

ORIGINS AND NATURE OF VESSELS IN MONOCOTYLEDONS. 3. LOWIACEAE, WITH COMMENTS ON RHIZOME ANATOMY

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SUMMARY

Sections and macerations of roots and stems of *Orchidantha maxillarioides* (Ridl.) K. Schum. (Lowiaceae) were examined with a scanning electron microscope (SEM). Vessels with long scalariform perforation plates occur in both roots and rhizome; perforation plates have more pit membrane remnants in rhizomes. At least a few tracheids are present. The degree of perforation plate specialization correlates with the moist forest understory habit of *Orchidantha*, and is similar to that in primitive families of monocotyledons that occupy marshy habitats. Vessel data suggest a primitive position for Lowiaceae within Zingiberales in accordance with recent phylogenies of monocotyledons, but recent molecular data point to a position more nearly terminal in the clade; this situation needs resolution. Raphides are figured with SEM, as are starch grains with rounded outlines, the shape of the latter newly reported for Lowiaceae.

INTRODUCTION

In our survey of vessels of monocotyledons, we have begun with genera in which vessels have been reported in roots only (e.g., Cheadle, 1942; Wagner, 1977). Thus far, we have examined Acoraceae (Carlquist & Schneider, 1997), Juncaginaceae, and Scheuchzeriaceae (Schneider & Carlquist, 1997). These studies have shown that in these three families, vessels occur in the rhizome as well as in the root. They also show remnants of pit membranes in at least some of the perforations, and a great variety in size of porosities in the pit membranes and in the extent of perforations on the end walls. SEM reveals a detailed and accurate picture of perforation plate morphology, and in our opinion is essential in advancing our understanding of vessel presence and histology in monocotyledons. Our selection of families that appear basal within monocotyledons in recent phylogenies (e.g., Duvall et al., 1993) is intended to reveal early stages in vessel evolution in monocotyledons. This information will be of value in comparison to xylem data on dicotyledon phylads proposed to be ancestral to monocotyledons. Reports to date claim that Lowiaceae have vessels with long scalariform perforation plates in roots; vessels have not been reported in rhizomes of Lowiaceae (Fahn, 1954; Tomlinson, 1959, 1969). Note should be taken that Lowiaceae do not lie in a basal or near-basal position within monocotyledons (Kress, 1995; Stevenson & Loconte, 1995). Thus, Lowiaceae may retain more primitive xylem on account of their ecological preference, and this situation makes the family an interesting one for investigation of xylem.

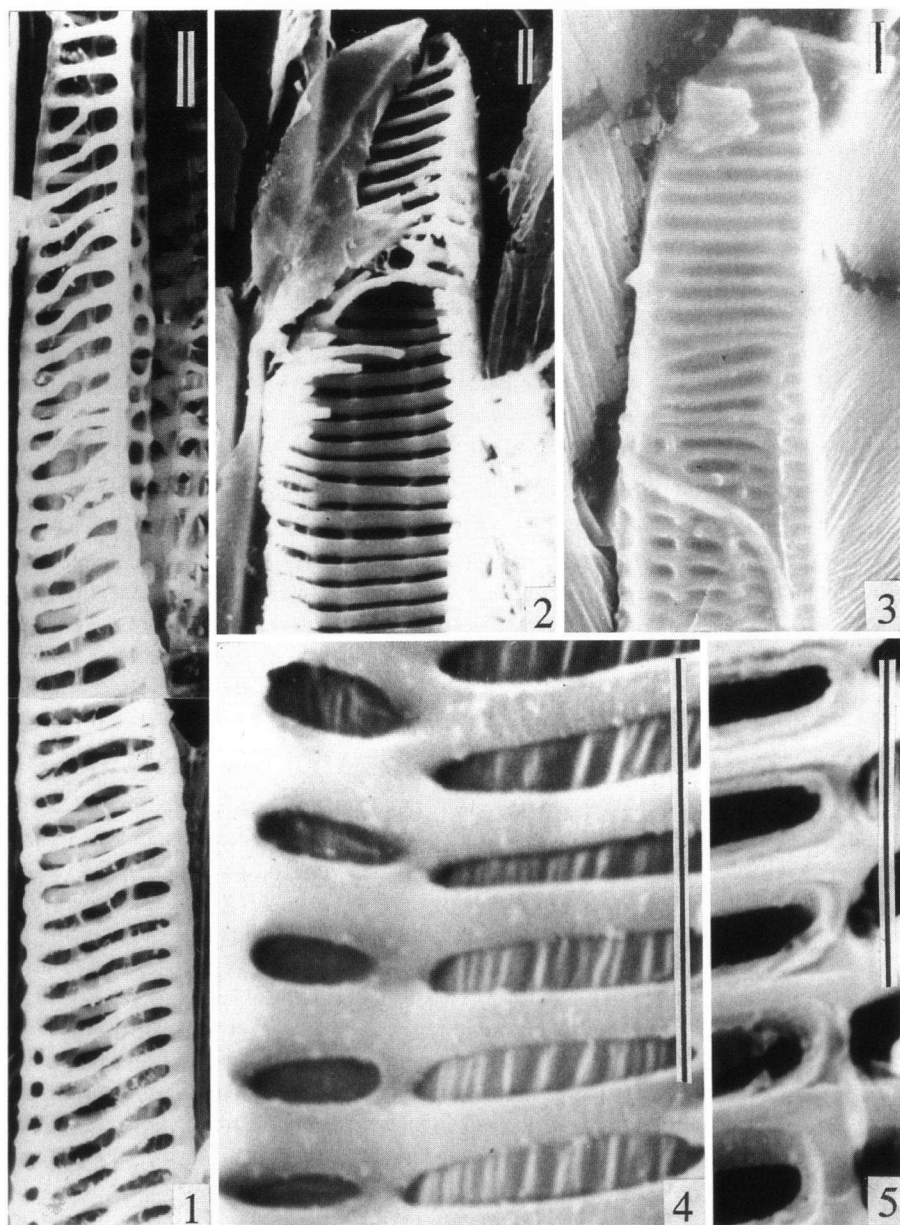


Fig. 1-5. SEM photographs of tracheary elements from roots of *Orchidantha maxillarioides*. — 1. Portion of long perforation plate from maceration. — 2. Short perforation plate, top (partly covered by debris) plus inside of vessel from section (below). — 3. Tracheary element with intact pits on end wall, from maceration. — 4. Lateral wall from vessel seen from inside vessel, showing scalariform pitting and striations in pit membranes, from section. — 5. Lateral wall portion of vessel seen from outside vessel, showing prominent borders on pits. — Scale bars at upper right in photographs = 10 μ m.

Lowiaceae consist of a single genus, *Orchidantha*, with ten species (Larsen, 1996); six of these are restricted to the Malesian area and are covered by Larsen's monograph. Although *O. maxillarioides* has been cultivated (Larsen, 1996), none of the species are common in the wild, and each has been collected only a few times. The genus occurs in moist, shady understory of wet lowland forests (Larsen, 1996). Monocotyledons for which such a habitat has been occupied without shift to drier areas (with or without reversals) apparently have the most primitive xylem among monocotyledons (Carlquist, 1975). Lowiaceae are thus significant in promoting a synthesis between ecology and anatomy.

A few details concerning rhizome histology have been uncovered by SEM; these are not mentioned in Tomlinson's account or differ from his findings. We have therefore added these to the account of tracheary elements.

MATERIAL AND METHODS

Our material was derived from a liquid-preserved specimen (likely in 50% aqueous ethanol) collected from a specimen cultivated at the Royal Botanic Gardens, Kew, U.K., by Cheadle (M-1458). Some roots and rhizomes were infiltrated, embedded in paraffin, and sectioned according to the schedules of Johansen (1940). Other portions of roots and rhizomes were macerated with Jeffrey's Fluid. Sections were mounted on aluminum stubs, cleansed of paraffin, sputter-coated, and examined with SEM. Macerations stored in 50% ethanol were spread onto aluminum stubs, sputter coated, and examined with SEM. We believe that the use of the two methods minimizes observations attributable to artifacts. In this study, as in our earlier studies of primary xylem using these methods, the consistency of results within specimens, species and families, as well as the entirely compatible results obtained from macerations as compared to sections, can be cited as evidence in the validity of the degree of pit membrane presence we have reported in perforation plates. Comparison of lateral walls with end walls also offers a source of data confirmation, as does the ease with which tears or other distortions can be recognized. Any appearance that could be attributed to torsion, breakage or other artifact was not included in our reports.

RESULTS

Tracheary elements of the roots (Fig. 1–5) possess scalariform perforation plates. Some of these (Fig. 1) are extremely long (about 3/4 of the perforation plate is shown). A much shorter perforation plate is seen in Fig. 2 (partially hidden by an overlying cell). Most perforation plates observed in roots fell within the range of those illustrated in Fig. 1 and Fig. 2, respectively. We observed clearly one tracheary element in which the end wall bore intact pit membranes (Fig. 3) and thus qualified as a tracheid. Some elements with a few perforations but mostly with pit membranes on the end wall were observed. Although enlargements of perforation plates are not presented, the perforations are vestigially bordered, and very slightly wider than the pits of the lateral walls. Typical scalariform lateral wall pitting is shown in Fig. 4. The lateral wall pits are fully bordered, as shown by the pits from which pit membranes were removed by sectioning (Fig. 5). In the vessel element of Fig. 4, pitting is scalariform,

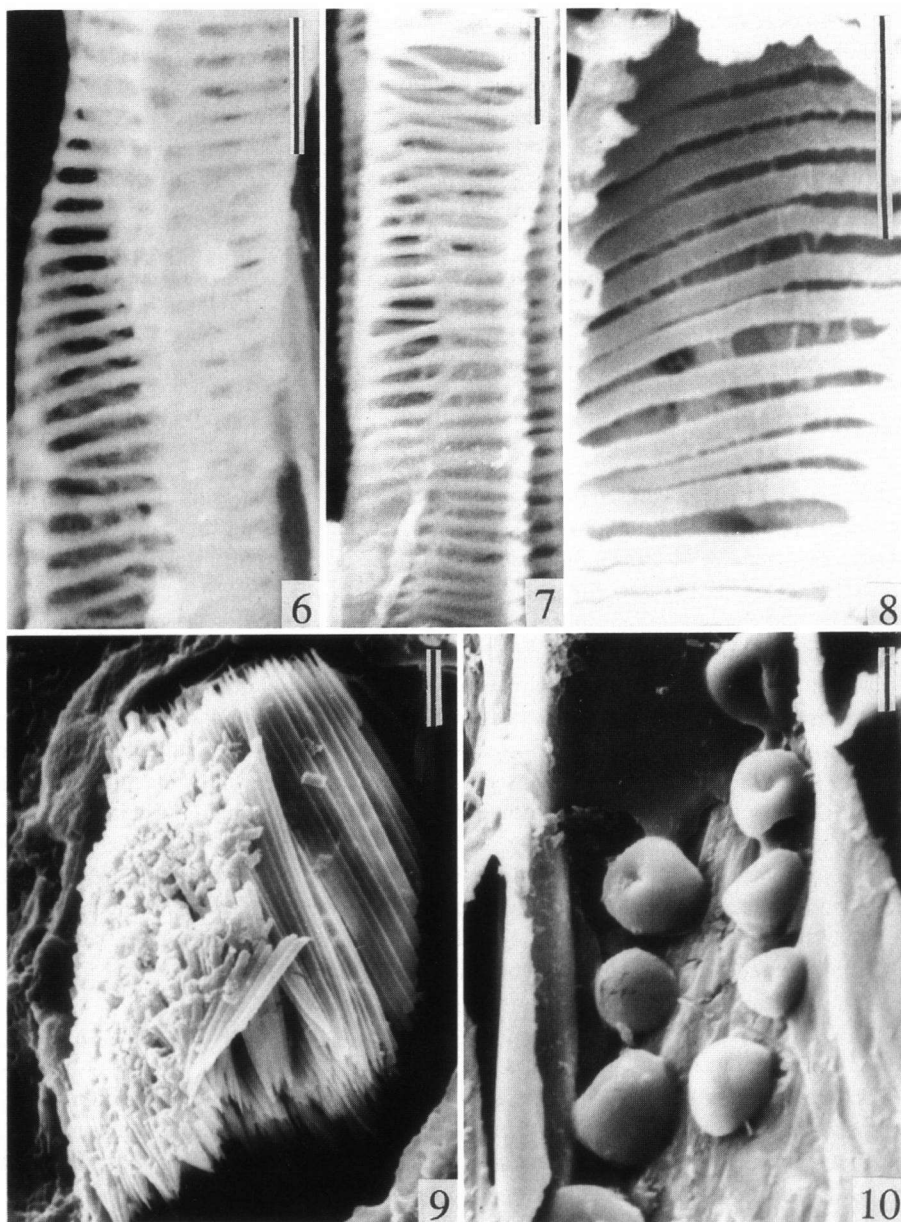


Fig. 6–10. SEM photographs of vessels (6–8) and other histological details (9–10) from rhizomes of *Orchidantha maxillarioides*. – 6. Vessel element from maceration, with perforation plate (left); lateral wall of a vessel at right; some remnants of pit membranes present in perforations. – 7. Perforation plate of a vessel element from maceration, with pit membranes absent in some portions of the end wall but present in others. – 8. End wall of vessel element from section, showing perforation plate seen from inside vessel: pit membranes with pores and various degree of lysis are present. – 9. Idioblast with raphides (intact at right, broken by sectioning at left). – 10. Starch grains from cortical parenchyma of sectioned rhizome. — Scale bars at upper right in all photographs = 10 μ m.

but the secondary wall portions running axially in the element are minimal, so that the element appears similar to an element with helical bands of secondary wall material.

In the rhizome (Fig. 6–8), vessel elements are also present. The perforation plate of Fig. 6 is typical of rhizome vessel elements in that pit membrane remnants occur in some of the perforations. The perforation plate of Fig. 7 shows some perforations clear of pit membranes, whereas remnants occlude others. An even more rudimentary perforation plate is shown in Fig. 8; porosities in the pit membranes are present, but lysis of the pit membranes is certainly incomplete. Lateral walls of rhizome tracheary elements are like those figured for the root.

Raphides have been reported to be common in Lowiaceae (Tomlinson, 1969). In our sections of the rhizomes, we confirmed that observation (Fig. 9). Tomlinson (1969) reports and figures only polyhedral starch grains for Lowiaceae. In our sections of rhizomes, we found starch grains with curved surfaces (Fig. 10), often with one or two indentations. The starch grains figured by Tomlinson may have come from cells in which starch accumulation was more extensive, and in which mutual compression had produced polyhedral shapes.

DISCUSSION AND CONCLUSIONS

We have shown that in three monocotyledon families in which vessels have been reported only in the root, vessels are also present in rhizomes when sections or macerations are studied with SEM. These families include Acoraceae (Carlquist & Schneider, 1997), Juncaginaceae (Schneider & Carlquist, 1997), and Scheuchzeriaceae (Schneider & Carlquist, 1997). To this list, we now add Lowiaceae. In all of these families, however, the perforation plates of the rhizomes are slightly less free from pit membranes than are those of the roots. This is in accord with the idea of Cheadle (1942) that if vessels occur in more than one organ of a monocotyledon, the specialization is greatest in roots, progressively less farther upwards in the plant. As an extension of this idea, our observations have revealed at least for the monocotyledonous taxa we have studied, that perforations and therefore vessel origin begin with formation of porosities in the pit membranes of perforation plates and progress to complete lysis of the pit membranes. The presence of pit membrane remnants in perforation plates of many of the monocotyledon vessel elements we have studied is a compelling reason to urge use of SEM in studies of whether or not vessels have been reported in any particular species or genus. Light microscopy cannot adequately resolve the presence of pit membranes or pit membrane remnants in perforations or pits of end walls of tracheary elements.

The vessel elements of Lowiaceae are only slightly more specialized than those of Acoraceae, Juncaginaceae, and Scheuchzeriaceae. The habitats of those three families are marshes or ponds. The minimal fluctuation in water availability can be correlated with the lower degree of specialization in perforation plates: in more seasonal habitats, sudden increase in peak flow seems to correlate with more specialized perforation plates in monocotyledons (Carlquist, 1975). The moist understory habitats of Lowiaceae are not aquatic habitats, but likely offer highly nearly continuous water availability. Thus, the fact that specialization level of vessels is only a little greater

than that of Acoraceae, Juncaginaceae, or Scheuchzeriaceae is in accord with ecology. These families are not closely related to Lowiaceae according to all phylogenetic systems of monocotyledons (Dahlgren et al., 1985; Takhtajan, 1987; Thorne, 1992; Duval et al., 1993).

Tomlinson (1969) stressed that Lowiaceae is an isolated family, well separated from other Zingiberales. Thorne (1992), however, placed it amidst other Zingiberales, although not in a basal position for the order. Dahlgren et al. (1985) did place Lowiaceae in a basal position within Zingiberales, and Takhtajan (1987) placed only Heliconiaceae more basally than Lowiaceae in the order. In the cladogram of Duval et al. (1993), which is based on *rbcl* sequence data, *Orchidantha* occupies a terminal or near-terminal position in the Zingiberales clade. Further investigations based on molecular studies (e.g., Kress, 1995; Stevenson & Loconte, 1995) and on tracheary elements of Zingiberales are producing a synthesis among various kinds of data.

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