Origin and nature of vessels in Monocotyledons. 7. Philydraceae and Haemodoraceae

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SCHNEIDER, E. L. AND S. CARLQUIST (Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105). Origin and nature of vessels in monocotyledons. 7. Philydraceae and Haemodoraceae. J. Torrey Bot. Soc. 132: 377–383. 2005.—SEM studies of macerated stems and roots showed that long scalariform perforation plates are present in roots and probably also stems of *Philydrum* (Philydraceae). In Haemodoraceae, clearly recognizable vessel elements are present in roots; perforation plates range from scalariform to simple. In stems of Haemodoraceae, however, less clearly recognizable vessel elements are present: the presence of thread-like pit membrane remnants is one criterion that argues for vessel presence. Such tracheary elements can be considered transitional between tracheids and vessel elements. End walls of transitional tracheary elements may have narrower bars between perforations, less prominent borders, and pit membrane remnants rather than non-porose pit membranes. However, only one or two of these three character expressions may be present, suggesting that clear definitions of vessel elements and tracheids may not be possible. Haemodoraceae show a marked difference, or disjunction, in morphology between vessel elements in roots and the vessel elements transitional to tracheids of stems. The physiological and evolutionary correlations of this morphological disjunction may be related to seasonality of water availability.

Key words: Haemodoraceae, Philydraceae, tracheids, vessel elements, xylem evolution

Philydraceae and Haemodoraceae have long been considered closely related to each other, an idea confirmed in recent DNA-based phylogenies (Chase 2004, Davis et al. 2004). These two families are now considered to form, along with Commelinaceae, Hanguanaceae, and Pontederiaceae, an order, Haemodorales (APG II 2003 Chase 2004, Davis et al. 2004). The present composition of this order, as noted by Chase (2004), results from molecular studies; in earlier phylogenies, these families were placed in several orders. Nomenclature follows MacFarlane et al. (1987), Simpson (1998), and Goldblatt and Manning (2000).

Philydraceae and Haemodoraceae are of special interest with respect to xylem histology because Cheadle (1968) claimed that they had clearly defined vessels in roots, but no vessels (or questionable ones in *Anigozanthos* of the Haemodoraceae) and thus only tracheids in stems. Such a mode of occurrence of tracheary elements offers the possibility of finding tracheary elements transitional between tracheids and vessel elements ("vessel-tracheids" of Fahn 1954). Such elements have been reported in the monocotyledon families Acoraceae (Carlquist and Schneider 1997) and Hanguanaceae (Schneider and Carlquist 2005). Such transitional tracheary elements are important in showing the phylogenetic origin of vessels in monocotyledons. Study of xylem by means of scanning electron microscopy (SEM) clarifies the nature of transitional tracheary elements, and thus illuminates the precise structural and ultrastructural nature of this transition. Studies by means of light microscopy can show only part of the nature of transitional tracheary elements, as is evident from Cheadle's (1968) notation of "questionable perforations" in stem tracheary elements of *Anigozanthos rufa* Labill.

Our sampling of Haemodoraceae and Philydraceae is not as large as that of Cheadle (1968). Cheadle studied the tracheary elements of 22 Haemodoraceae and three Philydraceae. Simpson and Dickison (1981) studied the tracheary elements of *Lachnanthes caroliniana* and report vessels with simple perforation plates in roots, vessels with scalariform perforation plates in rhizomes, and tracheids in leaves. We believe that the nature of tracheary elements in these Haemodoraceae and Philydraceae can be established on the basis of the material we have examined. Hopefully, our results offer a basis for further examination of transitional tracheary elements in a range of monocotyledons. The families we have studied to date (Carlquist and Schneider 1997, 1998a, 1998b; Schneider and Carlquist 1997, 1998, 2005) have been selected

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because they represent lineages in which transitional tracheary elements seemed likely to occur. Families in which vessel elements are clearly different from tracheids have not been included in this series of papers.

Materials and Methods. Roots and underground stems of living specimens of *Philydrum lanuginosum* Banks & Solander ex Gaertn., *Anigozanthos flavidus* DC. ex Réd., and *Wachendorfia thyrsiflora* Burm. were collected from plants under cultivation in Santa Barbara. Materials were fixed in 70% aqueous ethanol and then macerated with Jeffrey's Fluid (Johansen 1940). Macerations were spread onto aluminum stubs bearing electroconductive pads, dried in air, sputter coated with gold, and examined with a Hitachi S2600N SEM using an accelerating voltage of 25 kv. Care was taken to minimize exposure of delicate pit membranes to the electron beam, as such exposure at high power results in perceptible shrinkage and destruction of pit membranes.

Our criteria for recognizing perforation plates are as follows. Perforation plates are end walls distinguishable from lateral walls by one or more of these features: absence of pit membranes or presence of them as pit membrane remnants only; bars narrower between perforations than corresponding secondary wall portions of lateral wall pitting; and transitions between lateral wall pitting and perforation plates visible as porose thin pit membranes; or pit borders narrower in perforation plates than on lateral wall pitting.

Results. *Philydrum lanuginosum (Fig. 1–5).* Roots (Fig. 1–2) have scalariform perforation plates with numerous bars in metaxylem vessel elements (Fig. 1). These were identified not only because of being on end walls of tracheary elements, but also by virtue of having slender bars and no obvious pit membrane remnants in perforations. A curious protoxylem tracheary element, representing a cell with transitions between annular and helical thickenings and with conspicuous circular openings in primary wall areas, was observed (Fig. 2). We cannot present this with certainty as a vessel element, if only because so few protoxylem vessel elements have been identified and illustrated in monocotyledons, and thus available comparisons are few.

In stems of *P. lanuginosum*, a few tracheary element facets referable to the concept of perforation plates were observed (Fig. 3–5). The end wall facet shown (Fig. 3) appeals to us as a probable perforation plate because of its wide scalariform perforation plates, slender bars (often forked), and absence of pit membranes. To be sure, absence of pit membranes can occur because of handling of materials. Consequently, in attempting to identify perforation plates in stems, we sought features relating to pit membrane remnants. In Fig. 4, a portion of a perforation plate shows threads and porose pit membrane fragments in what may be perforations; the presumptive lateral wall (Fig. 4, left) possesses intact pit membranes. Pit membranes containing pores or holes of various sizes (Fig. 5) were observed near the end of a presumptive perforation plate. The delicate pit membranes illustrated in Fig. 5 are probably thinner than pit membranes of typical lateral wall pits, and thus can be interpreted as pits transitional to a perforation.

Anigozanthos flavidus (Fig. 6–9). Vessel elements are easily identified in the root (Fig. 6–8). Scalariform perforation plates may be seen in narrower (likely early metaxylem) vessel elements. (Fig. 6–7). Scalariform perforation plates, whether longer (Fig. 6) or shorter (Fig. 7), appeared sunken (collapsed inward toward the lumen) in our preparations, perhaps because the bars are so slender that they yield to the tension involved in drying. The difference between perforation plates and lateral wall pitting is readily apparent in these elements (Fig. 6–7). Vessel elements with simple perforation plates (Fig. 8) were somewhat more common than those with scalariform ones. Simple perforation plates are readily identifiable by their circular or oval outlines, their smooth edges, and their obvious contrast with lateral wall pitting (Fig. 8).

In stems, no clearly identifiable perforation plates were observed on tracheary elements. On end walls, a few adjacent pits were observed to contain threadlike pit membranes (Fig. 9) rather than laminar pit membranes. However, such pits are associated with thick intervening bars and have prominent borders (Fig. 9), features usually associated with lateral wall pitting.

Wachendorfia thyrsiflora (Fig. 10–13). In the roots of *W. thyrsiflora*, perforation plates appeared to be simple (Fig. 10–11). However, close examination of some perforation plates revealed probable bars at the end of the perforation plate near the cell tip (Fig. 10), and thus one might designate a few plates as scalariform, although not in the ordinary sense. Vessel ele-
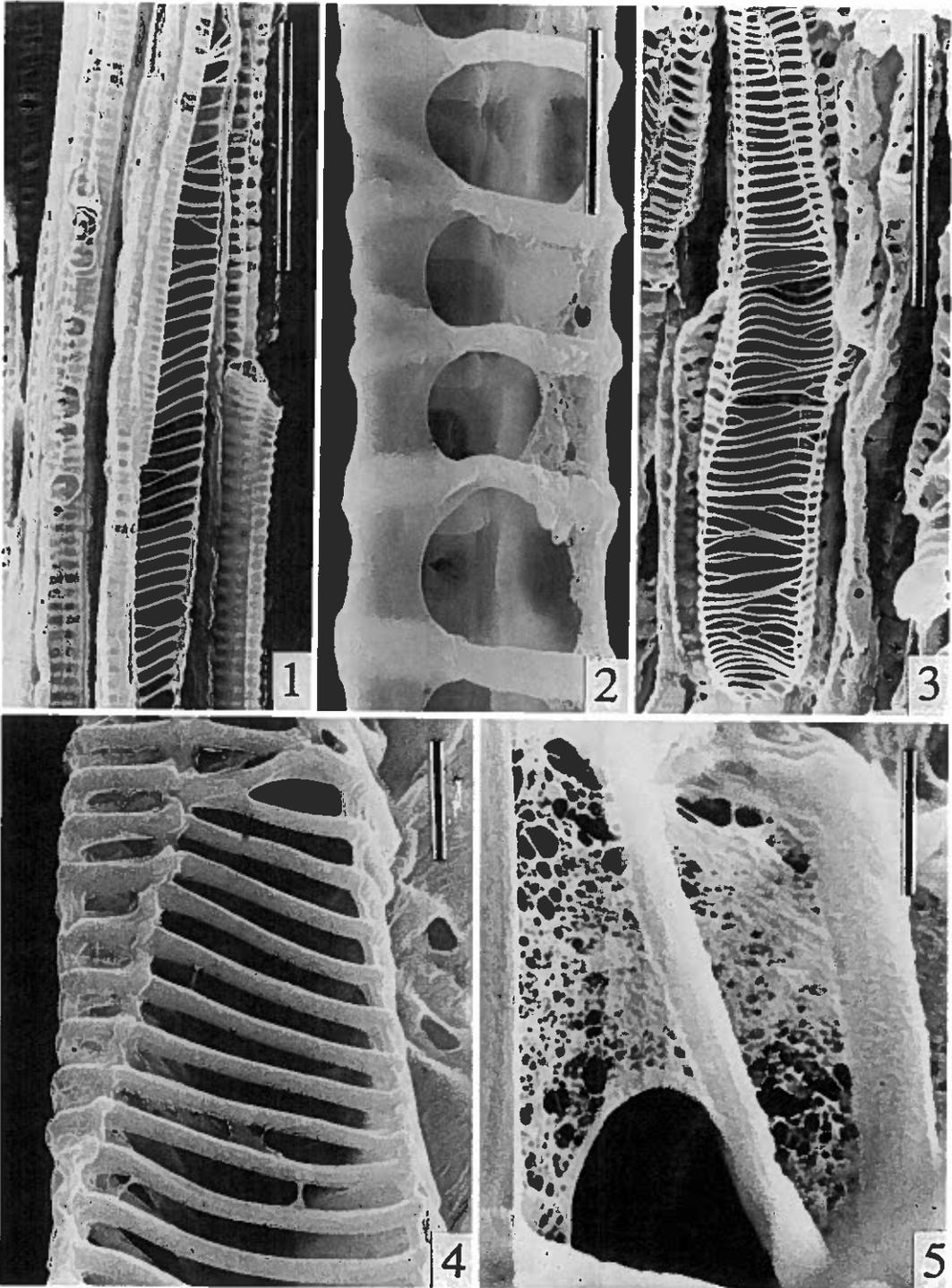
FIG. 1–5.   SEM photographs of tracheary elements in roots (Fig. 1–2) and stems (Fig. 3–5) of *Philydrum lanuginosum*. Fig. 1. Perforation plate of a metaxylem vessel. Fig. 2. Possible perforation plate of a protoxylem element. Fig. 3. Apparent perforation plate in a metaxylem element. Fig. 4. Portion of a facet of a tracheary element: threads and pit membrane portions suggesting the presence of perforations. Fig. 5. Thin pit membranes with pores and holes of various sizes, from an end-wall facet of a tracheary element. Fig. 1, 3, scale = 50 μm; Fig. 2, 4, scale = 5 μm; Fig. 5, scale = 1 μm.
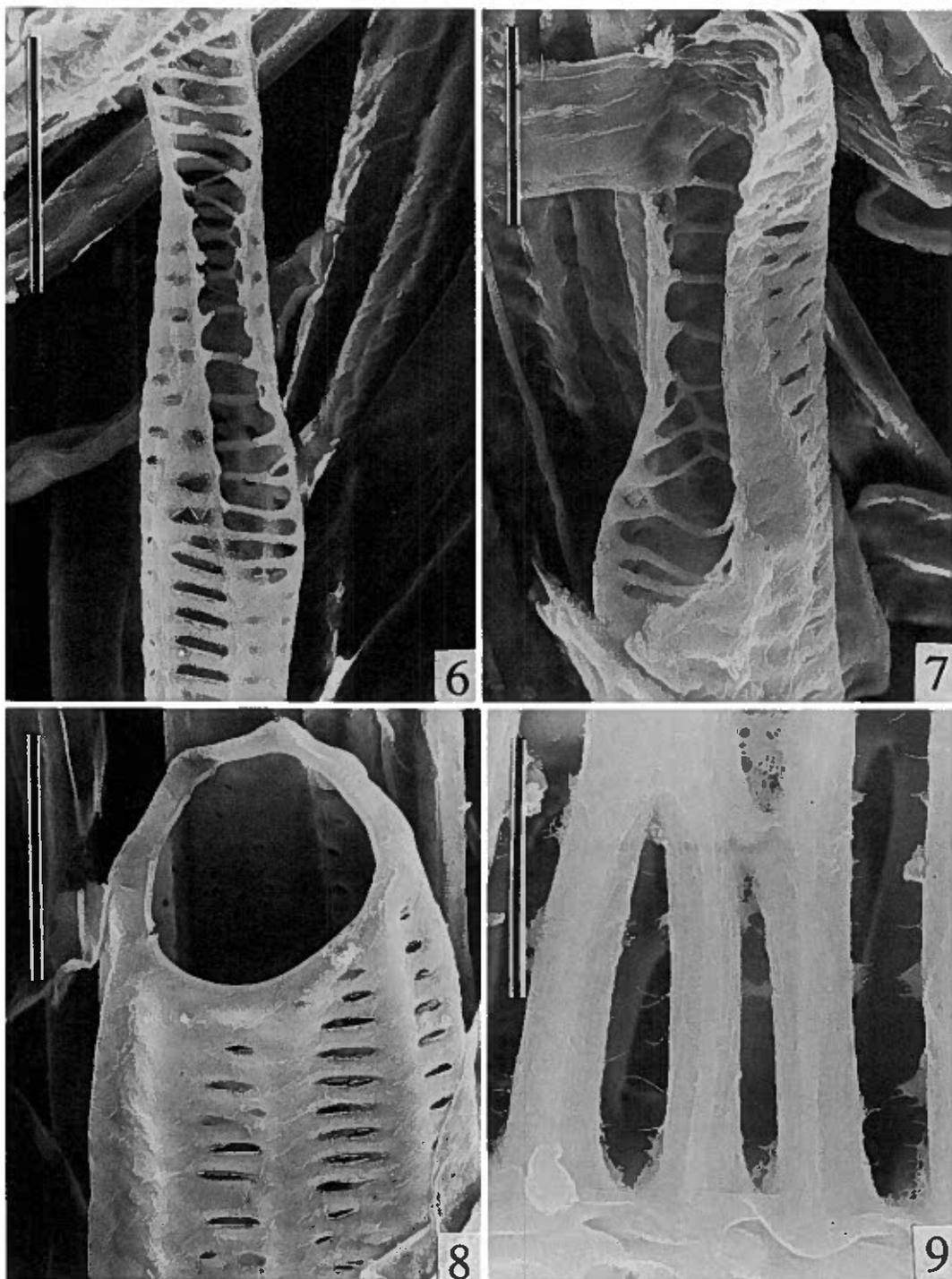
FIG. 6–9.　SEM photographs of tracheary elements in roots (Fig. 6–8) and stems (Fig. 9). of *Anigozanthos flavidus*. Fig. 6. Long scalariform perforation plate of an early metaxylem vessel. Fig. 7. Moderately long scalariform perforation plate of an early metaxylem vessel. Fig. 8. Simple perforation plate of a late metaxylem vessel. Fig. 9. Pits with threadlike pit membrane remnants from a tracheary element (tracheary element oriented transversely in this image). Fig. 6, scale = 50 μm; Fig. 7–8, scale = 20 μm; Fig. 9, scale = 5 μm.
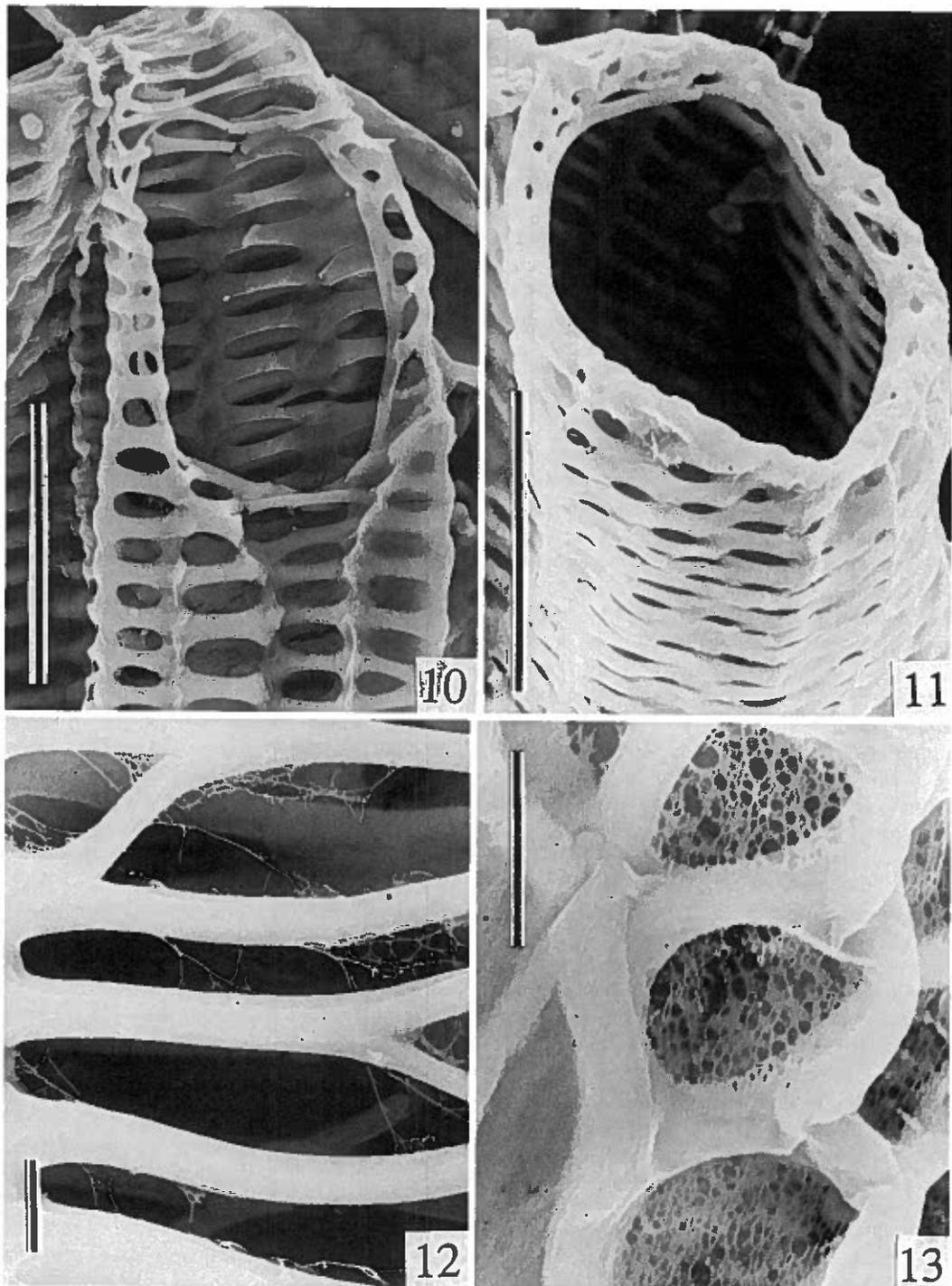
FIG. 10–13.   SEM photographs of tracheary elements of roots (Fig. 10–11) and stems (Fig. 12–13) of *Wach-endorfia thyrsiflora*. Fig. 10. Vessel element with scalariform lateral wall pitting; the perforation plate appears nearly simple, but has several bars at top. Fig. 11. Vessel element with a simple perforation plate and alternate lateral wall pitting. Fig. 12. Portion of a tracheary element facet with threadlike pit membrane remnants and vestigial borders on bars. Fig. 12. Tracheary element with non-porose pit membranes (left) and porose pit membranes (center, right). Fig. 10–11, scale = 20 μm; Fig. 12–13, scale = 5 μm.

ments have either scalariform (Fig. 10) or alternate (Fig. 11) pitting.

In stems, clearly defined vessel elements were not present. However, some end walls appear similar to perforation plates (Fig. 12). Threadlike pit membranes and relatively slender bars suggest that some elements have perforation plates, at least on the basis of these two criteria. Lateral walls of stem vessel elements (Fig. 13) contain both intact nonporose pit membranes (left) and porose pit membranes (center, right); the latter may be transitional to the kind of facet shown in Fig. 12).

Discussion and Conclusions. Cheadle (1968) found vessel elements with long scalariform perforation plates in roots of *Philydrum lanuginosum*, but did not find vessel elements in stems of that species. We confirm the observation of root vessels, but in addition, we located some vessels in stems of *P. lanuginosum* that are similar to those of the root. These stem vessels may not be frequent, however, and the possibility exists that tracheids as well as tracheidlike vessel elements are present in the stems of *Philydrum*.

In Haemodoraceae, Cheadle (1968) reported simple perforation plates in roots, except for *Anigozanthos manglesii* D. Don, *Dilatris pillansii* W. F. Barker, and *Tribonanthes australis* Endl.; in these species scalariform perforation plates were reported in roots. We can add *Anigozanthos flavidus* to this list. Cheadle (1968) illustrated a root perforation plate in *Haemodorum austroqueenslandicum* Domin in which there is a single large opening, with several bars distally. We reported such a perforation in the root of *Wachendorfia thyrsiflora* (Fig. 10). With the exception of the species named above in this paragraph, all of the vessel elements thus far described in roots of Haemodoraceae have simple perforation plates. The situation with respect to perforation plates on tracheary elements of stems of Haemodoraceae is much less clear. Cheadle (1968) figured a long scalariform end wall for a tracheary element of *Anigozanthos rufus*, with stippling on the pits (perforations?) of the end wall to indicate his uncertainty. He also reports similar questionable vessel elements in stems of *Lachnanthes tinctoria* (F. Gmel.) Sprague [= *Lachnanthes caroliniana* (Lam.) Dandy] and *Xiphidium album* Lam. [= *Xiphidium caeruleum* Aubl.]. With regard to shoot tracheary elements of Haemodoraceae, Cheadle states that "end walls of tracheids in stems appear much like perforation plates and may in-

deed have perforated pits." We would tend to concur with that judgment, for the threadlike pit membranes we located on end-wall facets in stem tracheary elements of *Anigozanthus flavidus* and *Wachendorfia thyrsiflora* contain threadlike pit membranes not unlike those illustrated for the perforation plates of dicotyledons with highly primitive wood (Carlquist 1992). SEM study shows the intermediacy of such tracheary elements, which might be called transitional elements or "vessel-tracheids" in the sense of Fahn (1954).

The stem vessel elements of Haemodoraceae and Philydraceae are illustrative of the stages of origin of vessel elements from tracheids, as in the monocotyledon family Hanguanaceae (Schneider and Carlquist, 2005). Those who wish a simple definition of vessel elements, a precise line between the two types of tracheary elements, are thus left with only at best an arbitrary demarcation. Narrowing of bars, lessening of borders, and increasing porousness of pit membranes in perforation plates (as compared to these features in lateral wall pitting in any species with transitional tracheary elements) do not occur in sharply demarcated stages. One of these can occur without similar expressions in the other two features, as in Acoraceae and Araceae (Carlquist and Schneider 1997, 1998b; Schneider and Carlquist 1998).

Philydraceae are notable for the retention of notably primitive vessel elements in roots, according the criteria of Cheadle (1942, 1944), who claimed that the most specialized vessel elements in any given species of monocotyledon are to be expected in the roots, with progressively less specialized vessel elements in stems and leaves in that order. Our data support those concepts, and also the marked disjunction in Haemodoraceae between (mostly) specialized vessel elements in roots combined with highly primitive vessel elements—arguably tracheids—in stems. As in that instance, the physiological advantage of such a disjunction may lie in the ephemeral functional life-span of roots that conduct rapidly (in the moist part of a highly seasonal environment) combined with perennial stems that persist through dry seasons and conduct more slowly (Carlquist 1975). These ideas have been confirmed by the work of Ewers et al. (1992).

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