

PENTAPHRAGMA: A UNIQUE WOOD AND ITS SIGNIFICANCE

by

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SUMMARY

Qualitative and quantitative data are given for wood anatomy of three species of *Pentaphragma* (Pentaphragmataceae); the woods of the three species are very similar. *Pentaphragma* is rayless, but eventually develops rays in at least one of the species studied. This is interpreted as related to secondary woodiness or upright habit within a predominantly herbaceous phylad. The vessel elements of *Pentaphragma* have features universally interpreted as primitive in dicotyledons: scalariform perforation plates with numerous bars; pit membrane remnants in perforations; scalariform lateral wall pitting; the genus also has fiber-tracheids with prominently bordered pits. These character states accord with the basal position in Campanulales accorded Pentaphragmataceae by Cosner et al. (1992), and suggests that order may have begun with more numerous primitive features than generally recognized. The presence of occasional scalariform perforation plates, often aberrant, in secondary xylem of families of Asterales *sensu lato* – Campanulaceae, Pentaphragmataceae, Valerianaceae, and even Asteraceae (e. g., certain Lactuceae) – can be attributed to paedomorphosis, extending these plates into secondary xylem from primary xylem. Raylessness in *Pentaphragma* can be described in terms of secondary woodiness or paedomorphosis. The fact that fiber-tracheids are shorter than vessel elements in *Pentaphragma* is believed related to raylessness also, because some fiber-tracheids are produced from 'potential' ray areas.

Key words: Asterales, Campanulales, paedomorphosis, raylessness, wood evolution.

INTRODUCTION

Pentaphragma Wall. ex G. Don, sole genus of Pentaphragmataceae (perhaps 30 species: Airy Shaw 1954; Lammers 1992), consists of sparsely branched or unbranched herbs that reach about 0.5 m at most. As understory herbs of moist places, some species are characteristically near streams, although others are in cool moist montane forest habitats (Airy Shaw 1942, 1953, 1954) from Burma and tropical China through Malaya, Borneo, and Java, to New Guinea (Airy Shaw 1954; Lammers 1992; Thorne 1992). Although a few authors have claimed that some features of the genus do not

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accord with placement of the family in Campanulales (notably Airy Shaw 1942, 1954; Dunbar 1978), relationship with families of Campanulales (or Asterales *sensu lato*) has been stressed on the basis of embryology (Kapil & Vijayaraghavan 1962), and, more recently, molecular data (Cosner et al. 1992). Two other features are often cited as characteristic of Campanulales: presence of inulin and presence of laticifers. *Pentaphragma* was not included in the inulin survey of Thulin (1978). Laticifers are absent in *Pentaphragma* according to Metcalfe and Chalk (1950) and were not observed in cortex or secondary phloem of the liquid-preserved stems included in the present study. All major phylogenies (see summary in Cosner et al. 1992) place Pentaphragmataceae in Campanulales. These phylogenies also recognize Pentaphragmataceae as distinct from Campanulaceae, a treatment urged by Airy Shaw (1942).

The questions of interest with respect to wood anatomy do not, therefore, involve whether the family is within Campanulales. Where within Campanulales Pentaphragmataceae should be placed, however, does concern data from wood anatomy, however. In the cladogram of Cosner et al. (1992), Pentaphragmataceae occupy a near-basal position. Their data show that if one recognizes two orders, Campanulales (Campanulaceae, Cyphiaceae, Lobeliaceae, Stylidiaceae) and Asterales *sensu stricto* (Asteraceae, Calyceraceae, Goodeniaceae, and Menyanthaceae), Pentaphragmataceae are almost equidistant between the two orders. Their data show a slightly greater affinity to Asterales than to Campanulales. Olmstead et al. (1993), analyzing *rbcl* data similar to those used by Cosner et al. (1992), show not two clades, but one, which they term Asterales *sensu lato*; Campanulaceae and Lobeliaceae are basal in that clade (Pentaphragmataceae is not included in their study). If Pentaphragmataceae are close to Campanulaceae, they would be basal either to the Campanulales of Cosner et al. (1992) or to the Asterales *sensu lato* of Olmstead et al. (1993), and thus one would expect wood features primitive for the group or clade, however defined, in which they occur.

If wood of *Pentaphragma* is construed as primitive (i. e., having wood features primitive for Campanulales or Asterales *s. l.*), that is of considerable interest, because only a few herbaceous families of dicotyledons have wood that is primitive, as judged, for example, by characteristic presence of scalariform perforation plates with 10 or more bars. Pentaphragmataceae are one of these (Fig. 3, 5–8). The only others that would qualify are Paeoniaceae (Keefe & Moseley 1978), Sarraceniaceae (DeBuhr 1977; Carlquist 1992a), and Saururaceae (Carlquist et al. 1995). A few species of *Chloranthus* (Chloranthaceae) are herbaceous and qualify as having scalariform perforation plates (Carlquist 1992b). *Cornus canadensis* L. (Cornaceae), although somewhat woody at the base, might be added to the list.

There are species in Campanulales or Asterales *s. l.* that have scalariform perforation plates to some extent. Short scalariform perforation plates with few bars characteristically occur in some Campanulaceae (Shulkina & Zikov 1980), but very few such plates occur in Lobeliaceae (Carlquist 1969). Occasional perforation plates that can be termed aberrant or variant scalariform perforation plates may be found in species of these orders that predominantly have simple perforation plates, such as Asteraceae, notably the tribe Lactuceae (Carlquist 1960, 1983a) and Valerianaceae (Carlquist 1983b). Thus, the clade 'Asterales *s. l.*' has a scattering of variant scalariform perforation plates,

whereas Pentaphragmataceae and, to a lesser extent, Campanulaceae are the only elements in the clade in which scalariform perforation plates occur characteristically. This has implications with respect to the position of these two families within the clade.

Pentaphragma has the unusual combination of raylessness (Fig. 2, 9) and primitive vessels (Carlquist 1975). The significance of this is worthy of further examination; both qualitative and quantitative data have been employed here to understand this situation. The species selected seem likely to represent an appreciable portion of wood variation that may occur in the genus because of their diversity in habitat and geographical distribution. SEM studies of the vessels in *Pentaphragma* (Fig. 5–8) were undertaken as a way of better understanding the nature of perforations and lateral wall pitting of vessels.

MATERIALS AND METHODS

A sample of stem of *Pentaphragma decurrens* Airy Shaw, Sarawak Museum 5253 (UC) was derived from herbarium material, treated with 5% aqueous NaOH, and stored in 50% aqueous ethanol. The specimen of *P. sp.* was collected by Dr. Robert Gustafson along a stream in Kubah National Park, Sarawak, Malaysia, July 6, 1995, preserved in cognac and transferred to 50% aqueous ethanol. No herbarium specimen of this collection was prepared. The material of *P. horsfieldii* (Miq.) Airy Shaw, Carlquist 4421 (RSA), was collected in moist forest understory on Bukit Maxwell, Malaya, Malaysia, and preserved in 50% aqueous ethanol. Wood from near the bases of stems have been selected for study. Upper stems have less wood, and root wood is excessively sinuous. For paraffin sectioning, wood was softened with ethylene diamine and treated as described in Carlquist (1982), and sections were stained in a safranin-fast green combination. Sections of *P. sp.* for SEM studies were prepared on a sliding microtome, dried between glass slides, and sputter coated with gold. Macerations were prepared with Jeffrey's fluid and stained with safranin.

Vessels are measured as lumen diameter; diameter of vessels oval in transection were computed as averages between the widest and narrowest diameters. Numbers of vessels per group is a mean computed on the basis that a solitary vessel = 1, a pair of vessels in contact = 2, etc. Terminology of the IAWA Committee on Nomenclature (1964) has been followed. In the descriptions that follow, the Borneo species precede the Malayan species.

ANATOMICAL RESULTS

Pentaphragma decurrens, Sarawak Museum 5253 (UC) (Fig. 1–3) — Growth rings absent, although a shift in angle of cell deposition can be noted at the top of Figure 1 (there is no evidence that this shift corresponds with a seasonal event in this specimen). Vessels commonly solitary; mean number of vessels per group, 1.42. Mean number of vessels per mm², 57. Mean vessel diameter, 32 μ m. Mean vessel element length, 758 μ m. Vessels angular to somewhat rounded in transection. All vessels with scalariform perforation plates (Fig. 3); mean number of bars, 36.2. Lateral wall pitting scalariform. Mean vertical height of lateral wall pits about 5 μ m, apertures widely ellipti-

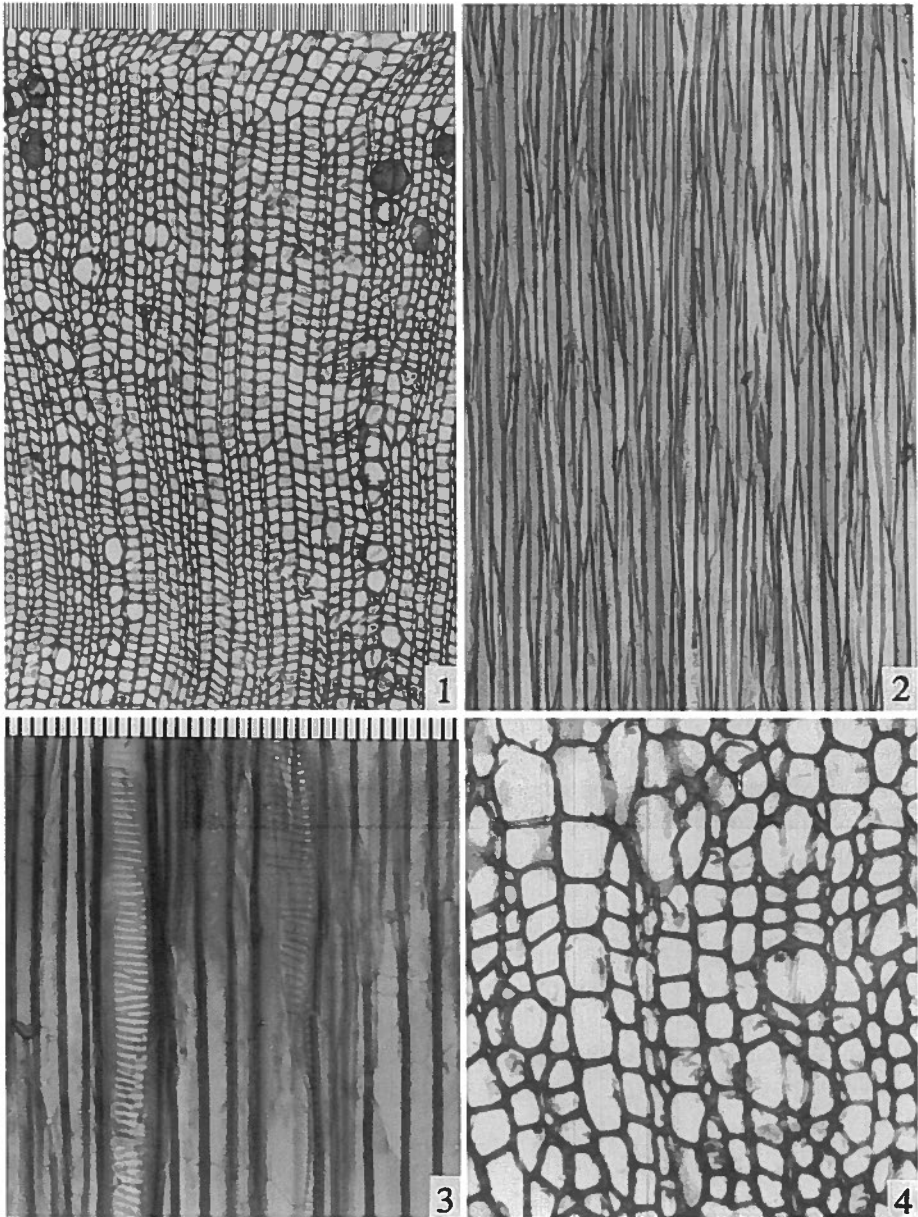


Fig. 1–4. Wood sections of *Pentaphragma*. — 1–3. *P. decurrens*. — 1: Transection; central third of wood in photo lacks vessels. — 2: Tangential section, showing rayless condition. — 3: Portion of radial section, showing a long scalariform perforation plate (left) and portion of another (right). — 4. *P. sp.*, transection; imperforate tracheary elements diverse in diameter. — Fig. 1 & 2, scale above Fig. 1 (divisions = 10 μm); Fig. 3 & 4, scale above Fig. 3 (divisions = 10 μm).

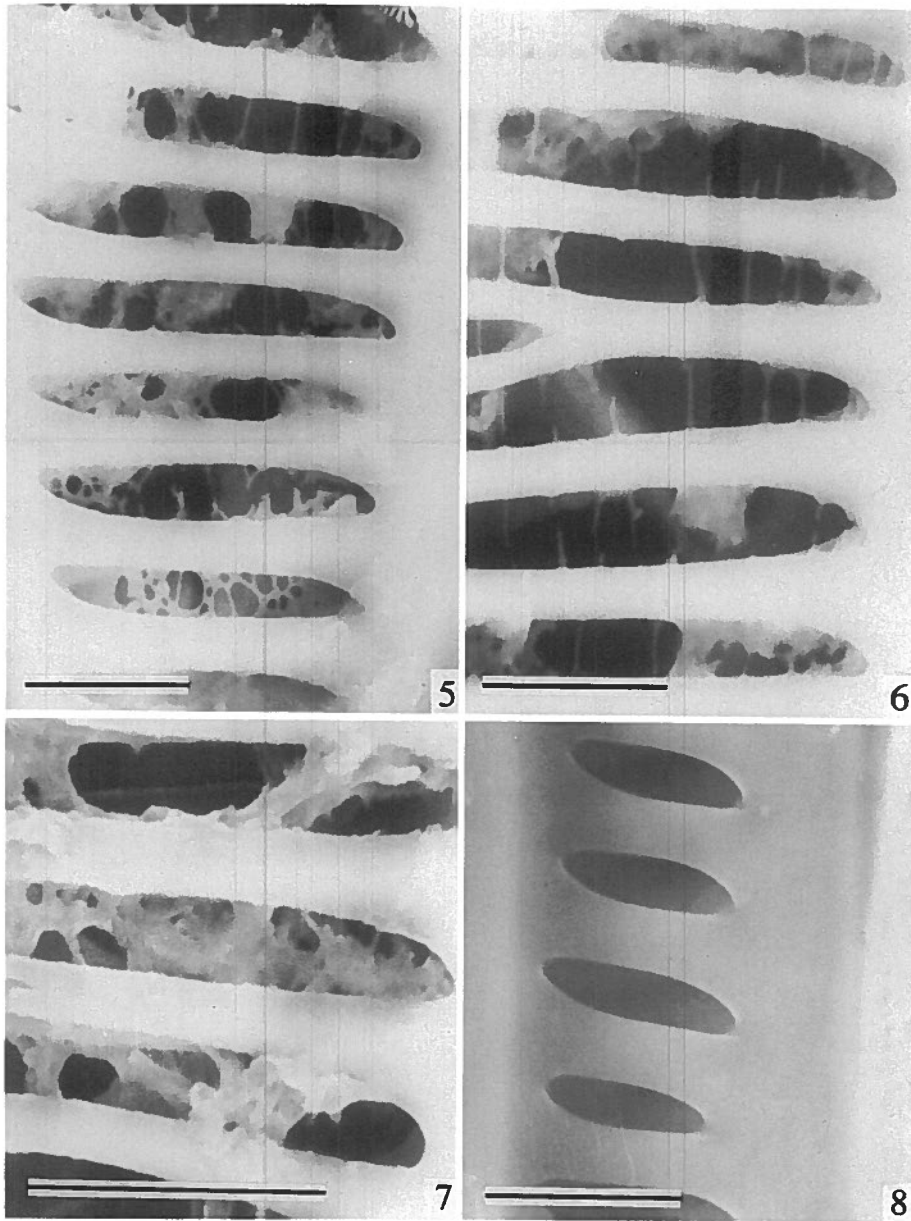


Fig. 5–8. SEM photographs of *Pentaphragma* sp. (Gustafson, 6 July 1995) wood to show details of vessels. — 5–7. Portions of perforation plates from radial sections. — 5: Plate with various degrees of pit membrane remnants. — 6: Plate with only threadlike remnants of pit membranes. — 7: Plate with extensive remnants of pit membranes. — 8: Lateral wall of vessel element from radial section. — Fig. 5–8, bars = 10 μ m.

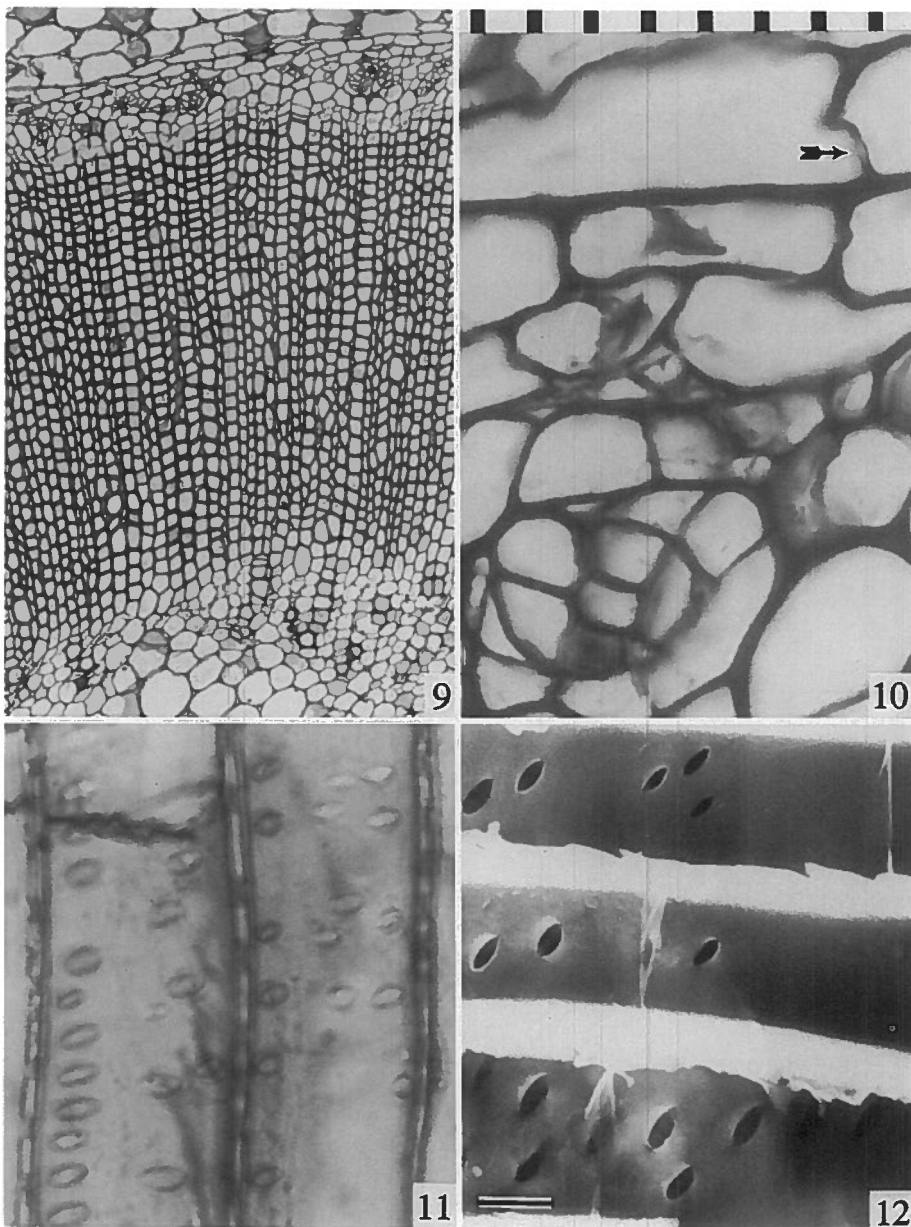


Fig. 9–12. Sections of *Pentaphragma* wood and stem tissues. — 9–11. *P. horsfieldii*. — 9: Trans-section of secondary xylem, pith below, secondary phloem and portion of cortex at top; vessels relatively sparse. — 10: Trans-section of secondary phloem with endodermis above (Casparian strip indicated by arrow). — 11: Portions of two septate fiber-tracheids (septum at upper left); pits are bordered. — 12. *P. sp.*, SEM photograph of three septate fibers from radial section of wood to show septa, wideness of pit apertures. — Fig. 9, scale above Fig. 1; Fig. 10 & 11, scale above Fig. 11 (divisions = 10 μ m); Fig. 12, bar = 10 μ m.

cal. Mean vessel wall thickness, 2.7 μm . All imperforate tracheary elements are fiber-tracheids, many of them septate one or more times; pits bordered, about 5 μm in diameter, with widely elliptical pits. Mean fiber-tracheid length, 603 μm . Mean fiber-tracheid wall thickness, 1.3 μm . Axial parenchyma absent. Rays absent. Wood nonstoried. Crystals and deposits absent.

Pentaphragma sp., Gustafson s. n., 6 July 1995 (Fig. 4–8, 12) — Growth rings absent (wood may differ somewhat in pattern in successive years, however). Vessels mostly solitary (Fig. 4); mean number of vessels per group, 1.32. Mean number of vessels per mm^2 , 30. Mean vessel diameter, 36 μm . Mean vessel element length, 641 μm . Vessels angular to rounded in transection (Fig. 4). All vessels with scalariform perforation plates (Fig. 5–7), mean number of bars per plate, 31.1. Perforations with remnants of pit membranes, rarely free from such remnants and sometimes with nearly intact membranes (Fig. 5–7). Lateral wall pitting scalariform (Fig. 8); pits about 5 μm in vertical diameter, pit apertures widely elliptical. Mean vessel wall thickness, 2.7 μm . All imperforate tracheary elements are fiber-tracheids, many septate one or more times, with bordered pits about 5 μm in diameter and widely elliptical apertures (Fig. 12). Mean fiber-tracheid length, 506 μm . Mean fiber-tracheid wall thickness, 2 μm (the apparently greater thickness of fiber walls in Figure 12 results from the fact that walls are sectioned obliquely). Axial parenchyma not observed. A few uniseriate and biseriate rays composed of upright cells present in outer portions of the secondary xylem, walls about as thick as those of libriform fibers and lignified. Wood nonstoried. Crystals and deposits absent.

Pentaphragma horsfieldii, Carlquist 4421 (Fig. 9–11) — Growth rings absent (Fig. 9). Vessels commonly solitary or in pairs (Fig. 9), mean number of vessels per group, 1.80. Mean number of vessels per mm^2 , 72. Mean vessel diameter, 31 μm . Mean vessel element length, 867 μm . Vessels angular to somewhat rounded in transection (Fig. 9). All vessels with scalariform perforation plates; mean number of bars per perforation plate, 46.3. Lateral wall pitting of vessels scalariform, mean vertical height of pits about 5 μm , pit apertures widely elliptical. Mean wall thickness of vessels, 2.5 μm . All imperforate tracheary elements are fiber-tracheids, most septate one or more times (Fig. 11), pits bordered, about 5 μm in diameter, with widely elliptical pit apertures (Fig. 11). Mean fiber-tracheid length, 677 μm . Mean fiber-tracheid wall thickness, 2.4 μm . Axial parenchyma not observed. Rays absent in the stems studied. Wood nonstoried. Crystals and deposits absent.

The material of *P. horsfieldii* was suitable for showing several histological details of the stem in addition to secondary xylem. In Figure 10, one can see an endodermal cell with the Casparian strip indicated. The secondary phloem in *Pentaphragma* is noteworthy in that, although phloem parenchyma forms a continuous cylinder around the stem, sieve tube elements and companion cells are arranged in strands which are identifiable because of the narrow diameter of their component cells (Fig. 9). One such strand is shown in Figure 10 (bottom). The sieve-tube elements and companion cells are narrow and almost alike in diameter. The parenchyma cells are much wider.

DISCUSSION AND CONCLUSIONS

The wood of *Pentaphragma* is unique among Campanulales (either as included within Asterales *s.l.* or considered separately) in that it has vessel features judged to be highly primitive according to the criteria of Frost (1930) and Carlquist (1992a) – scalariform perforation plates with numerous bars, remnants of pit membranes in perforations, and scalariform lateral wall pitting. The fiber-tracheids are primitive in that the pits have borders, a fact noteworthy in that septate imperforate tracheary elements relatively infrequently have borders (Carlquist 1988). However, these primitive features are combined with raylessness, a feature that has been regarded as a specialization (Barghoorn 1941). Raylessness may not be so much a specialization as an insertion of paedomorphosis into the developmental pattern of a wood (Carlquist 1962, 1988). The wood of *Pentaphragma* sp. is not entirely rayless: it eventually develops rays, just as do some woods in other families (Barghoorn 1941; Carlquist 1970; Carlquist & Hoekman 1986). Raylessness appears associated with secondary woodiness (Carlquist 1970) and certainly occurs in groups that as a whole can be characterized as herbaceous, such as Plantaginaceae or Polemoniaceae. Therefore, *Pentaphragma* could be a basal element in Campanulales. This would mean that herbaceousness is primitive in Campanulales, a conclusion in line with data provided for Lobeliaceae (Carlquist 1969) and Campanulaceae (Shulkina & Zikov 1980), both of which families are characterized by paedomorphic wood features indicative of secondary woodiness, such as preponderance of upright wood cells.

Campanulaceae are not rayless, but they do possess, to various degrees, scalariform perforation plates (Shulkina & Zikov 1980). The occurrence of scalariform perforation plates is more common in primary xylem and earlier-formed secondary xylem, suggesting paedomorphosis, in Asteraceae, Campanulaceae, and Valerianaceae (Carlquist 1960, 1983a, 1983b; Shulkina & Zikov 1980). This circumstance suggests that increase in woodiness is a specialization, or secondarily acquired feature, in the Campanulales (or Asterales *s.l.*). The data also suggest that groups basal within Asterales *s.l.* retain more primitive features than one might have guessed from the terminal position often accorded to families such as Asteraceae in most phylogenies of dicotyledons constructed before the availability of molecular data.

The perforation plates of *Pentaphragma* are primitive not merely by virtue of having numerous bars, but also the retention of pit membrane remnants in the perforations (Fig. 5–7). Presence of membrane remnants has been considered a primitive expression in vessel elements of dicotyledons at large (Carlquist 1992a), and there seems no reason why Pentaphragmataceae should be considered an exception.

Tracheids with clearly bordered pits are another primitive feature of *Pentaphragma*, as noted above: relatively few septate fibers in dicotyledons at large retain borders on pits to any appreciable degree, leading one to the conclusion that selective value for bordered pits decreases markedly when imperforate tracheary elements have indefinite longevity and thus are unlikely to function in water-conduction to any appreciable extent (Carlquist 1988). Therefore, the bordered pits of *Pentaphragma* septate fibers are all the more remarkable. The wide apertures on these bordered pits, like the wide

apertures on lateral wall pitting of *Pentaphragma* vessels, are indicative of pedomorphosis (Carlquist 1962).

The occurrence of a stem endodermis in *Pentaphragma* proves to be of systematic significance. Stem endodermis occurs not merely in Pentaphragmataceae, but in Asteraceae, Campanulaceae, Dipsacaceae, and Valerianaceae (Metcalf & Chalk 1950). This distribution suggests that stem endodermis may be primitive in Campanulales or Asterales *s. l.*

One feature worthy of mention is the fact that imperforate tracheary elements are shorter than the vessel elements they accompany. This condition would not be expected in a typically woody plant, in which vessel elements show little elongation compared with the fusiform cambial initials from which they were derived, whereas imperforate tracheary elements are longer because they experience considerable intrusive growth. The comparative shortness of imperforate tracheary elements of *Pentaphragma* could be explained by the fact that some of the fiber-tracheids are derived from areas of the cambium that would correspond to ray initials (e. g., note absence of vessels in the central part of Figure 1, indicating that fiber-tracheids in the central third of that photograph would correspond to a potential ray area). Interestingly, bordered pits of the imperforate tracheary elements in *Pentaphragma* that can be said to be derived from potential ray areas are like the bordered pits of the septate fibers derived from the same cambial zones from which vessel elements are derived. One might expect simple pits commonly on ray cells, and therefore if imperforate tracheary elements were derived from a potential ray area, one might expect those elements to have simple pits. The fiber-tracheids derived from the 'potential ray areas' differ little from those associated with vessel elements; the latter fiber-tracheids tend to be somewhat longer and more frequently septate. Imperforate tracheary elements shorter than the vessel elements they accompany have been reported in a rayless species with a habit much like that of *Pentaphragma*, *Plantago princeps* Cham. (Carlquist 1970), although this condition is not true of other species of *Plantago* (Carlquist 1970). A search of other rayless species, particularly those with elongate stems like those of *Pentaphragma*, might reveal other instances of imperforate tracheary elements shorter than the vessel elements they accompany.

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