

Origins and nature of vessels in monocotyledons. 9. *Sansevieria*

S. Carlquist, E.L. Schneider *

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

Received 9 June 2006; received in revised form 3 November 2006; accepted 7 November 2006

Abstract

Sections of fixed material of four collections of three species of *Sansevieria* were studied by means of scanning electron microscopy (SEM) to initiate study of distribution of vessel elements and the ultrastructural nature of tracheary elements in the genus. Roots of *Sansevieria* have scalariform perforation plates in vessels; only tracheids are present in stems (=rhizomes) and leaves. This distribution is similar to that of genera of Asparagales claimed in recent molecular phylogenies to be close to *Sansevieria*: *Dracaena*, *Ophiopogon*, and *Ruscus*. Also similar in tracheary element types is Orchidaceae, now considered a member of Asparagales. Ultrastructural study of *Sansevieria* tracheary elements reveals intermediacy between vessel elements and tracheids because porose pit membranes extend across entire end walls of tracheids, and portions of scalariform perforation plates of vessel elements. This correlates with longevity of roots in *Sansevieria*, and probable moderate transpiration rates in leaves. In *Sansevieria*, as in other monocotyledons, vessel type occurrence, organographic distribution, and tracheary element ultrastructure relate primarily to ecology, although molecular-based trees, in fact, help understand the patterns of shift in ecological adaptation with attendant change in tracheary element structure.

© 2006 SAAB. Published by Elsevier B.V. All rights reserved.

Keywords: Asparagales; Pit membranes; Ruscaceae; Tracheary elements; Ultrastructure; Xylem

1. Introduction

Sansevieria is a genus of about 60 species, native to tropical and subtropical areas from warmer parts of South Africa to islands east of Africa, northeastern and northern Africa, the Arabian peninsula, India, Burma, and Java (Brown, 1915; Morgenstern, 1979). In earlier classifications, *Sansevieria* was placed in Liliaceae. After the subdivision of that family (Dahlgren, 1983; Dahlgren et al., 1985), *Sansevieria* was placed in Agavaceae. However, Duvall et al. (1993) signaled a close relationship between *Danae* (Asparagaceae), *Nolina* (Nolinaceae) and *Sansevieria*. Recent molecular work, reviewed by the APG II (2003) shows that *Sansevieria* should be placed close to *Dracaena* and *Ophiopogon* in Ruscaceae (=Dracaenaceae), in Asparagales. One can place “asparagoid families” (Asparagaceae and Ruscaceae) together with other families (including Orchidaceae, for example) into a more inclusive version of Asparagales (APG II, 2003) or one can opt for other familial and ordinal concepts. As noted by Chase (2004), this decision is one

of convenience at present. Molecular phylogenies reveal that families and genera with widely divergent habits, such as *Dracaena* and *Asparagus*, may be closely related. If grouping genera with such divergent habits into a single family, Asparagaceae, seems awkward to some, future systematists may find rapid habit diversification an evolutionary phenomenon that should be stressed by phylogenetic systems and employed in teaching. The latter preference would find more inclusive families and orders acceptable. Treatments diverge at present, but for the purposes of the present paper, the concept of Ruscaceae that includes *Dracaena*, *Ophiopogon*, *Ruscus*, and *Sansevieria* will be employed.

The summary of Cheadle (1942) mentions Liliaceae as a family in which vessels are present in roots, but not elsewhere in the plant, with minor exceptions. Presumably that generalization applies to *Sansevieria*, which he does not mention specifically. In a later paper that describes vessels in several genera of Ruscaceae, Cheadle (1970) reports scalariform perforation plates on vessels in roots of *Ruscus*, but only tracheids in the stems of that genus. Cheadle (1970) reports simple to scalariform perforation plates in vessels of roots, combined with scalariform perforation plates in stems in the ruscaceous genera *Danae* and *Semele*. In *Asparagus*,

* Corresponding author.

E-mail address: eschneider@sbbg.org (E.L. Schneider).

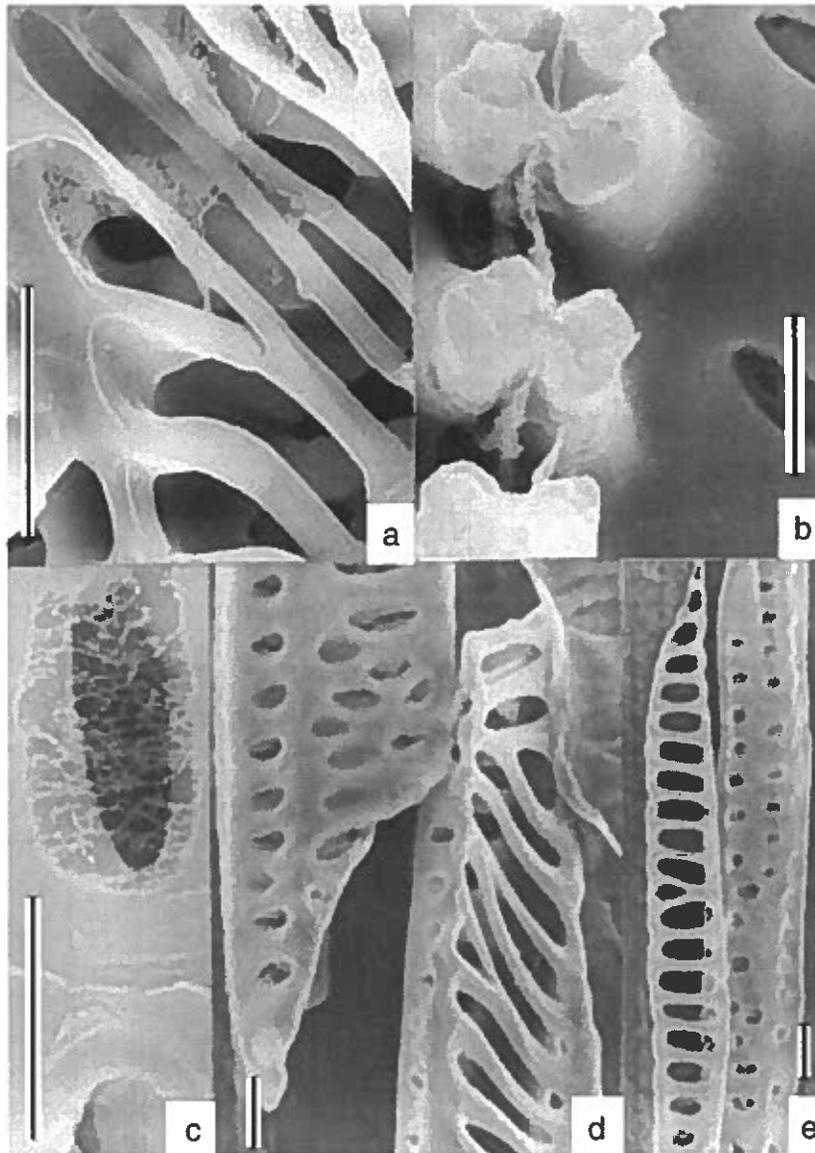


Fig. 1. SEM micrographs of xylem from longisections of roots of *S. deserti* (a–c) and *S. trifasciata* var. *laurentii* (d–e); (a) portion of perforation plate with pit membrane remnants in some of the perforations; (b) sections of bordered pits in tracheary elements (left), with lateral wall pits (right); (c) pit at distal end of perforation plate, showing reticulate pit membrane; (d) tips of two vessels elements, dislodged from each other by sectioning, perforation plate at right; (e) long narrow perforation plate (left) and lateral wall with pits (right). Scale bars=5 μ m.

Cheadle (1970) finds vessel types and distributions like those in *Danae* and *Semele*. Cheadle and Kosakai (1971) figure root vessels with long scalariform perforation plates for *Ophiopogon*. In *Dracaena*, Cheadle (1942) reported simple perforation plates in vessels in roots together with scalariform perforation plates in vessels of leaves. Thus, morphology of vessels at the level of light microscopy is known for most of the asparagoid genera, but no details concerning the vessels of *Sansevieria* have been reported. The literature contains no details concerning the ultrastructure of tracheary elements in the asparagoid genera, although in preparation for the present study, we investigated, using scanning electron microscopy (SEM), tracheary elements of several species of *Dracaena* and *Ophiopogon*.

Tracheary elements of *Sansevieria* are potentially of interest with respect to ecology. *Sansevieria* is a genus of tropical or subtropical areas that rarely or never experience frost (Brown,

1915; Morgenstern, 1979). The habitats of *Sansevieria* in the Old World are often described as open, sunny places, but frequently with subsurface moisture availability. For example, *Sansevieria deserti* N. E. Brown grows along lake margins or riverbanks in areas that otherwise could be described as desert. Clearly, some habitats mentioned by Brown (1915), such as sandy areas near seashores and uplifted coral plateaus are dry if humid, and the succulence of rhizomes and leaves in *Sansevieria* correlates with the dryness of such habitats. *Sansevieria* rhizomes are mostly underground (*S. deserti*, *Sansevieria trifasciata* Prain), but production of elongate surface rhizomes in a few species (*Sansevieria dooneri* N. E. Brown) permits exploitation of microhabitats. The underground rhizomes are potentially valuable for escaping heat and fire. The leaves of *Sansevieria* are variously oriented, from cylindrical and vertical (*S. deserti*) to flat and nearly horizontal (*S. trifasciata* "hahnii"),

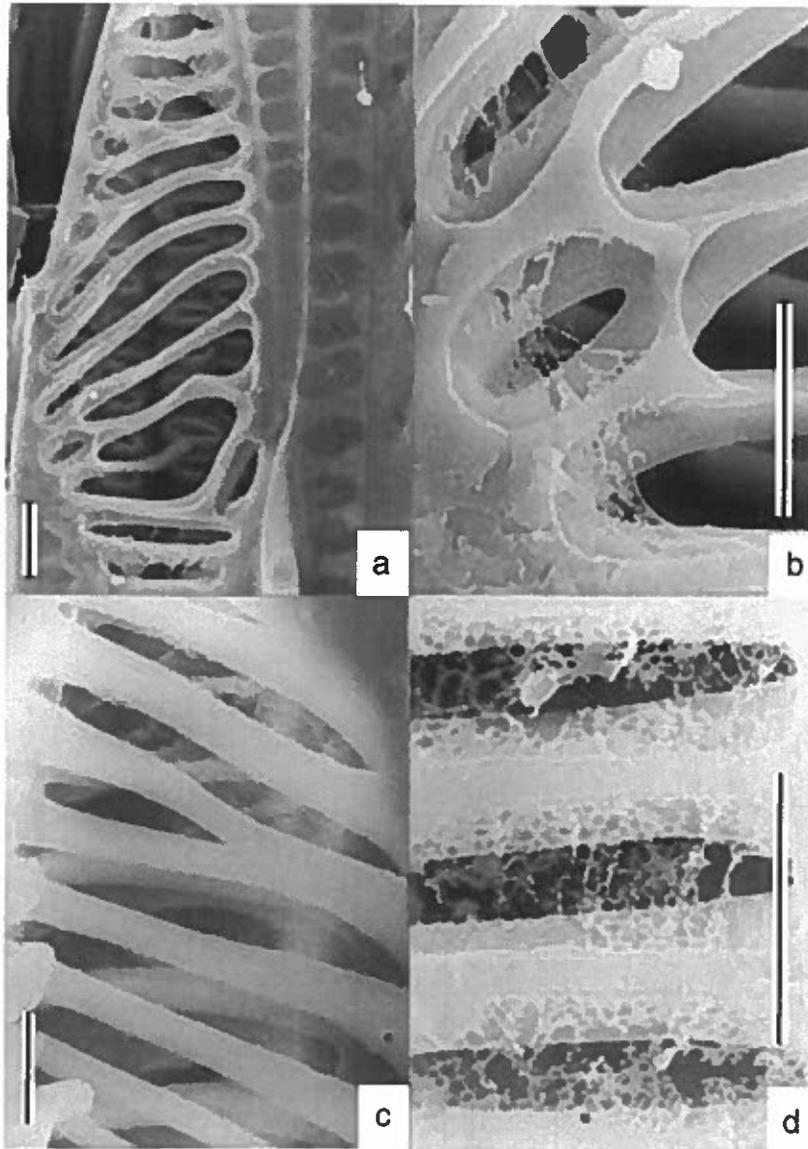


Fig. 2. SEM micrographs of xylem from longisections of roots of *S. trifasciata* "hahnii" (a–b) and *S. dooneri* (c–d); (a) perforation plate in face view seen from outside of vessel element; note pit membrane remnants in pits at upper and lower end of plate; (b) enlarged area of perforation plate, showing webbed nature of pit membrane remnants; (c) perforation plate seen from inside of vessel element, showing sparse pit membrane remnants; (d) view of pits from outside of vessel; pit membrane is reticulate. Scale bars = 5 μ m.

thereby with a potential range in photosynthetic capacity suited to high light intensity as well as moderate. Juvenile plants of species with flattened leaves tend to have leaves that are more nearly horizontal than those on adult plants. The number of leaves per rhizome is variable depending on the habitat and growth condition of the plant. Thus, *Sansevieria* provides a distinctive range of forms that invite interpretation with respect to the adaptive nature of tracheary elements. In monocotyledons in general, tracheary element types and distribution within a plant sensitively reflect habitat and ecology primarily, systematic relationships secondarily (Carlquist, 1975).

2. Materials and methods

Plants in actively growing condition were obtained from the grounds of the Lotusland Foundation, Santa Barbara. These

plants (species cited above) represent accessions identified by that Botanic Garden. Root, stem (rhizome), and leaf portions were preserved in 50% aqueous ethanol. As with our study on orchid xylem (Carlquist and Schneider, 2006), freehand longitudinal sections were prepared by means of single-edged razor blades. Sections were washed in three changes of distilled water, dried between glass slides, mounted on aluminum stubs, sputter-coated with gold, and examined with a Hitachi S2600N scanning electron microscope. This methodology, which is similar to that of Sano (2005), minimizes formation of artifacts. The use of relatively thick (ca. 1 mm) freehand sections permits study of more extensive portions of larger numbers of tracheary elements, and in addition, the thickness offers a form of strength that minimized breakage of delicate primary walls during handling. Rips and corrugation in pit membranes, where they occur, are artifacts and can easily be differentiated from

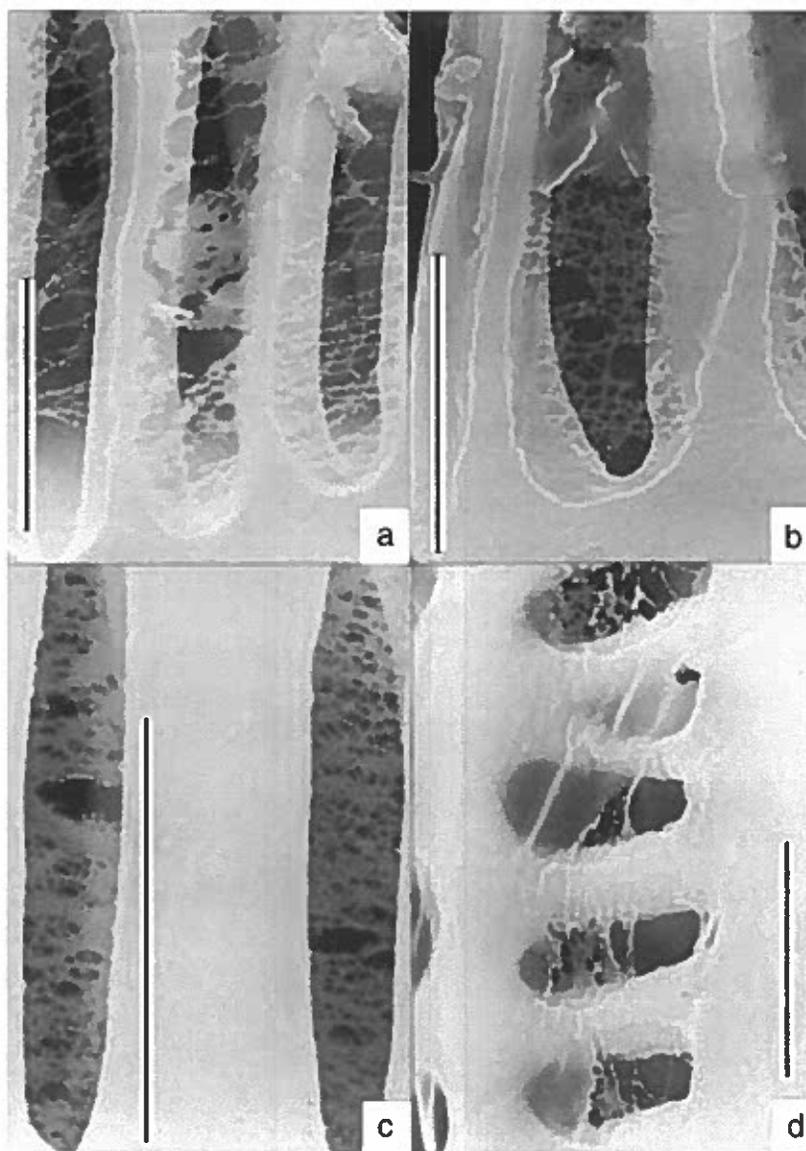


Fig. 3. SEM micrographs of xylem from long sections of stems of *S. deserti* (a–b) and *S. dooneri* (c–d); (a) linear to reticulate pattern of pit membrane, seen from outside of tracheid; (b) finely reticulate pattern of pit membrane, seen from outside of tracheid; (c) porose pit membrane, seen from inside of tracheid; (d) probable parenchyma-tracheid interface, showing intact membranes on parenchyma side, porose membranes on tracheid side. Scale bars = 5 μ m.

occurrences of threads and pores we report as natural appearances. Distribution of porose membranes and nonporose membranes within tracheary elements cannot be illustrated here in detail. Our knowledge of those distributions depends on extensive examination of sections, although we report what we believe to be representative conditions.

3. Results

3.1. Roots

Roots of *Sansevieria* contain vessels with scalariform perforation plates (Figs. 1 and 2). The details of those scalariform plates are diverse, however. In *S. deserti* (Fig. 1a), porose remnants of pit membranes are present in some of the distal perforations, whereas those in the central portion of the perforation plate lack such pit

membranes in this particular plate. Porosities penetrate the dual (but fused) pit membranes on end walls of adjacent tracheary elements, as shown in Fig. 2b. Some pit membranes in distal perforations of perforation plates may be networklike (Fig. 2c). The tips of two vessel elements, adjacent to each other but dislodged by the sectioning process, are illustrated in Fig. 2d. Pit membrane remnants were not observed on the perforation plate in Fig. 2d. The distinction in secondary wall architecture between the perforation plate of the vessel element tip at right and the lateral wall pitting on the vessel element tip at left is clear, as is the presence of pit membranes in the lateral wall pitting. This distinction is also evident in a pair of tracheary elements from a root of *S. trifasciata* var. *laurentii* N. E. Brown (Fig. 1e). Although both elements are slender, the relatively large perforations on the perforation plate (Fig. 1e, left) differ in size markedly from the lateral wall pitting on the tracheary element at right.

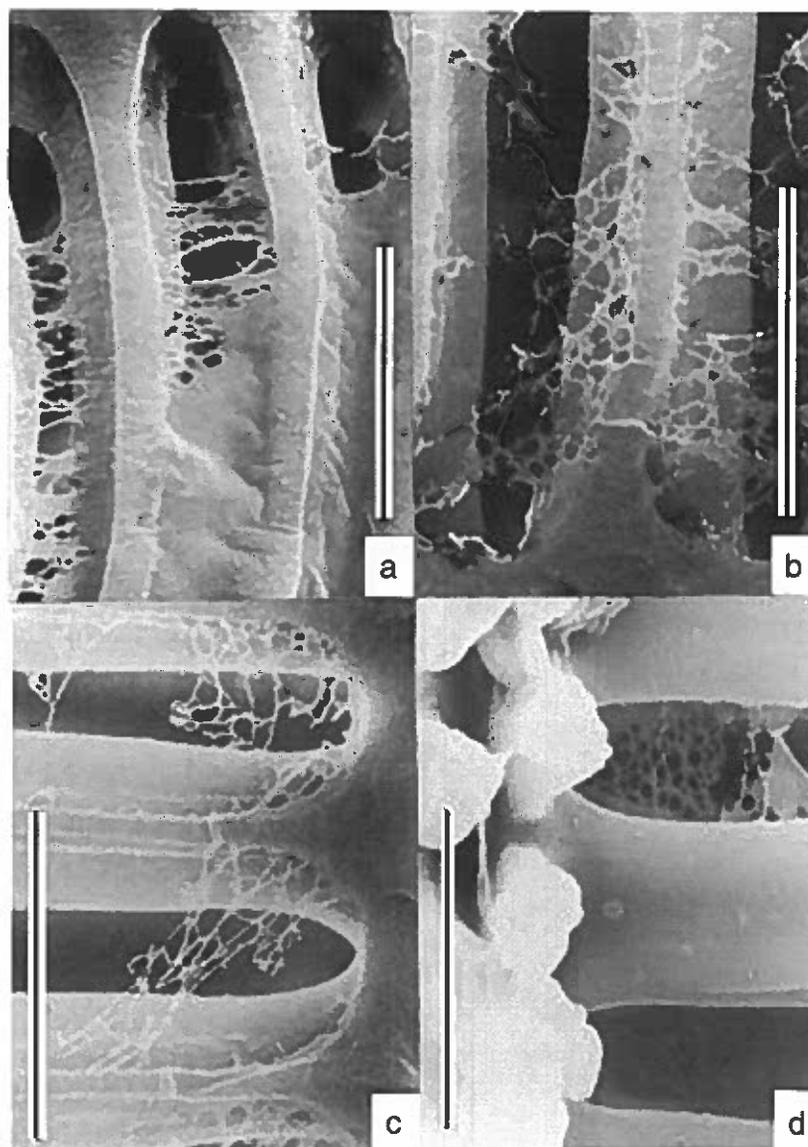


Fig. 4. SEM micrographs of xylem from longisections of stems of *S. trifasciata* "hahnii" (a–c) and *S. trifasciata* var. *laurentii* (d); (a) portions of pits from probable tracheid-parenchyma interface, showing intact membrane below, porose membrane center, and absence of pit membrane above, due to degrees of shaving away of pit membrane portions; (b–c) finely reticulate pit membrane portions, seen from outside of tracheids; (d) tracheid wall in sectional view (left) and face view (right), showing circular pores on the pit membrane at upper right. Scale bars = 5 μ m.

Similar patterns were evident in other collections. Clear differentiation into a perforation plate is evident in the end wall of a vessel of a *S. trifasciata* "hahnii" root (Fig. 2a), although pit membrane remnants occur at the lateral ends of perforations as well as in the most distal (upper and lower) ends of the perforation plate. These pit membranes, shown enlarged in Fig. 2b, are porose. Although some distortion of the networklike pattern can be attributed to drying, the basic pattern seems clear. Absence of pit membrane remnants in perforation plates contrasts with presence of nonporose pit membranes in lateral walls of tracheary elements (Fig. 2a, right). A view of a perforation plate of *S. dooneri* reveals a few threadlike pit membrane remnants (Fig. 2c, upper left). Because this view shows a perforation plate from the inside of a vessel element, removal of pit membrane remnants due to separation of adjacent elements is unlikely to be present. The reticulate pattern present

in pit membranes of some end walls of tracheary elements of *S. dooneri* roots is shown in Fig. 2d; some ripping of these delicate pit membranes due to handling is evident.

3.2. Stems (=rhizomes)

The tracheary elements of stems of *Sansevieria* (Figs. 3 and 4) may be defined as tracheids, because the elements do not show clear differentiation in pit morphology and size between end walls and lateral walls, and because no instances of pit membrane absence that appeared natural were observed. In *S. deserti* rhizomes (Fig. 3a–b), tracheids have pit membranes that are threadlike (Fig. 3a) or reticulate (Fig. 3b). However, attention is called to the fact that some portions of the membranes in both Fig. 3a and b are relatively nonporose (e.g., Fig. 3b, above). This difference is attributed to the shaving

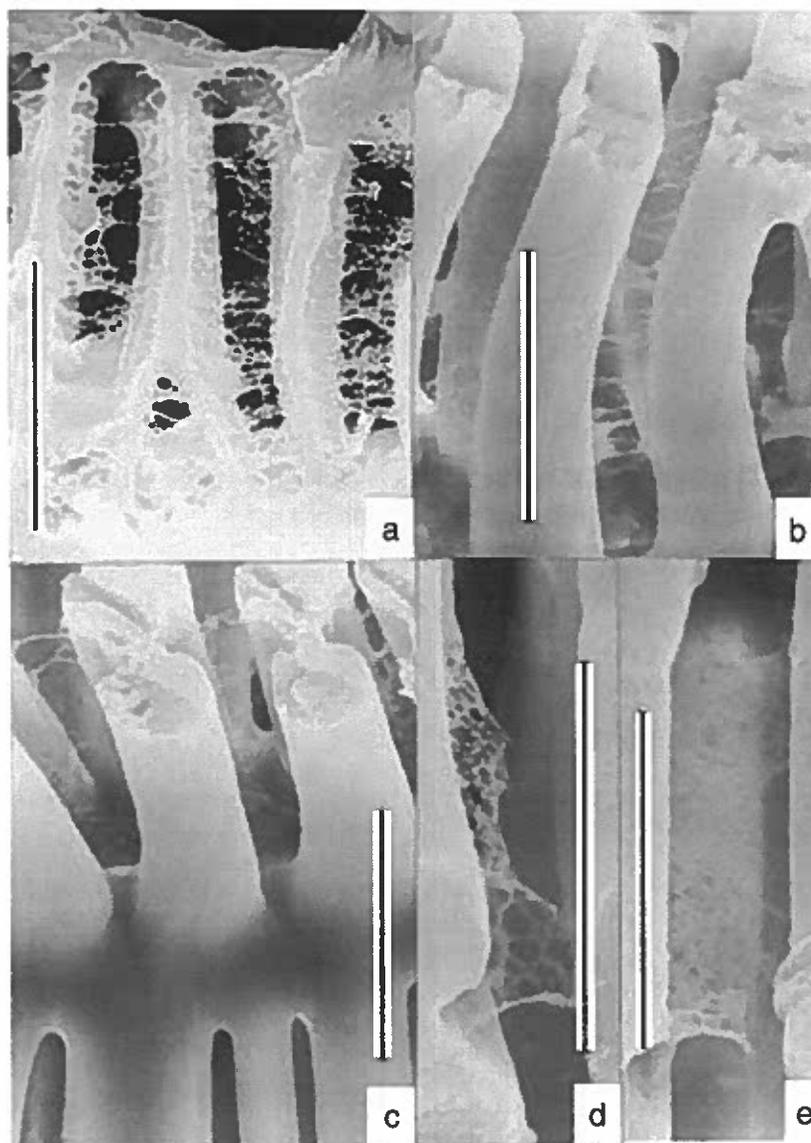


Fig. 5. SEM micrographs of xylem from longisections of leaves of *S. trifasciata* var. *laurentii* (a), seen from outer surface of tracheid, and *S. trifasciata* "hahnii" (c–e), seen from inner surface of tracheid, with wall obliquely sectioned; (a) finely reticulate pit membranes; (b) finely threadlike pit membrane remnants in pits; (c) finely reticulate pit membranes, above, contrast with intact pit membranes, below; (d) torn portion of coarsely porose pit membrane; (e) finely porose pit membrane. Scale bars=5 μ m.

action of sectioning, so that both thicknesses of the dual pit membrane structure of adjacent cells are exposed in some places (less porose), whereas a single thickness (more porose) is exposed in other places. Although identification of the nature of cell contacts in sections is difficult, we believe that the cell faces shown in Fig. 3a–b) may be contacts between tracheary elements and parenchyma cells, with the more porose of the two thicknesses of the primary wall on the tracheary element side. The tracheid pit membranes of *Sansevieria volkensii* rhizomes shown in Fig. 3c–d) illustrate a similar story, although pores in pit membranes are smaller. Because the pits seen in Fig. 3c are seen from the inside of the tracheid, and pit borders in the background indicate that the pits represent an intact contact between two tracheids, a porose tracheid-to-tracheid pattern can be claimed. The presence of both nonporose and porose pit membrane portions in Fig. 3d suggests that a tracheid-to-parenchyma contact, as in Fig. 3a–b, may be illustrated.

The rhizome tracheids of *S. trifasciata* "hahnii" (Fig. 4a–c) and *S. trifasciata* var. *laurentii* (Fig. 4d) confirm the above patterns. In Fig. 4a, both porose and nonporose pit membrane areas are present, suggesting that the two thicknesses of the primary wall are present, below right, but only one thickness is present in the reticulate pit membrane portion. The shaving away of pit membrane portions by the sectioning process would correspond with the entire absence of pit membrane portions at the top of Fig. 4a. In Fig. 4b–c, only porose pit membrane portions are present. Note that pit borders may be seen behind the porose pit membranes, indicating that the pit membranes are not adherent to the pit borders. The delicate nature of the reticulate membrane remnants in Fig. 4b–c is evident in the tearing of the meshwork. The degree of tearing in these two photographs probably represents the best renditions of such delicate strands that are possible with our methods. The porose pit membrane of Fig. 4d is seen from the inside of a tracheid, its

pattern probably represents an intact condition. The pit membrane in the lower pit is absent, probably from handling.

3.3. Leaves

The tracheary elements of the leaves may be categorized as tracheids because their end walls are not different from the lateral walls. Pit membranes in a probable end wall as seen from the outside of a tracheid are illustrated for *S. trifasciata* var. *laurentii* in Fig. 5a. A reticulate pattern of the pit membrane is evident. The remaining photographs of leaf tracheids (Fig. 5b–e) represent views of pit membranes from the insides of tracheids, as seen in *S. trifasciata* “*hahni*”. The tenuous nature of threadlike pit membrane remnants in the center pit of Fig. 5b suggests minimal artifact formation. Such threadlike membranes are evident in the upper pits of Fig. 5c. Note the cut edges of the secondary wall, above in Fig. 5b–c. The pits at bottom in Fig. 5c contain nonporose pit membranes, and represent a lateral wall of a tracheid. The pit membranes of Fig. 5d–e are from oblique sections much like those of Fig. 5b–c, but the cut edges of the wall are at bottom. The two membrane portions illustrated in Fig. 5d–e represent different degrees of pore presence in tracheid-to-tracheid pit membranes.

4. Conclusions

Sansevieria has vessels in the root, but tracheids in the stems and leaves. The vessels in roots have scalariform perforation plates; lateral walls of vessels have scalariform to circular bordered pits. Porose pit membrane remnants are common in the perforation plates, although areas apparently naturally devoid of pit membrane remnants were observed. These vessel elements are not markedly dissimilar from the tracheids of stems and leaves in *Sansevieria*. Stem and leaf tracheids have scalariform pitting in which porose, reticulate, or strandlike pit membranes occur. Pit membranes represent two thicknesses of primary walls, and the pit membrane on the tracheid side of the contact may differ in texture and ultrastructure from the pit membrane on the parenchyma side. The sectioning technique we have employed permits exposure of the two layers. Where tracheid to parenchyma contacts occur, the pit membrane on the tracheid side may be porose, whereas the pit membrane on the parenchyma side is laminar and nonporose. Both thicknesses of the pit membrane in pits of end walls of leaf and stem tracheids, and of pit membrane remnants in perforations of roots, may be porose, so that when one looks from the inside of one tracheid through a pit into another tracheid, strandlike or networklike pit membranes are evident.

Vessels with scalariform perforation plates in roots combined with tracheids in stems were observed by Cheadle (1970) in *Ruscus* and by Cheadle and Kosakai (1971) for *Ophiopogon*. Vessels with simple to scalariform perforation plates were observed in roots of *Semele* but with tracheids in stems and leaves (Cheadle 1970). *Asparagus* (Cheadle and Kosakai, 1971) has vessels with simple perforation plates in roots, but vessels with scalariform perforation plates in stems. *Dracaena* offers the anomaly of having vessels with simple perforation

plates in roots, combined with tracheids in stems and vessels with scalariform perforation plates in leaves (Cheadle, 1942). However, Cheadle’s sampling of *Dracaena* was limited.

Cheadle (1942, 1970) and Cheadle and Kosakai (1971) view organographic distribution of vessels within monocotyledon in terms of levels of specialization, and interpret these to implied phylogenetic trees, although phylogenetic trees are not formulated or cited in their work. The specialization levels, stated in terms of a five-point scale, are expressed in terms of generalizations for families and subfamilies, and thus do not highlight individual differences of species and genera. Character state reversions are apparently not considered by Cheadle and coworkers. More importantly, ecological interpretations were not taken into account.

When organographic distributions of vessels and degree of perforation plate specialization are compared to ecology (Carlquist, 1975), remarkable correlations are evident. Members of monocot clades in more highly seasonal environments, where soil moisture availability fluctuates, show presence of vessels to be more widespread within the plant body. For example, allioids have simple perforation plates in roots, which are ephemeral, but no vessels in the very short stems and succulent leaves of bulbs, which are perennial. Such a vessel distribution would correlate with rapid conduction of water in roots during a short season of soil moisture, but slow conduction in leaves and stems. Placed against the templates based on ecology, the vessel types and their distribution in *Sansevieria* shows an intermediate kind of pattern in that root vessels, with scalariform perforation plates, are seemingly adapted to less rapid rates of conduction. Such a correlation is understandable in view of the fact that roots in *Sansevieria* are often perennial—a fact that suggests that soil moisture availability is relatively prolonged in sites where *Sansevieria* grows as compared with sites where *Allium* typically occurs. The absence of vessel elements in stems and leaves of *Sansevieria* parallels the succulent nature of leaves and rhizomes in the genus. The limited transpiration of leaves of *Sansevieria*, as evidenced by thick leaf cuticles, and frequent vertical leaf placement, also correlates with absence of vessels in stems and leaves. These considerations apply also to *Ophiopogon* and to *Ruscus*, which occupy similar ecological situations, although *Ruscus* has phylloclades rather than leaves. One could also offer the asparagalean family Orchidaceae in comparison: they too, have similar vessel types and distributions, as well as ecology (Carlquist and Schneider, 2006).

Our sampling of *Sansevieria* is too small to provide any variations within the genus with respect to systematics or ecology, nor do the species selected suggest any appreciable variation in these respects. The three species were, in fact, selected for diversity in habit.

The presence of pit membrane remnants in scalariform perforation plates of *Sansevieria* roots suggests a primitive mode of structure, almost a degree of intermediacy between tracheids and vessel elements. Such a degree of intermediacy was reported in roots of such monocotyledons as *Acorus* (Carlquist and Schneider, 1997) and *Hanguana* (Schneider and Carlquist, 2005), as well as in the orchids (Carlquist and Schneider, 2006).

Likewise, stem tracheary elements in these same genera and families are difficult to categorize, because end walls can have pit membranes that are highly porose. We stress the presence of pit membrane remnants and porose pit membranes because in systematics as well as in ecological plant anatomy, those unacquainted with ultrastructure may be tempted to think in terms of two divergent cells types. The porous, reticulate, or threadlike nature of pit membranes in end walls of tracheids in the groupings mentioned above in this paragraph are not merely intermediate in morphology, they are probably intermediate in ability to conduct water. The enhanced water conduction ability of a highly porous end wall (as compared with that of nonporous pit membranes) needs study. More importantly, the ability of porose end walls to restrict passage of air bubbles, and thereby enhance conductive safety, needs study by plant physiologists. Our studies, by offering instances of where porose pit membranes may be present in tracheary elements of monocotyledons, can offer the basis for such studies.

References

- APG II, The Angiosperm Phylogeny Group, 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* 141, 399–436.
- Brown, N.E., 1915. *Sansevieria*. A monograph of all the known species. Royal Botanic Gardens, Kew. *Bulletin of Miscellaneous Information* 5, 185–261.
- Carlquist, S., 1975. *Ecological Strategies of Xylem Evolution*. University of California Press, Berkeley.
- Carlquist, S., Schneider, E.L., 1997. Origins and nature of vessels in monocotyledons. 1. *Acorus*. *International Journal of Plant Science* 158, 51–56.
- Carlquist, S., Schneider, E.L., 2006. Origins and nature of vessels in monocotyledons. 8. *Orchidaceae* 2006. *American Journal of Botany* 93, 963–971.
- Chase, M.W., 2004. Monocot relationships: an overview. *American Journal of Botany* 91, 1645–1654.
- Cheadle, V.I., 1942. The occurrence and types of vessels in the various organs of the plant in the Monocotyledoneae. *American Journal of Botany* 29, 441–450.
- Cheadle, V.I., 1970. Vessels in Pontederiaceae, Ruscaceae, Smilacaceae, and Trilliaceae. *Botanical Journal of the Linnean Society* 63 (Supplement 1), 45–50.
- Cheadle, V.I., Kosakai, H., 1971. Vessels in Liliaceae. *Phytomorphology* 21, 320–333.
- Dahlgren, R., 1983. General aspects of angiosperm evolution and macrosystematics. *Nordic Journal of Botany* 3, 119–149.
- Dahlgren, R.M.T., Clifford, H.T., Yeo, P.F., 1985. *The Families of the Monocotyledons: Structure, Evolution, and Taxonomy*. Springer Verlag, Berlin.
- Duvall, M.R., Clegg, M.T., Chase, M.W., Clark, W.D., Kress, W.J., Hills, H.G., Eguiarte, L.E., Smilth, J.F., Gaul, B.S., Zimer, E.A., Learn Jr., G.H., 1993. Phylogenetic hypotheses for the monocotyledons constructed from *rbcL* sequence data. *Annals of the Missouri Botanical Garden* 80, 607–619.
- Morgenslern, K.D., 1979. *Sansevierias in Pictures and Words*. Illertalern Offsetdruck & Verlag GMBH. Kempten, Germany.
- Sano, Y., 2005. Inter- and intraspecific structural variations among intervacular pit membranes, as revealed by field-emission scanning electron microscopy. *American Journal of Botany* 92, 1077–1084.
- Schneider, E.L., Carlquist, S., 2005. Origins and nature of vessels in monocotyledons. 6. *Hanguana*. *Pacific Science* 59, 393–398.