

Pit membrane remnants in perforation plates of Hydrangeales with comments on pit membrane remnant occurrence, physiological significance and phylogenetic distribution in dicotyledons

SHERWIN CARLQUIST FLS* and EDWARD L. SCHNEIDER

Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105, USA

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Perforation plates from ten species of seven genera of Hydrangeales *sensu* Thorne were studied using scanning electron microscopy (SEM). The presence of pit membranes in perforations ranges from abundant, as in *Carpenteria* and *Hydrangea*, to minimal, as in *Deutzia*, *Escallonia* and *Philadelphus*. Abnormally great pit membrane presence may result from the presence of secondary compounds that inhibit lysis, as in *Quintinia serrata*; such interference with the natural lysis process may or may not be evident from coarseness and irregularity of pit membrane surface and of threads composing the pit membrane remnants. The presence of pit membrane remnants in perforation plates is hypothesized to be a symplesiomorphy, found in a fraction of dicotyledons with scalariform perforation plates (but still in an appreciable number of species). Pit membrane remnant presence may represent incomplete lysis of primary wall material (cellulose microfibrils) in species that occupy highly mesic habitats, where such impedance in the conductive stream does not have an appreciable negative selective value. This physiological interpretation of pit membrane remnants in perforations is enhanced by the phylogenetic distribution as well as the strongly mesic ecological preferences of species that exemplify this phenomenon in dicotyledons at large. Families with pit membrane presence in perforations are scattered throughout phylogenetic trees, but they occur most often in basal branches of major clades (superorders) or as basal branches of orders within the major clades. Further study will doubtless reveal other families and genera in which this phenomenon occurs, although it is readily detected only with SEM. Phylogenetic stages in the disappearance of pit membrane remnants from perforation plates are described, ranging from intact pit membranes except for presence of pores of various sizes, to presence of membrane remnants only at lateral ends of perforations and in one or two perforations (arguably pits) at the transition between a perforation plate and subadjacent lateral wall pitting. Developmental study of the mechanism and timing of lysis of pit membranes in perforations, and assessment of the role of the conductive stream in their removal, are needed to enhance present understanding of vessel evolution. © 2004 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2004, 146, 41–51.

ADDITIONAL KEYWORDS: Cornales – ecological wood anatomy – Escalloniaceae – Ixerbaceae – Saxifragaceae – vessel evolution – wood evolution.

INTRODUCTION

Pit membrane remnants tend to occur in genera and families with more numerous primitive features (Carlquist, 1992). Hydrangeales as defined by Thorne (2000) form a plexus of families that correspond to this description, and serve to conclude our survey of

this phenomenon in woody dicotyledons. We have selected a range of species that show diversity in this phenomenon. Because this survey has presented considerable data not hitherto available, we are attempting to interpret the occurrence of pit membrane remnants in dicotyledons with scalariform perforation plates in terms of ecology, phylogeny, physiology and development.

The Hydrangeales of Thorne (2000) and Takhtajan (1987) correspond closely to the groups called

*Corresponding author. E-mail: s.carlquist@verizon.net

Hydrangeaceae by Soltis, Xiang & Hufford (1995) and Fan & Xiang (2003), or woody families of Saxifragales (see summaries of treatments by 12 phylogenists in Goldberg, 1986). Thorne (2000) and Takhtajan (1987) regard Cornales and Hydrangeales as sister orders of superorder Cornanae. Although classification of these families is in flux, and changes are occurring as more species are included in DNA-based phylogenies, the definition of Thorne (2000) is used here for convenience. Thorne's classification is comprehensive, because it defines families, the generic contents of which can be determined from references cited therein. More recent phylogenies sample only a small proportion of the genera in a family (Soltis *et al.*, 2000; Angiosperm Phylogeny Group, 2003) and thus may not reflect familial placement for any given genus. The genera covered in the present paper include some (e.g. *Carpenteria*, *Carpodetus*) that have been treated variously in recent phylogenies. The present study makes no pretence of clarifying such classification problems, because data on only a limited number of vessel features for a limited number of species are presented.

Although further instances of presence of pit membrane remnants in perforation plate remnants will doubtless be discovered, we believe that those we have presented are the more conspicuous uncovered to date. These include Carlquist, 1991, 1992, 1999, 2001a, 2003; Carlquist & Schneider, 2002, in press a, b; Schneider & Carlquist, 2003a, b, in press b). These studies, in turn, build on reports in SEM studies of wood structure from particular regions by Meylan & Butterfield (1978) and Ohtani & Ishida (1978); these two studies present excellent illustrations, and their findings have not been challenged. In the work of Meylan & Butterfield, the presence of pit membrane remnants (which they call 'microfibrillar webs') was not a central issue; nor was this phenomenon the sole focus of the study of Ohtani & Ishida, and so this feature was neglected until the survey offered earlier (Carlquist, 1992). We hope workers will be alert to the possible occurrence of this phenomenon. Separating genuine occurrences from artefacts is easily done (see Carlquist, 1990). We hope further data will contribute to building a picture of early stages in perforation plate evolution.

MATERIAL AND METHODS

The collections studied are as follows: *Carpenteria californica* Torr., several collections studied, cult. Santa Barbara Botanic Garden; *Carpodetus serratus* J.R. & G. Forst., cult. University of Auckland, Carlquist 8094 (RSA); *Deutzia gracilis* Sieb. & Zucc. cv. *Nikko*, cult. Santa Barbara, California, Carlquist 8193 (SBBG); *Escallonia bifida* Link & Otto, cult. Santa Barbara,

California, Carlquist 8195 (SBBG); *Escallonia macrantha* Hook. & Arn., cult. Santa Barbara, California, Carlquist 8196 (SBBG); *Escallonia* sp., accession no. 577-56, cult. Washington Park Arboretum, Seattle, Washington; *Hydrangea macrophylla* (Thunb.) Ser. cv 'Blue Wave', accession no. 1081-57-C, cult. Washington Park Arboretum, Seattle, Washington; *Hydrangea paniculata* Sieb., cult. Santa Barbara, California, Carlquist 8192 (SBBG); *Hydrangea quercifolia* Bartr., cult. Santa Barbara, California, Carlquist 8194 (SBBG); *Philadelphus purpureo-maculata* Lemoine, cult. Santa Barbara, California, Carlquist 8191 (SBBG); *Quintinia serrata* A. Cunn., W. of Auckland, New Zealand, Braggins s.n.

The specimens of *Carpodetus* and *Quintinia* were preserved by drying. Portions for sections were boiled in water and stored in 70% aqueous ethanol. Wood portions of the remaining collections were taken from living specimens and preserved in 70% aqueous ethanol. Radial sections of wood were cut on a sliding microtome at about 40 µm; no softening of wood samples prior to sectioning was required. The sections were dried between clean glass slides, mounted on aluminium stubs, sputter-coated with gold, and examined using a Hitachi S2600N scanning electron microscope at full rather than partial vacuum. Despite the use of 25 kv accelerating voltage, the resolution and contrast of our photographs are not ideal. Concave surfaces, which return fewer electrons than convex surfaces, present special challenges for SEM, and because the portions of interest in this study are sunken below the surface of the wood section, some charging in the form of bands (Fig. 5) is inevitable.

Artefacts are readily identified in the material. These take the form of (i) tears or rips and (ii) impregnation of the pit membrane with secondary compounds. The presence of tears and rips is signalled by irregular outlines (Fig. 6), as opposed to the smooth outlines of pores or other naturally formed spaces in the pit membranes of perforations. Rips and tears are believed to be caused by handling of sections. Impregnation of pit membranes with secondary compounds, which results in inhibition of lysis and can suggest a lesser degree of pit membrane dissolution than is to be expected for a given species, is evident by irregularity in the surface of a pit membrane or in coarseness of fibrils or strands within the pit membrane remnant. Membranes impregnated with secondary compounds were shown in Chloranthaceae by Carlquist (1990) for *Ascarina maheshwarii* Swamy and *A. philippinensis* C. B. Robinson. In the present study, these conditions are illustrated by *Carpodetus serratus* (Figs 3, 4, 6) and *Quintinia serrata* (Figs 29, 30).

Terminology is according to the IAWA Committee on Nomenclature (1964) and Carlquist (1992, 2001b). Arrangement of species is alphabetical.

RESULTS

Carpenteria californica (Fig. 1). Sections from several plants showed that a majority of the perforation plates were multiperforate, although true scalariform plates were also present. Perforations varied from being devoid of pit membranes to having intact membranes, even within a single perforation plate. This tendency toward random absence of pit membranes in perforation plates was observed in the several plants studied. Pit membrane remnants are more abundant in the multiperforate perforation plates than in the scalariform plates.

Carpodetus serratus (Figs 2–6). Meylan & Butterfield (1978) report that 'microfibrillar webs occasionally traverse the individual openings at each end of the scalariform perforation plates.' They present such webs solely at lateral ends of perforations, but our material shows more extensive and less porous pit membrane remnants. This more extensive presence should probably be ascribed to impregnation of the pit membrane with secondary compounds prior to lysis of the pit membrane. However, such extensive pit membrane remnants usually are not reported from perforation plates, scalariform or otherwise, in which pit membrane remnants are not observed to occur. In our material, several to numerous perforations at the region of transition between the perforation plate and the lateral wall pitting were observed to be completely covered by pit membranes (Figs 2 and 3), with larger holes or nearly clear perforations in the central portion of the perforation plates (Fig. 4). Several plates clear of pit membrane remnants or nearly so are certainly also present. An occasional perforation plate was observed to bear pit membranes that are entirely intact (Fig. 6). On the left in Figure 6 are rips in several membranes which serve to show that membranes do cover the perforations. Lateral wall pits always bear intact membranes (Fig. 5). The helical sculpture observed in vessel walls of this species by Meylan & Butterfield (1978) is much like that in our material (Fig. 5), although ridges that vary in prominence are evident in our material.

Escallonia (Figs 7–12). The collections of *Escallonia* we studied present a consistent pattern. Perforations are relatively few per perforation plate in the genus. Pit membranes are present chiefly at lateral ends of the perforations (Figs 9, 11). However, perforations in regions transitional between lateral wall pitting and perforation plates contain more extensive remnants (Figs 7, 10, 12), usually in the form of threads. These threads are delicate and are often torn, apparently by handling of sections. Vessel wall pits (Fig. 8) are narrow and slit-like, but the pit membranes of lateral wall

pits are intact and nonporous. Helical thickenings irregular in orientation and prominence occur on vessel walls of *E. bifida* (Fig. 8).

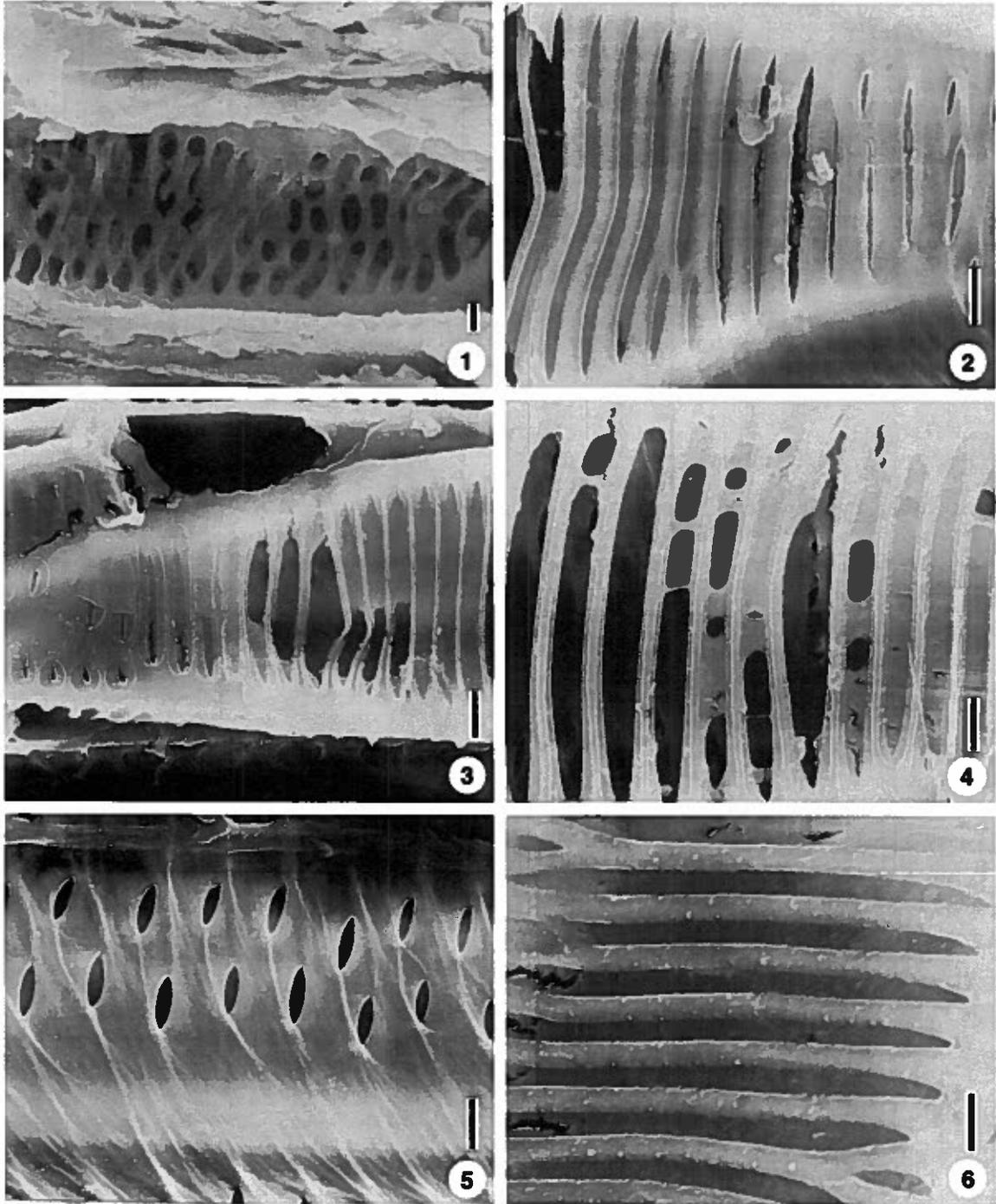
Hydrangea. In the commonly cultivated *Hydrangea macrophylla*, pit membrane remnants are abundantly present (Figs 13–19). The wood studied was taken from an old shrub, and the portions studied were not close to the cambium, so the pit membranes illustrated represent developmentally mature patterns. Degrees of pit membrane presence are arranged from most to least abundant. In Figure 13, the pit membrane is present but with rift-like gaps in it (these are natural, not tears). In Figure 14, the pit membrane is extensive, fenestrated by axial rifts but also (left) mesh-like patterns. Predominantly axially orientated threads are visible in Figure 15, but a patch of intact pit membrane (lower left) is also present. Intermediacy between threads and sheet-like pit membrane remnants is shown in Figure 16. Threads running in various directions plus perforated laminar pit membrane remnants are illustrated in Figure 19. Pit membrane absence characterizes some perforation plates in this species.

A wide range of pit membrane presence is also found in *H. paniculata* (Figs 20–25). The pit membranes of Figure 20 are delicately porous, as are portions in Figure 21 with thread-like remnants present elsewhere. The pit membrane remnants of Figure 22 range between thread-like and reticulate, whereas those of Figure 23 are clearly thread-like (some slightly displaced by handling). Threads in the lateral ends of perforations are illustrated in Figure 24. In Figure 25, a transition between perforation plate and lateral wall is represented: lateral wall to the left, perforation plate on the right. The transitional pits on the left have small pores in pit membranes; the perforations on the right have reticulate or thread-like pit membrane remnants.

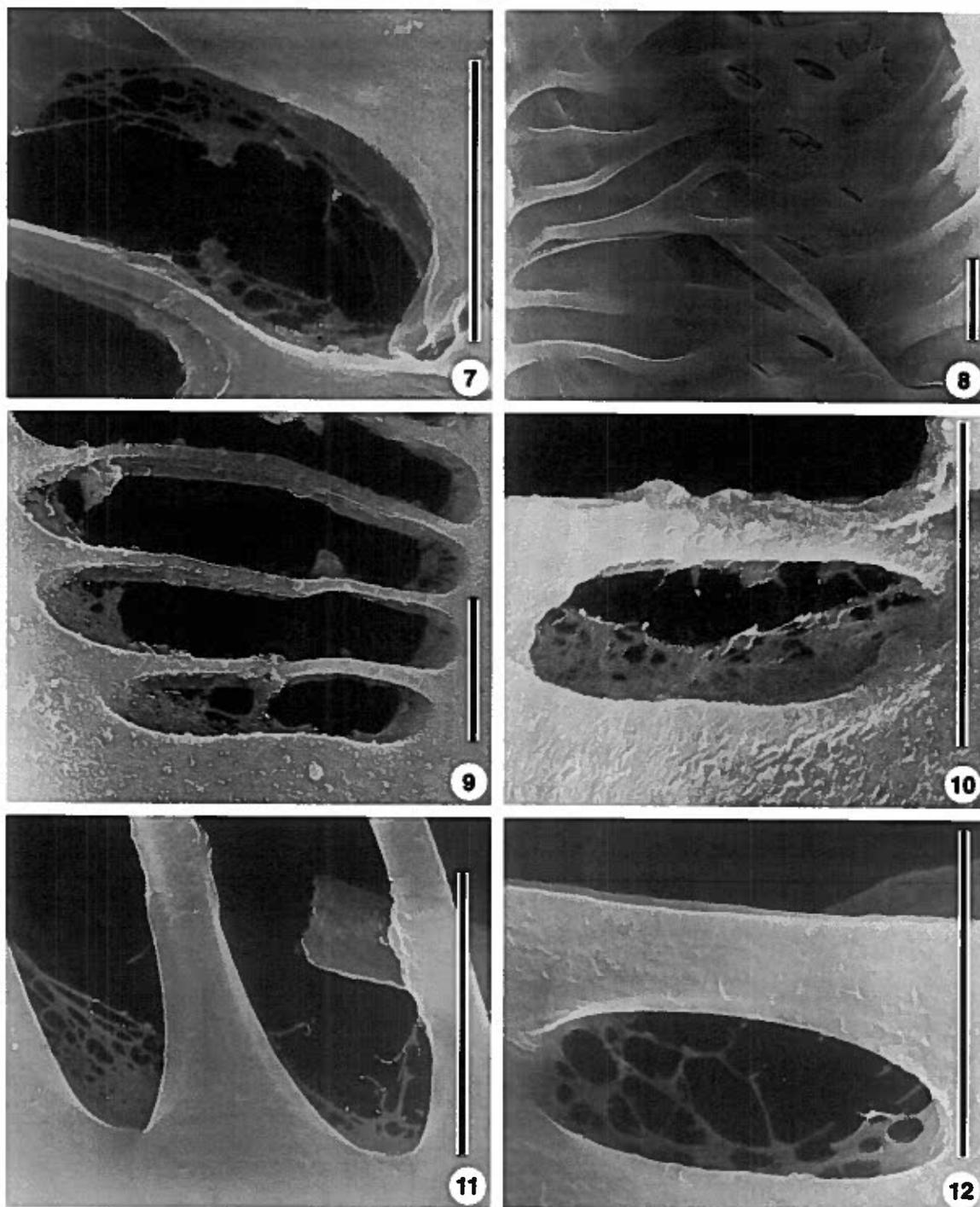
Hydrangea quercifolia (Figs 26, 27) has more numerous perforation plates clear of pit membrane remnants than the other species studied: pit membrane remnants are present in regions transitional between pits and perforations (Fig. 26), where holes in sheet-like pit membranes are common. Elsewhere, similar pit membrane remnants may be found at lateral ends of perforations (Fig. 27).

Philadelphus. The sole specimen studied has pit membrane remnants in lateral ends of perforations only (Fig. 28). The membrane remnants are porose.

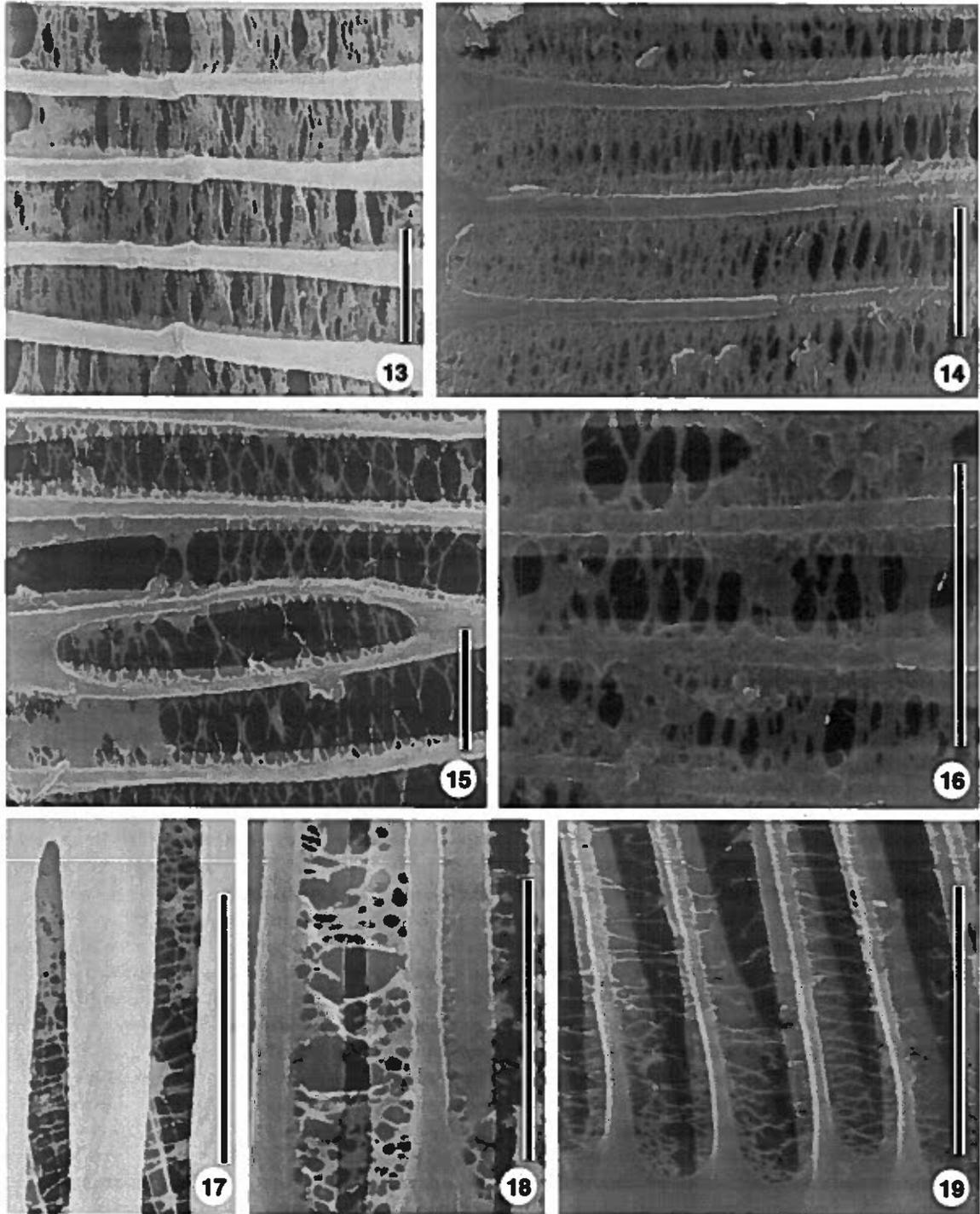
Quintinia serrata (Figs 29–32). This species has pit membrane remnants in perforations. However, the conditions that are most representative for the species may not be illustrated. The pit membranes of



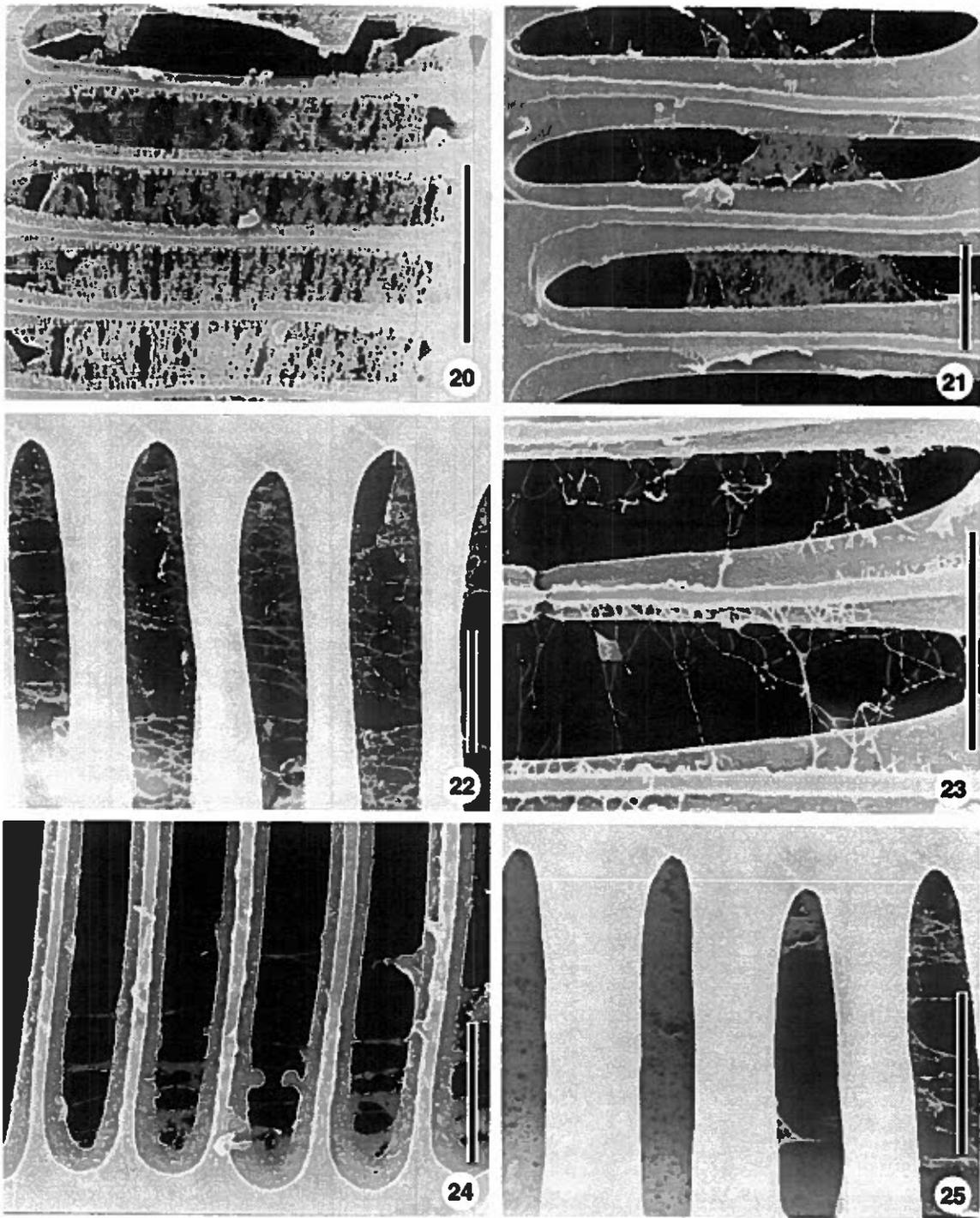
Figures 1-6. Vessel details from radial sections of wood of *Carpenteria* and *Carpodetus*. Scale bars = 5 μ m. Fig. 1. *Carpenteria californica*, multiperforate perforation plate; pit membranes occur in a portion of the perforations. Figs 2-6. *Carpodetus serratus*. Fig. 2. Transition region between perforation plate, left (about five perforations completely covered by pit membranes) and lateral wall pitting at right (identifiable by narrower pit apertures). Fig. 3. Transition region between lateral wall pitting, left, and perforation plate, right; large holes occur in pit membranes in six of the perforations. Fig. 4. Portion of perforation plate, illustrating various degrees of pit membrane presence in perforations, ranging from membranes completely intact (near right) to membranes with large holes, to (left) absence of pit membranes. Fig. 5. Lateral wall of vessel, showing narrow pit apertures through which may be seen intact pit membranes, and helical thickenings on the vessel surface. Fig. 6. Portion of perforation plate in which pit membranes are entirely intact (tears in four membranes, left), possibly the result of inhibition by deposition of a secondary compound.



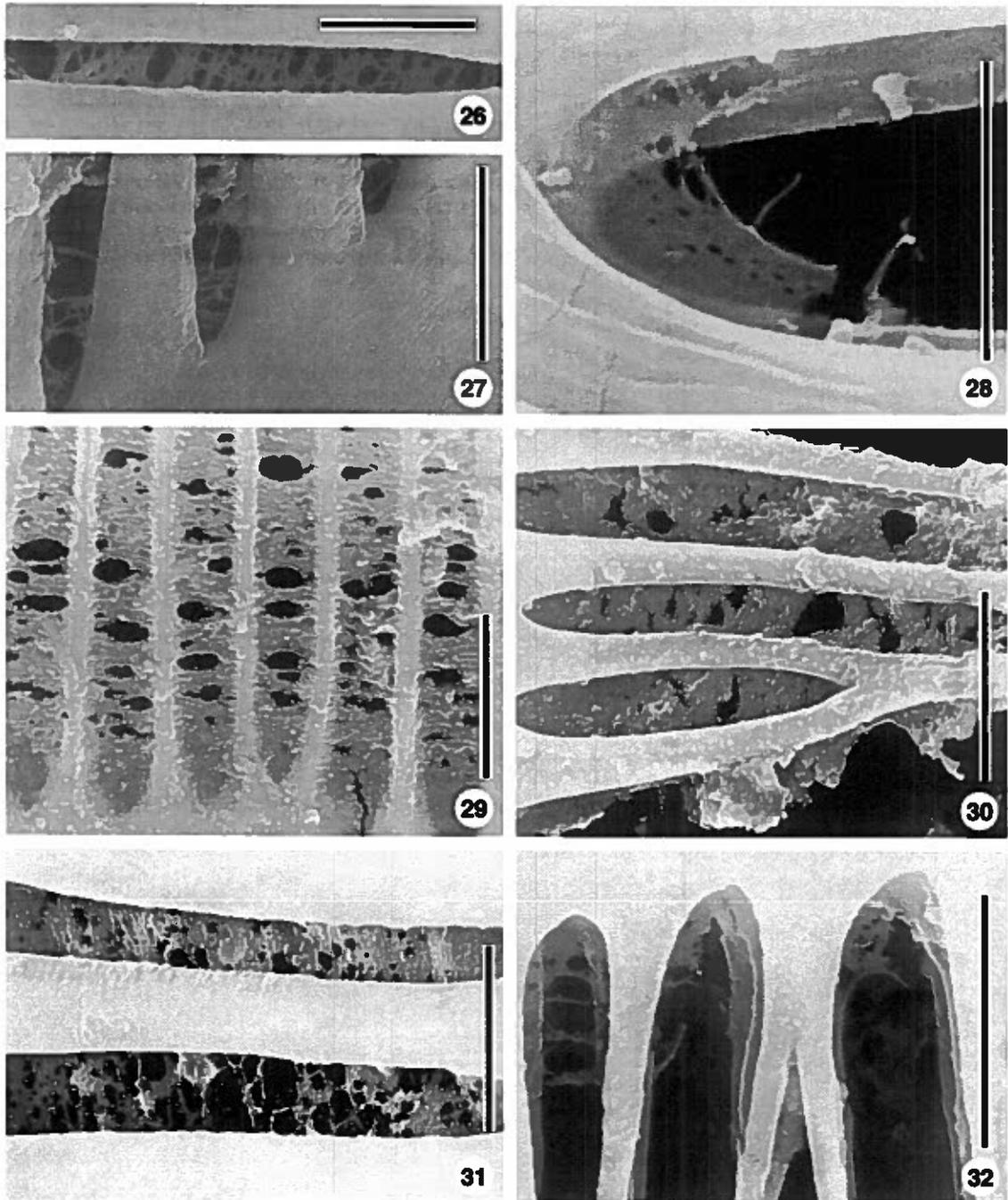
Figures 7–12. Vessel portions from radial sections of three species of *Escallonia*. Scale bars = 5 μ m. Figs 7, 8. *E. bifida*. Fig. 7. Terminal perforation of a perforation plate, showing a network-like pit membrane remnant; some tearing probably has occurred. Fig. 8. Vessel wall surface, showing varied thickenings and narrow pit apertures of lateral wall pits. Figs 9, 10. *E. macrantha*. Fig. 9. Terminal three perforations of a perforation plate, showing more pit membrane remnants in the terminal pit. Fig. 10. Pit from region transitional between perforation plate and lateral wall pitting; the large tear is probably an artefact. Figs 11, 12. *Escallonia* sp. Fig. 11. Network-like or thread-like pit membrane remnants in lateral ends of two perforations. Fig. 12. Terminal perforation of a perforation plate (below) with nearly intact network-like pit membrane remnants; another perforation (above) lacks pit membrane remnants.



Figures 13–19. Portions of perforation plates from radial sections of *Hydrangea macrophylla* wood. Scale bars = 5 µm. Fig. 13. Central portions of perforations, showing axially elongate rifts judged to be natural. Fig. 14. Portions of four perforations (lateral ends at left), showing axially elongate pores less common at lateral ends of perforations. Fig. 15. Portions of several perforations in which the pit membrane is reduced to threads except for a patch of nearly intact pit membrane at lower left. Fig. 16. Portions of three perforations, the pit membranes of which show transitions from sheet-like with circular pores, to isolated threads. Fig. 17. Portions of two perforations from end of perforation plate; transitions from porose pit membrane (above, left) to threads with various orientations. Fig. 18. Portions of two perforations with network-like pit membrane remnants; two large rifts (centre) may represent artefacts. Fig. 19. Portions of perforations (lateral ends at bottom) traversed by numerous thread-like pit membrane remnants.



Figures 20–25. Portions of perforations from radial sections of wood of *Hydrangea paniculata* wood. Scale bars = 5 μm . Fig. 20. Membranes mostly intact, with small pores; wider openings may indicate some tearing. Fig. 21. Pit membrane remnants ranging from laminar with small pores (centre) to sparse threads (above). Fig. 22. Pit membranes transitional between network-like to thread-like. Fig. 23. Delicate thread-like pit membrane remnants, some dislocated. Fig. 24. Pit membrane remnants at lateral ends of perforations only. Fig. 25. Area transitional from lateral wall pitting (to the left) to perforation plate (at right); the pits (perforations?) at left have intact membranes bearing numerous small pores, whereas the perforations at right have pit membrane remnants typical of the species.



Figures 26–32. Portions of perforations from radial sections of wood of *Hydrangea*, *Philadelphus* and *Quintinia*. Scale bars = 5 μ m. Figs 26, 27. *H. quercifolia*. Fig. 26. Pit membrane with relatively few pores from end of perforation plate. Fig. 27. Lateral ends of perforations with thread-like pit membrane remnants. Fig. 28. *P. purpureo-maculata*, lateral end of perforation, showing porose pit membrane remnant. Figs 29–32. *Q. serrata*. Fig. 29. Perforations with pit membranes containing axially orientated holes; some degree of lysis inhibition may be present. Fig. 30. Pit membrane remnants with a few holes; the large areas of intact membrane probably represent inhibition of pit membrane dissolution because of deposition of secondary compounds. Fig. 31. Portions of two perforations from terminus of perforation plate (lateral wall pitting would be above the upper perforation); porous and network-like patterns of pit membranes are judged to be natural. Fig. 32. Pit membrane remnants at lateral ends of perforations only.

Figures 29 and 30, are apparently laminar, minimally interrupted by holes. Threads and surfaces of these pit membranes, however, are not smooth and suggest accretion of a secondary compound. Deposition of a gummy compound during the maturation of the vessel element may have inhibited enzymatic removal of portions of pit membrane portions. The pit membranes in some perforations of Figures 31 and 32 appear to have experienced less inhibition of pit membrane lysis (Fig. 32 probably shows the least inhibition). The reticulate appearance of the lower perforation in Figure 31 is unlikely to represent much artefact formation, however.

CONCLUSIONS: REVIEW OF PIT MEMBRANE REMNANTS IN PERFORATION PLATES

Hydrangeaceae and families thought to be allied (at least in some systems) were selected for study because several species of these families have long scalariform plates with numerous bars. Such perforation plates are more likely to have pit membrane remnants than plates with few bars, although a small number of families with few bars per plates (Bruniaceae, Sarracenaceae) can have pit membrane remnants. Presence of scalariform perforation plates is correlated with mesic habitats (Carlquist, 1975). This ecological correlation extends to presence of pit membrane remnants (Carlquist, 1992), although the list of families with pit membrane remnants is shorter than the list of families with scalariform perforation plates. The search for families with pit membrane remnants in perforations (Carlquist, 1992) focused mainly on families with numerous bars per plate.

The presence of pit membrane remnants can only be interpreted as an impedance to conduction. Such an impedance has no positive selective value. Even if scalariform perforation plates act as sieves to remove air bubbles in vessels, as alleged by Zimmermann (1983), the distribution of species with pit membrane remnants would not suggest that these remnants enhance this function: the majority of species with the remnants occur in frost-free localities (e.g. Illiciaceae). The highly mesic sites occupied by those species with pit membrane remnants suggests that moderate impedance in the conductive flow is of little negative selective value, assuming that peak flow rates are never as rapid as they are in areas with strong fluctuation in moisture availability and therefore conductive rates. Not surprisingly, those species with minimal pit membrane remnants outnumber those with more extensive remnants. This suggests that there is moderate selection for removal of pit membrane remnants.

The existence of vessel-free flowering plants, most of which are restricted to mesic, frost-free localities (Carlquist, 1975), suggests that the difference

between woods with vessels that feature diminished conductive capability in end walls and woods without vessels is not appreciable. One notes the occurrence in conifers of margo porosities that probably improve conduction of water through the pit membrane (as compared to nonporous pit membranes, e.g. in ferns). The improvement in conduction cannot be very great, but the porose margo of a conifer tracheid is comparable to the pit membrane of a perforation in a dicotyledon with retention of extensive areas of pit membranes (e.g. *Hydrangea macrophylla*).

One can question how pit membranes can be dissolved in part but not wholly in the perforations of dicotyledons described in papers of the present series. The same question, however, can be applied to the margos of conifer tracheid pit membranes. Many conifers do not have tori in tracheid pit membranes, so porous and nonporous pit membrane portions of the same thickness can be produced during tracheid maturation (see Meylan & Butterfield, 1978). We have been aware of this phenomenon in gymnosperms, but the occurrence of a similar phenomenon in perforation plates of angiosperms has been neglected.

The ecological and systematic distribution of pit membrane remnants in dicotyledon vessel perforations suggests that the phenomenon is relictual. This is in contrast with conifer tracheids, in which all species have intact pit membranes, and the development of margos in pit membranes represents a specialized condition, with more prominent pores in species that are not highly primitive within conifers.

The systematic distribution of perforation plate pit membranes underlines this. To the instances cited in Carlquist (1992) are added families with incipient vessels, in which pit membranes are present but intact with holes and pores: Amborellaceae (Carlquist & Schneider, 2001), Nelumbonaceae (Schneider & Carlquist, 1996a), Nymphaeaceae and Cabombaceae (literature for these latter two families is cited in Schneider & Carlquist, 1996b).

Where most abundant, as in Aextoxicaceae, pit membrane remnants take the form of intact pit membranes in all perforations, but with pores of various sizes in the pit membranes. As pit membrane presence disappears phylogenetically, pit membranes take the form of threads or networks of strands traversing the perforations (e.g. Hydrangeaceae). Minimal retention of pit membranes is shown where pit membrane remnants are restricted to lateral ends of perforations and to one or two perforations (which alternatively could be termed pits) in the transitional region between the perforation plate and lateral wall pitting, as in Ericaceae (Carlquist & Schneider, in press a). In these transitional pits, membranes may be intact but with pores, or they may cover only a portion of a perforation (as in *Escallonia*).

Superimposing our data onto a molecular phylogeny would be unjustified and premature. Only a limited number of dicotyledon species have been studied with respect to presence of pit membrane remnants in perforation plates. On the other hand, molecular phylogenies do not at present include some of the genera and even families for which pit membrane remnants in perforations have been reported. The genera and families with pit membrane presence in perforations have an abundance of features that are considered primitive in woods (e.g. most of them have tracheids as the imperforate tracheary element type, diffuse axial parenchyma, and Heterogeneous Type I rays). A number of the genera and families with pit membrane remnants appear in molecular phylogenies as outgroups to major clades (e.g. Aextoxicaceae of Berberidopsidales as an outgroup to Caryophyllales), rather than in 'terminal' branches of clades.

The developmental significance of pit membrane remnant presence remains to be studied. Is the primary wall of the pit membrane completely developed when enzymatic action dissolves pores in it, or are pores present before the primary wall is mature? What is the role of the conductive stream in removing pit membranes from perforations? Understanding of the developmental nature of formation of pit membrane remnants will help complete our picture of how vessels have evolved, and by what mechanisms incomplete achievement of more specialized stages of structure advancement occurs.

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