which alternatively may be termed perforations) in the transition between the the perforation plate (usually scalariform) and lateral wall pitting. The pit membrane remnants take the form of sheets of primary wall perforated by pores of various sizes, or threads that traverse the perforation; transitions between the two types often occur. We sampled only genera with scalariform perforation plates, because

pit membrane remnants are so scarce in simple perforation plates of dicotyledons as to be almost nonexistent. Our sampling did cover all three subfamilies and enough species to show a consistency in the patterns described above.

Within Ericales, the degree of membrane remnant presence in perforations of vessels of Ericaceae can be described as vestigial. Two explanations are possible, and they may not be mutually exclusive. Ericaceae may be in a moderately basal position with Ericales and represent an intermediate stage in disappearance of pit membrane remnants compared to Clethraceae, Cyrillaceae, and Sarraceniaceae. In turn, this explanation makes the assumption that Ericales as a whole are relatively primitive in numerous features, because scalariform perforation plates with pit membrane remnants and similarly primitive features are lacking in numerous clades of dicotyledons. The presence of pit membrane remnants has been interpreted as a very primitive feature in dicotyledon wood, a kind of vestige of a tracheidlike condition (Carlquist 1992).

Pit membrane remnants in theory would form an appreciable impedance to flow in vessels, unless sap flow rates are very slow (in terms of volume per unit time). One can hypothesize that dicotyledons with primitive secondary xylem that has scalariform perforation plates retaining pit membrane remnants occur in mesic conditions. Certainly this is true in the three other families of Ericales cited above as having more extensive pit membrane remnants than do Ericaceae. Although some Ericaceae certainly do grow in highly mesic conditions, the family ranges rather widely with respect to soil moisture availability in sites where species occur. The genera of Ericaceae with simple perforation plates tend to occur in areas with wide fluctuation in moisture availability, where simple perforation plates would be of selective value for accommodating more rapid flow rates during relatively brief periods of abundant water availability. The genera of Ericaceae with scalariform perforation plates, especially those with presence of pit membrane remnants in perforations, tend to grow in moister habitats, where severe fluctuation in water availability does not occur. Pit membrane remnants, because they represent an impedance to conduction, would be of neutral selective value where flow rates are slow, and where both moisture availability and transpiration are steady, as in Clethraceae (Carlquist & Schneider 2004) or Cyrillaceae (Schneider & Carlquist 2003).

The occurrence of helical thickenings in vessels of Ericaceae is interesting, because they have been reported only in a limited number of genera. These genera (see Introduction) occur in sites where

reduction in soil moisture occurs at least briefly, or where freezing conditions (which can be considered physiologically a form of drought) are present. The increasing percentage of helical thickenings with increasing xeric conditions was demonstrated within a single large family, Asteraceae (Carlquist 1966). This tendency occurs within dicotyledons at large, and may represent a method of deterring embolism formation in vessels or of removal of embolisms in vessels, or conceivably, both (Carlquist 1975, 2001). The reports of helical thickenings in *Leucothoe* and in *Pieris* are new records, as far as we know. The thickenings in *Leucothoe* are of a novel type not often encountered in dicotyledons; those of *Pieris* are more typical. However, the more we view helical sculpturing in vessels in dicotyledons with SEM, the more we realize that helical sculpturing is not a single phenomenon ("helical thickenings") but a series of phenomena, representing many distinctive patterns (Carlquist 2001).

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## THE RUPERT BARNEBY AWARD

The New York Botanical Garden is pleased to announce that Vidal de Freitas Mansano, of the Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, and Benjamin M. Torke, currently a graduate student in the Department of Biology, Washington University, St. Louis, are the joint recipients of the Rupert Barneby Award for the year 2005. They will be studying the systematics and diversification of *Swartzia* (Leguminosae, Papilionoideae, Swartzieae), a prominent neotropical tree genus of approximately 140-180 species, with species diversity concentrated in lowland rainforests of the Guianas and Amazonia.

The New York Botanical Garden now invites applications for the Rupert Barneby Award for the year 2006. The award of US\$ 1,000.00 is to assist researchers to visit The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a detailed letter describing the project for which the award is sought, and the names of 2-3 referees. Travel to the NYBG should be planned for sometime in the year 2006. The application should be addressed to Dr. James L. Luteyn, Institute of Systematic Botany, The New York Botanical Garden, 200th Street and Kazimiroff Blvd., Bronx, NY 10458-5126 USA, and received no later than December 1, 2005. Announcement of the recipient will be made by December 15th.