Pit membrane remnants in perforation plates and other vessel details of Cornales

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Introduction

The species studied here belong to Cornaceae and two families segregated from it by various authors: Aucubaceae and Griseliniaeae. Ohtani and Ishida (1978) reported pit membrane remnants in Japanese Cornaceae, although these structures were not reported by Meylan and Butterfield (1978) in the two New Zealand species of Griselinia that they studied with SEM. Whether pit membrane remnants occur more widely in Cornaceae has not been hitherto investigated, and the present paper is a contribution to knowledge of this distribution. Earlier papers on wood anatomy mostly have not used that technique (see Gregory, 1994). More recent studies of wood anatomy of Cornaceae (Li & Chao, 1954; Noshiro & Baas, 1998) were not concerned with fine details of perforation plate structure, although a few SEM photographs of wood details were offered in the Noshiro and Baas (1998) paper. Both Li and Chao (1954) and Noshiro and Baas (1998) reviewed the taxonomic problems associated with traditional alliances that include Cornaceae. Recent molecular data analyzed cladistically (e.g., Soltis et al., 2000) showed that Cornales (from which they studied Cornus) and Garryales (in which they in-
location within perforation plates are aspects that have remained unexamined. Because our reports are based on viewing large areas of radial sections, we believe we can address these questions at least in a preliminary way. As these aspects of pit membrane presence become better known, the physiological and evolutionary significance of these structures can be assessed. In addition, studies such as the present one provide a basis for selection of species for experimental work on pit membrane remnants. The way in which these form and the conditions under which they persist need to be elucidated. Cornaceae (s.l.) are a woody family ideal as subjects for examining such questions, since they grow in a range of habitats from frost-free to markedly temperate, and thus the relationship between nature of perforation plates and formation of ice within the conductive system could be examined. Because Cornaceae characteristically occupy moist habitats, the effect of drought on the conductive stream should not be a complicating factor.

Although our sampling of Cornaceae and allied families is small, the fact that all three genera examined do possess pit membrane remnants is of potential significance in resolution of familial definitions and relationships in this complex (for information on various phyllogenetic treatments, see Goldberg, 1986; Noshiro & Baas, 1998; Thorne, 2000).

Materials and Methods

Samples of stems were taken from living plants cultivated in Washington Park Arboretum, Seattle (Aucuba japonica Thunb. #215-76-A, Cornus stolonifera Mich. #638-41, Griselinia littoralis Raoul) and Santa Barbara Botanic Garden (Cornus glabrata Benth. #75-147). The stems used were between three and five years old, and thus a mature wood pattern is represented. No observations are based on vessel elements that might be immature by virtue of being near the cambium.

Stem segments were cut into portions suitable for sectioning and fixed in 50% acetic acid for that procedure. Only radial sections were prepared; thick sections (>30 μm) were employed because of ease of handling and the chance that in thick sections, larger portions of perforation plates would be intact. The sections were dried between clean slides, mounted on aluminum stubs, sputter-coated with gold, and examined with a Hitachi S2600N scanning electron microscope.

Descriptions of species are arranged in alphabetical order. The pit membranes figured are believed to represent natural appearances, such as would be present in the living plant (see Schneider & Carlquist, 2003, for a discussion of identification of artifacts). There are obvious artifacts (e.g., the transverse tear in pit membrane of the top perforation, Fig. 2A), but other than such clear structural disruptions, the pit membranes represented are considered reliable representations. Prolonged exposure to the electron beam, especially at accelerating voltages above 20 kV, can result in tearing, and therefore we have adjusted voltage strength and exposure carefully so as to avoid any such artifact formation. We would point, as one evidence of the validity of our observations, to the fact that entirely intact and pore-free pit membranes occur in lateral wall pits of vessels, forming a kind of control to what is observed in perforation plates. For additional criteria for separation of artifacts from valid pit membrane remnants, see Carlquist and Schneider (2001). The steps in formation of pit membrane remnants in vessels would be worthy of study, but at present, no literature on this exists to the best of our knowledge.

Results

Aucuba japonica (Fig. 1). More than half of the perforation plates examined lack appreciable pit membrane remnants. The remainder range from perforation plates in which pit membrane remnants are abundant (Fig. 1A) to present only at lateral ends of the perforations (Fig. 1C). The appearance of these remnants is mostly intermediate
Fig. 1  Aucuba japonica. Portions of radial sections of wood. A–C, Portions of perforation plates. A, Several companion elements; B, Perforation plate with elongated pits; C, Perforation plate with large circular pits.
The tendency for the pit membranes to form fine reticulate webs in lateral ends of perforations is illustrated. The wide borders of the perforations (Fig. 1C) are similar in tone to the pit membrane remnants, and therefore the patterns formed by the remnants are clearest in areas overlying the inner pit aperture of the vessel. Vessel wall areas that are free from pits tend to show widely spaced, shallow thickenings (Fig. 1D). These thickenings are transverse and not helical in the sense of forming a continuous gyre, but they would fall under the phenomenon of "helical thickenings" in the all-inclusive sense of the term as used by most comparative wood anatomists. Helical thickenings have been reported for Cornaceae previously in Corokia (Patel, 1973) but not, apparently, in Aucuba.

**Cornus stolonifera** (Fig. 3). The features illustrated are similar to those of *C. glabra*, but with somewhat different texture in the pit membrane remnants. Pits transitional between the lateral wall pitting and the perforation plate of vessel elements are shown in Figure 3A—B, left. In Figure 3D, the entire transition from lateral wall pit with intact membrane (left) to perforation with no perceptible pit membrane remnants in the central portion is shown. The perforation to the left of the one at far right in Figure 3D does show, bottom, a pit membrane remnant at the lateral end, reinforcing what is a typical pattern for the family. One can see a similar instance in Figure 3B, above right, in the form of a few threads. Threadlike pit membrane remnants in lateral ends of perforations are illustrated in Figure 3C, left. The similarity of the transitional pit in Figure 3A to the transitional pit in Figure 3D is striking: in both cases, the perforated portion is more abundant on one side (left in Fig. 3A, right in Fig. 3D).

**Griselinia littoralis** (Fig. 4) shows pit membrane features very similar to those of *Cornus*. Pit membrane remnants are chiefly threadlike and confined to the lateral ends of perforations (Fig. 4A), although more than half of the perforation plates examined do not show perceptible pit membrane remnants. A degree of intermediacy between laminar pit membrane and pit membrane in the form of slender threads may be seen in Figure 4A—C. The pit membrane of Figure 4D, laminar but perforated by small pores, is unusual, and others like it were not observed in our material. The three pits/perforations of Figure 4B show the transition region from lateral wall pitting (top) to perforation plate (bottom), and illustrate the difficulty in defining the terms "pit" and...
Fig. 2. *Cornus glabra*. Portions of perforation plates from radial sections of wood. A. Ends of perforations, to show laminar pit membrane remnants perforated by pores; tear in top membrane is an artifact. B. Several perforations to show remnants which form similar threadlike and flake-like configurations. C, D. Transition.
Fig. 3. *Cornus stolonifera*. Portions of perforation plates from radial sections of wood. A. Perforation in zone intermediate between lateral wall pitting and perforation plate, to show pore pit membrane. B. Two perforations, one at left (nearer to lateral wall pits, which are not shown) contains more abundant pit membrane remnants. C. Several adjacent perforations, each with threadlike membrane remnants at lateral ends of perforations. D. Transition between lateral wall pitting (extreme left) and perforation plate (remainder of photograph). Scale bars: A = 2 μm; B–D = 5 μm.
Fig. 4. Gosselinia littoralis. Portions of perforation plates from radial regions of wood. A. Three perforation plates. B. Single perforation plate. C. Close-up of a perforation plate. D. Denser view of the perforation plate.
term that indicates intermediacy between the two categories. Certainly the perforation at the bottom in Figure 4E shows the restriction of threadlike pit membrane remnants to lateral ends of perforations, typical in perforation plates of Cornaceae (s.l.) that retain pit membranes in perforations. The apparent shrinkage of a pit membrane remnant to one side of the perforation, shown in Figure 4B, center, and Figure 4C, appeals to us as probably an artifact. However, we have no way of knowing whether such deformation occurs in the xylem of a living plant or is the result of the drying required for examination of sections with SEM.

Conclusions

Our sampling of Cornaceae (s.l.) is admittedly very small, and was influenced by the desire to find whether pit membrane remnants could be found in several genera of the family as broadly defined. We therefore selected species with more numerous bars per perforation plate. In the cornalean alliance, some species have few bars, some none, and species with few or no bars would, in our experience, probably lack pit membrane remnants. Pit membrane remnants have been found in only a few genera with relatively few bars per perforation plate (e.g., Bruniaceae & Sarracenioideae; Carlquist, 1992).

Despite the small sampling, the similarity of the three genera with respect to types and distribution of pit membrane remnants is considerable. This similarity is not necessarily indicative of close relationship, however.

More significantly, though, the patterns reported here are not unique, but occur in families and orders in which pit membrane remnants are relatively vestigial. The similarity to occurrence of pit membrane remnants in Ericaceae (Carlquist & Schneider, in press), a family that has not been proposed to be related to the cornalean families in any phylogenetic scheme, is striking. In both Cornaceae s.l. and Ericaceae s.l., pit membrane remnants are present in fewer

the remnants are mostly confined to lateral ends of the perforation plates. An exception occurs in the transitional zone between lateral wall pitting and the perforation plate. In this area, one or two pits (perforations) contain more extensive pit membranes, but the pit membranes are abundantly perforated or threadlike. The occurrence of such a transitional pit/perforation shows that at least in families with pit membrane remnants of this sort, designating any particular structure as a pit or a perforation may be difficult.

The vestigial nature of the pit membrane remnants suggests possible correlations with the conductive stream. If the remnants are considered an impedance to the conductive stream, the remnants present in the Cornaceae studied represent a minimal interruption to that stream. Remnants occur in fewer than half of the perforation plates. In the perforation plates where they are present, most perforations contain remnants only at lateral ends of the perforation, and most of the length and width of the perforations are free from the remnants. One or two perforations intermediate between true perforations and lateral wall pits occur in the transition between lateral wall pitting and perforations. These constitute only a minor impediment to conduction and, indeed, if they were viewed as modifications of pits rather than of perforations, would represent an enhancement of conduction.

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Literature Cited


