PIT MEMBRANE REMNANTS IN PERFORATION PLATES OF PRIMITIVE DICOTYLEDONS AND THEIR SIGNIFICANCE

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Perforations of vessel elements characteristically retain remnants of pit membranes (primary walls) in woods of species of more than 30 families of dicotyledons. Scanning electron microscopy is necessary to demonstrate presence and type of membrane remnant. Species with these remnants in perforations given in earlier literature as well as those newly reported here are listed. Perforation membrane remnants may take the form of flakes, strands, or webs, and particular types may characterize particular families (e.g., strands or bands in Illiciaceae). Some families have abundant perforation membrane remnants (e.g., Chloranthaceae, Illiciaceae). Where membranes are nearly intact, they are porose and closely resemble the porose pit membranes on end walls of Tetracentron tracheids. In Tetracentron, however, tracheary elements are monomorphic, so vessel origin cannot yet be said to have occurred. Membrane remnants in perforations are regarded as a relictual primitive feature that should be added to the list of primitive character states claimed for vessel elements in angiosperms; alternative hypotheses are considered and discussed, and evidence from DNA phylogenies is needed. In vessel-bearing dicotyledons with membrane remnants in perforations, many perforations are relatively clear, but an appreciable proportion of perforation plates do have membrane remnants.

Vessel elements are considered to be derived from tracheids phylogenetically (e.g., Bailey, 1944). Once vessels have originated in a particular phylad, a progressive division of labor between vessel elements and imperforate tracheary elements occurs. Once the phylogenetic divergence between these cell types has begun, any intermediacy between them ought to vanish rather rapidly over time, because intermediate cells would be expected to be of minimal selective value. In dicotyledons in which vessel origin has occurred but specialization is still at a minimal level, one would expect to find more numerous tracheid-like features in vessel elements. Because tracheids have pit membranes in pits of end walls at maturity, whereas in vessel elements, membranes in perforations of the end wall (= perforation plate) undergo lysis at maturity, a tracheid-like vessel element might be expected to retain membranes, or portions of them, in the perforations in the mature vessel element. There have been a number of reported occurrences of membrane remnants in perforations (see Systematic Distribution, below). These occurrences are nearly all in primitive dicotyledons with scalariform perforation plates in vessels. In order to ascertain if there is indeed a phyletic pattern in occurrence of membrane remnants in perforations, I have attempted to summarize the literature on this topic and to explore dicotyledon woods for additional instances.

Membrane remnants in perforations are potentially interesting in showing the transition between vessel elements and tracheids. The patterns of occurrence of these remnants may lead us to believe that the transition from tracheids to vessel elements is not a sharp one, and that the traditional character of membrane presence vs. absence in end walls used to differentiate the two cell types must be modified. For this reason, pit membranes in end walls of the tracheids of vesselless dicotyledons (notably Tetracentron) are compared with membrane remnants in perforations of vessel-bearing dicotyledons.

Use of scanning electron microscopy (SEM) has permitted not only discovery of pit membrane remnants in scalariform perforation plates of a number of dicotyledons, but also provided examples of a number of different modes of occurrence. Some of these remnants have been called "microfibrillar webs" (e.g., Meylan and Butterfield, 1978) because they may occur as a meshwork of strands. The terms "remnants of partitions" and "fibrillar strands" have also been applied (Ohiani and Ishida, 1978, p. 71). In calling attention to the possible phyletic significance of membrane remnants in perforations, I used the terms "flakelike," "strandlike," and "porose membranes that are nearly intact" to describe types of membrane remnants that are not at all weblike in appearance. There are other instances in which some perforation plates are entirely clear whereas other nearby perforation plates bear intact pit membranes: Geissoloma (Fagerlind and Dunbar, 1973) and Myrothamnus (Carlquist, 1988, Fig. 3.10.4). I am therefore suggesting the term "membrane remnant" to cover this phenomenon in perforation plates in general, with other adjectives added to describe the appearance in a particular case. Description of these diverse types of membrane remnants is one of the goals of the present paper. Strands of primary wall material in perforations should not be confused with strands of secondary wall material that traverse perforations, forming interconnections between bars. Examples of this latter phenomenon have been reported for perforation plates of vessels of several genera of Myristicaceae (Garratt, 1933; Metcalfe and Chalk, 1950) and Carpenteria of the Hydrangeaceae (Carlquist, 1961). Both primary wall remnants and strands of secondary material may occur together in perforations occasionally, as in Neomyrtus (Meylan and Butterfield, 1978). The strands of secondary wall material that cross...
scalariform pits on tracheids of lepidodendroids (Cichan, Taylor, and Smoot, 1981) may be a similar phenomenon. Data from the literature and from my original observations show that presence of membrane remnants in perforations is not a chance occurrence, but is characteristic of particular species. Because of the potential phylogenetic interest, a listing of all instances, reported in the literature and newly uncovered, is assembled below.

Care must be taken in reporting occurrence of pit membrane remnants in perforations, because examples of membrane presence that involve artifact formation or noncharacteristic modes of occurrence can be involved. For example, in woods of Ascarina (Chloranthaceae), some vessels contain deposits of yellowish "resinlike" compounds. These deposits appear to inhibit lysis of pit membranes in perforations when they coat the perforation plate. Attention must also be paid to artifact formation that results from processing of wood samples; such processing, however, in all likelihood merely lessens the quantity and intactness of membrane remnants, since the delicate nature of the membrane remnants makes them vulnerable to destruction; certainly they are not enhanced by handling.

MATERIALS AND METHODS

In order to present as many instances of membrane remnants in perforations as possible, wood of species of families with scalariform perforation plates was examined. In most instances, the occurrence of perforation plates of a primitive sort, with numerous bars, was used as a basis for selection. Examination of perforation plates in face view (in radial sections of woods) with the light microscope can reveal appearances that are suggestive of membrane remnant occurrence: granular dots in the perforations, for example. Many of the woods with this appearance under the light microscope do indeed prove to have characteristic presence of membrane remnants in perforations when viewed with SEM. For the majority of species, wood samples were not sectioned especially for this study. Rather, slides from the wood slide collection accumulated at the Rancho Santa Ana Botanic Garden were used as a source of sections. The slides were disassembled by soaking in xylene, with several changes of xylene used in order to remove all residues of the mounting resin from the sections.

Sections derived from disassembly of prepared slides as well as those especially prepared for the present study were obtained by sectioning on a sliding microtome. Softening techniques were not employed for these species. Sections not derived from prepared slides were dried between clean glass slides after sectioning and prior to examination with SEM. The wood samples used were mostly available in dried form. These samples were boiled in water and stored in aqueous 50% ethyl alcohol preparatory to sectioning. Liquid-preserved wood samples were used for a few genera (see Acknowledgements).

Terminology follows the usages proposed by the IAWA Committee on Nomenclature (1964). That terminology does not cover structures likely to be seen clearly only with electron microscopy, and like other authors, I offer simple descriptive phrases or adjectives for such structures.

RESULTS

The present study focused primarily on species with long scalariform perforation plates, but did not exclude species with shorter scalariform perforation plates. Aextoxicum punctatum (Aextoxicaceae) has unusually long scalariform perforation plates (Fig. 1). At lower magnification (Fig. 1), one sees minute irregularities in the perforations. At higher magnifications (Figs. 2, 3), these irregularities prove to be kinds of membrane remnants. In Aextoxicum, these remnants range between flakes (Fig. 2) and strands (Fig. 3).

In Illicium, sole genus of Illiciaceae, presence of primary wall remnants in perforations is extensive and quite varied: none of the species 1 examined lacked remnants altogether. In I. cubense there are perforation plates in which pit membranes in perforations are nearly intact but porous (Fig. 4). In other perforation plates, bandlike or strandlike portions of primary walls can be found; these are porous where remnant strands are wider (Fig. 5). Illicium tashiroi (Figs. 6–11) shows a wide range in strands and bands of membrane remnants. In Fig. 6, one can see that almost half of the area of the perforations is covered by pit membrane bands or strands. In Fig. 7, one can see the nature of this pattern clearly: the pit membranes seem subject to localized lysis. The remnants in the perforation plate shown in Fig. 8 are more often flakelike, although a few strands are present. In Fig. 9, on the contrary, the remnants take the form of slender strands. Where vessel elements are split away from each other by sectioning so that one can view the perforation plate of a single cell without the corresponding half from the cell removed by sectioning, one can see that the strands in Illicium perforations are indeed primary wall portions. The perforation plate in Fig. 10 is that of a single cell at left, whereas the superimposed perforation plates of both adjacent cells are present at right. In Fig. 11, one can see portions of perforations of a single cell viewed from the outside of


Figs. 6–11. SEM photographs of perforation plates from radial sections of Illicium tashiroi, SJRW-24057. 6. Perforation plate portion with more than half perforation area covered by membrane remnants. 7. Perforations to show extensive bandlike remnants. 8. Flakelike membrane remnants in perforations. 9. Delicate strands in perforations. 10. Perforation with wall from one cell shaved away at left, strands and bands evident. 11. Perforation portions of one cell, viewed from exterior of cell: strands of primary wall material extend from primary wall of bars. Figs. 6, 10, bar in Fig. 2; Figs. 7, 9, bar in Fig. 3; Fig. 11, bar = 1 μm.
that cell. The preparations of Figs. 10 and 11 are particularly valuable in showing that the strandlike remnants are not extensions of the pit border (in which case they would be secondary wall portions) but extensions of the primary wall. The tendency for membrane remnants to be in the form of strands and bands is characteristic of all of the species of *Illicium*. Such perforation membrane remnants were illustrated for *I. floridanum* earlier (Carquist, 1988).

*Paracryphia* (Paracryphiaceae) shows a wide range of expressions (Figs. 12–17); the pit membrane remnants may be flakelike, although in some perforation plates (Carquist, 1988, Fig. 3.7.1) the membranes are essentially intact but porose. The strands in perforations of Fig. 12 recall those of *Illicium*, but the lateral ends of the perforations contain nearly intact membranes that are porose. In Fig. 13, pit membranes cover more than half the area of the perforations, and the membranes are porose. Pit membranes may also be flakelike and less porose (Fig. 14) in *Paracryphia*. The flakes of the pit membranes can develop a clotted appearance (Fig. 16). Two collections of *Paracryphia* were examined. In *Carquist 15575*, the membrane remnants in perforations are relatively few and limited to edges of the perforations (Fig. 17) in contrast to the abundance of membrane remnants in *McKee 4993*.

*Heliamphora* (Sarraceniaceae), like *Paracryphia* and *Illicium*, shows a range of expressions with regard to membrane presence in perforations (Figs. 18–22). *Heliamphora* is noteworthy in that membrane remnants are characteristically present, although the perforation plates of *Heliamphora* have fewer bars than is typical of most of the dicotyledons examined in the present study. Most perforation plates of *Heliamphora* have less than half of the area of the perforations covered by flakelike membrane remnants (Fig. 19). Close examination shows that the flakes are porose (Fig. 19). Within a perforation plate in *Heliamphora*, some perforations are clearer than others (Fig. 20). Many perforations in the specimen studied are clear or nearly so (Fig. 21), although objects dislodged during sectioning can become attached to the perforation plate (arrow). The perforation plate of *Heliamphora* shown in Fig. 22 has remnants that are like a coarse fibrillar mesh. I believe that in this case, accumulation of deposits of a secondary plant product may have inhibited lysis of the membrane (such deposits were seen in sections examined by light microscopy).

Inhibition of lysis of a pit membrane is suggested by the contrast between Figs. 24 and 25, representing two perforation plates from the same section of wood of *Ascarina maheshwarty* Swamy. The typical condition in this species, porose membranes, is shown in Fig. 24. In Fig. 25, the membrane appears coated, and the pores are partially occluded. Sections of this wood studied with the light microscope showed that in some vessels, yellowish resinlike deposits were present. The contrast of Figs. 24 and 25 is clear, but one must be alert for possible instances of membrane lysis inhibition that are less marked. The strands between perforations in *Cliftonia monophylla* (Fig. 28) are slightly coarser than strands in other woods examined typically are, and presence of a coating by some natural deposit may be suspected (the wall adjacent to the perforations also appears coated). The failure of membrane lysis in the perforation of *Euptelea polyandra* shown in Fig. 32 may in part be due to inhibition produced by a natural secretion in the wood. However, in species such as those in the present study in which membrane remnants characteristically occur in perforations, very slight chemical changes in the vessel element as it matures might inhibit membrane lysis in perforations to a degree greater than is typical. One almost never sees inhibition of membrane lysis in a perforation that is large, as in species with simple perforation plate, even in those woods with conspicuous accumulations of resinlike compounds in wood cells; in these species, inhibition of lysis must be much more difficult than in species with longer scalariform perforation plates.

*Berzelia cordifolia* (Bruniaceae) has numerous perforation plates in which pit membranes are highly porose (Fig. 26). Such plates were also observed in another species of Bruniaceae, *Lonchostoma esterhysenae*.

*Hydrosymum cumbalense* Karsten has perforation plates that show a gradual transition between the perforation plate (Fig. 27, left) and lateral wall pitting (Fig. 27, right). Remnants of pit membranes are greatest in the perforations toward the ends of the plate, and least in the centers of the plates.

The most common type of remnant in the perforation plates of dicotyledon woods I observed is that of sparsely

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*Figs. 12–17.* SEM photographs of perforation plates from radial sections of wood of *Paracryphia alticola*. 12–16. Wood from *McKee 4993*. 12. Strands and porose flakelike membranes in perforations. Bar = 5 μm. 13. Porose membrane portions in perforations. 14. Flakelike membrane remnants. 15. Porose membrane remnants at lateral ends of perforations. 16. Flakelike membranes with clotted appearance. 17. Wood from *Carquist 15575*: perforations with small quantities of membrane remnants along their edges. Figs. 13, 14, 16, bar in Fig. 2; Fig. 15, bar in Fig. 11; Fig. 17, bar in Fig. 5.

*Figs. 18–23.* SEM photographs of perforation plates from radial sections of woods of *Heliamphora* (Sarraceniaceae) and *Hibbertia* (Dilleniaceae). 18–23. *Heliamphora nutans*. V. Funk s.n. 18. Perforations typical for the species in membrane remnant presence. 19. Porose flakelike remnants. 20. Strands, flakes, and bands in perforations. 21. Perforation plates with a few flakelike remnants; starch grain lodged on perforation plate as a result of processing (arrow). 22. Extensive membrane presence in perforations, probably the result of failure of lysis because of natural secretions in the wood. 23. *Hibbertia argentea*. *Carquist 5689*: numerous flakelike remnants in perforations. Figs. 18, 22, bar in Fig. 2; Figs. 19, 23, bar in Fig. 5; Figs. 20, 21, bar in Fig. 12.
spaced strands, as illustrated for Cliftonia monophylla (Fig. 28), Sphenostemon lobosporus (Fig. 29), and Euptelea polyandra (Figs. 30, 31). Species with an extremely large number of perforations in perforation plates seem the most likely to retain membranes in perforations at maturity of the vessel element. Hibbertia argentea (Fig. 23) exemplifies this. Euptelea polyandra also represents both a large number of bars per perforation plate and abundant presence of membrane remnants (Figs. 30–32). In Euptelea, these remnants most often take the form of strands stretching across the perforations (Fig. 31).

Euptelea is generally placed in a monogenic family of the order Hamamelidales, close to the vesselless families Tetracentraceae and Trochodendraceae. Tetracentron and Trochodendron both have well-marked annual rings in which the wider earlywood tracheids bear scalariform pits on end walls (Figs. 33–35) and lateral walls. Pits from the end walls of earlywood tracheids of Tetracentron sinense are shown in Figs. 33 and 34. Figure 33 shows pit membranes that are markedly porose. The pit membranes of Fig. 34 are almost as porose as those of Fig. 33. In Trochodendron aralioides, pores are present in end wall pit membranes, but they are much smaller than those of Tetracentron (Fig. 35). These facts are introduced in order to see if vessel elements can still be defined in terms of membrane absence in perforations, as has traditionally been done, or whether other criteria must be used.

With regard to differentiation between vessel elements and tracheids, one should keep in mind a generalization not evident from the above descriptions. In the vessel-bearing dicotyledons on which reports are made here, most perforations are relatively free from strands, flakes, or webs of primary wall material; a small but appreciable proportion of perforation plates have conspicuous remnants. However, there are notable exceptions in which the majority of perforation plates bear remnants of membranes: Bruniaeae (Berzelia cordifolia); Cercidiphylaceae (Cercidiphyllum japonicum; Ohtani and Ishida, 1978); Cornaceae (Cornus controversa; Hemsley: Ohtani and Ishida, 1978); Eupomeriaceae (Eurya grandidentata; Sieb. & Zucc. (Ohtani and Ishida, 1978)); Chloranthaceae: Aesculus lucida Hook. f. (Meylan and Butterfield, 1978); Berzelia cordifolia Schlechter, Carlquist 4690; *Lonchochomma esterhuyseae Strid, Carlquist 4982; Caprifoliaceae: Viburnum spp. (Ohtani and Ishida, 1978); Cercidiphylaceae: Cercidiphyllum japonicum Sieb. & Zucc. (Ohtani and Ishida, 1978); Chloranthaceae: Aesculus lucida Hook. f. (Meylan and Butterfield, 1978); *Aesculus spp. (Carlquist, 1990); Chloranthus spp. (Carlquist, 1992a); Hedyosmum spp. (Carlquist, In press c); Sarcandra glabra (Thunb.) Nakai (Carlquist, 1987).


**SYSTEMATIC DISTRIBUTION OF MEMBRANE REMNANTS IN PERFORATIONS IN DICOTYLEDONS**

**Known species**—The following list incorporates new reports, including instances described above. These are indicated by an asterisk (*) and citation of a collection; slides are represented in the Rancho Santa Ana Botanic Garden wood slide collection. Additional instances are quite likely to be found, especially in the larger families listed below.


Monimiaceae: *Atherosperma* sp., *Carlquist* 1155; *Laurera nova-zelandiae* A. Cunn. (Meylan and Butterfield, 1978; ontogenetic stages shown in Butterfield and Meylan, 1980).
Myrtaceae: *Neomyrtus pedunculata* (Hook. f.) Allan (Meylan and Butterfield, 1978).
Paracyrphiaceae: *Paracyrphya alitica* (Schlechter) van Steenis (Carlquist, 1988, and the present paper).
Sarraceniaceae: *Heliamphora nutans* Benth., *Vicki Funk* s.n.
Sphenostemonaceae: *Sphenostemon lobosporus* (F. Muell.) L. S. Smith, *Carlquist* 15253.
Theaceae: *Cleyera japonica* Thunb. and *Ternstroemia gymnanthera* (Wight & Arn.) Sprague (Ohtani and Ishida, 1978).

The above list omits two minor instances. Butterfield and Meylan (1980) figure a simple perforation plate of *Knightia excelsa* R. Br. (Proteaceae) with a large membrane remnant; they concede this is a very rare occurrence. Ohtani and Ishida (1978) figure perforation plates of *Sorbus alnifolia* (Sieb. & Zucc.) C. Koch that are basically simple but traversed by a few irregular fragments of secondary wall material; they figure a few strands of primary wall remnants attached to these fragments. Both of these are exceptions that prove the rule that membrane remnants in perforations are essentially confined to scalariform perforation plates.

Species investigated — The above list needs to be placed into perspective. Some of the families are small and have been relatively thoroughly investigated with respect to membrane remnants. Ohtani and Ishida (1978) offer SEM pictures of numerous species of Theaceae, but only two of these bear membrane fragments in perforations. Although all of the species presented by Meylan and Butterfield (1978) were studied by SEM, not all with numerous bars per perforation plate and narrow perforations possessed membrane remnants: no remnants are reported or figured in *Ackama* (Cunoniaceae), *Archeria* (Epacridaceae), or *Pennantia* (Icacinaeae), for example. In my own investigations for the present paper, I studied at least five species in each of the following families: Bruniaceae, Caprifoliaceae, Cornaceae, Dilleniaceae, Hamamelidaceae, Hydrangeaceae, and Monimiaceae. The species chosen for investigation in these families were selected because they had numerous bars per perforation plates, and the narrowness of the perforations might be thought to favor retention of membrane remnants. However, only a fraction of the species fitting this description do, in fact, have membrane remnants. Thus, narrowness of perforations is not directly related to membrane remnant presence. Moreover, in a number of the species in which membrane remnants do characteristically occur, many perforations lack remnants, and the perforations that lack the remnants are apparently no wider than the perforations in which the membranes are retained. Notably wide perforations occur in Bruniaceae and moderately wide ones in *Heliamphora* of the Sarraceniaceae, and yet membrane remnants may be found in perforations of these plants.

**DISCUSSION**

The evidence presented above suggests to me that the presence of membrane remnants in perforations of vessel elements at maturity is a primitive feature in dicotyledons, although alternative hypotheses that are conceivable will be discussed below. Presence of membrane remnants should be added to the list of features considered primitive in vessel elements of dicotyledons by Frost (1930). The systematic distribution alone is suggestive, but the tendency for membrane remnants to be most abundantly represented in species with long scalariform perforation plates with numerous bars is also evident. Beyond the primitiveness of membrane remnants in perforations, there are some interesting additional implications of the data.

The remnants in perforations are, when most extensive, unlike the porose pit membranes in tracheids of *Tetracentron* (Figs. 33, 34) and of *Bubbia* of the Winteraceae (Carlquist, 1983). The pores in these pit membranes are smaller than those seen in pit membrane remnants of *Hedyosmum* (and other Chloranthaceae), *Illicium*, and *Paracyrphia* — but not much smaller. In fact, one could question on the basis of pore size in membranes of tracheid end wall pits whether *Tetracentron* does have tracheids or an early stage in vessel evolution. I believe we must continue to designate *Tetracentron sinense* Oliver as vesicular (although with a tendency toward vessel evolution) because the tracheary elements in *Tetracentron* are monomorphic: there are not two groups of tracheary elements in terms of diameter or length in this species. One should note that there is very little dimorphism between vessel elements and tracheids in the root of *Sarcandra* of the Chloranthaceae (Carlquist, 1987), however. An additional reason why one should designate the tracheary elements of *Tetracentron* as tracheids is that the end walls of tracheids uniformly have porose membranes. In all of the vessel-bearing dicotyledons listed above as having membrane remnants, however, even in those species with the most abundant retention of membrane portions there are always other perforation plates in which the perforations are relatively clear.

If membrane remnants in perforations are relictual in the genera listed earlier, one may ask why there is a persistence of these membranes. One can hypothesize that these plants grow in humid areas with soil that never dries; thus, transpiration rates would be rather steady, and the selective pressure for maximal clear areas in per-
forations to accommodate strong fluctuation in flow rates would be minimal. Another feature, likely of much lesser importance but not negligible, is that the vast majority of the species listed earlier as having membrane remnants in perforations also have tracheids rather than fiber-tracheids or libriform fibers (terms according to IAWA Committee on Nomenclature, 1964) as their imperforate tracheary element type (see listings, Carlbjnst, 1988). However, such a species would not offer help to the cladistics workers who wish to hypothesize vessel loss several times in woody dicotyledons, and the *Sarcandra glabra* kind of instance is not what concerns them, because loss of vessels in a species that has barely attained them is really not a character state reversion of significance. For their cladograms to be maximally parsimonious, they might wish, for example, to derive vesselless wood like that of *Tetracentron* from wood like that of vessel-bearing Hamamelidales such as Hamamelidaceae or Eupteleaceae. Although the vessels in these two families are indeed primitive, they are clearly defined vessel elements, with much greater diameter than tracheids, shorter length than tracheids, and with lateral wall pitting of vessels quite unlike the perforations of the end wall in pit size, pit morphology, and pit density. Were Eupteleaceae, for example, imagined as ancestors of *Tetracentron*, not only would lysis in membranes of perforations have to fail (not a difficult event to imagine), one would have to erase the genetic information for vessel diameter and for differentiation between end wall and lateral walls in a series of character states. Selective factors and ecological scenarios that could lead to erasure of such genetic information have never been offered by those who wish to hypothesize such secondary vessellessness. These are of importance because in lysis of pit membranes in perforation plates, as has been shown (Esau and Hewitt, 1940; Esau, 1965, p. 231 and Fig. 11.3), loss of the pit membranes in perforation plates of vessels occurs late in ontogeny, well after all other features of the vessel wall have been established. Those who would like to envision secondary vessellessness as having occurred several times in woody dicotyledons tend to contrast the rigor of cladistic methodology with what they regard as the arbitrary nature of "Baileyan" dicta. The evolutionary interpretations of I. W. Bailey and his students, in fact, were based on statistical considerations that were presented in tabular form rather than calculated according to current statistical procedures—a presentation that should not make one conclude the methods are less than rigorous. The conclusions of Bailey were compelling precisely because the statistical likelihood of driving wood evolution backwards to supposedly primitive conditions is so low when the various wood features are not functionally or developmentally related to each other, as recalculation by current statistical procedures would doubtless show. One must concede that a conflict in interpretations by those who view vesselless dicotyledons from different perspectives does exist at present.

Attention must be called to noncharacteristic persistence of membrane remnants in perforations by virtue of inhibition of membrane lysis through the secretion in the wood of "resinlike" or other compounds. One can suspect these not only because surfaces of the membranes and adjacent secondary walls appear coated, but also because such membranes have localized distribution within the wood. Light microscopy can confirm presence of deposits in the vessel elements. On the other hand, if one observes riffs and tears in the membrane remnants one sees in perforations, one can suspect that wood sample preservation and processing methods may have contributed to alteration of the membranes, and that in the living plant, the membranes may have been somewhat more intact.

Another interpretation that might be offered for presence of membrane remnants is that the presence of these is tolerated because they offer minimal obstructions to flow. In this interpretation, where perforations are wider, remnants should be absent. One should note that in species with membrane remnants, the majority of perforation plates usually have relatively clear perforations. If perforation plates with minimal obstruction are in the minority, selective pressure for removal of the vestigial membrane remnants ought to be minimal. Membrane remnants, where present, are often in the form of slender threads that would offer minimal impediment to flow. Another circumstance worthy of comment is the tendency for membrane remnants to be confined to small areas at the lateral ends of the perforations; this is mentioned by Meylan and Butterfield (1978), Middleton (1987), and Ohtani and Ishida (1978) for a number of species. In my own preparations, I saw this tendency in only a few of the species with membrane remnants. More significantly, if one looks at the species with narrow perforations that lack membrane remnants (see second section under Systematic Distribution, above), one finds many species that lack membrane remnants but should be expected to have them if a correlation between perforation width and membrane presence is operative. In other words, transpiration stream has not removed membrane remnants in an appreciable number of species with narrow perforations. To be sure, we do not know the speed of water flow in these species, and this interpretation cannot be dismissed entirely at present.

Another interpretation that can be invoked is that instances of membrane remnants in perforations could be indicative that vessel elements are being converted into tracheids, and that therefore secondary vessellessness could occur in woody dicotyledons. This phyletic sequence is particularly appealing to workers in cladistics whose most parsimonious cladograms for "primitive" dicotyledon families require such a hypothesis. Young (1981) is a representative of this view, but other workers can be cited also. Such workers may wish to emphasize the comments of Takahashi (1988), who in his study of *Sarcandra glabra* (Thunb.) Nakai (Chloranthaceae) came to the conclusion that the difference between a vessel and a tracheid can be very slight—as it is indeed in that species—and that if the transpiration stream were strong, it might lead to formation of vessels, whereas a weaker flow would lead to formation of tracheids in such a species. I can readily agree that if a species were teetering on the brink of vessel origin, small factors might push it in either direction.

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There is every reason to believe, however, that the majority of membrane remnants in perforations figured by Meylan and Butterfield (1978) and Ohtani and Ishida (1978), as well as the remnants in the present study, are free from artifacts.

**LITERATURE CITED**


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