

Wood anatomy of Penaeaceae (Myrtales): comparative, phylogenetic, and ecological implications

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Accepted for publication May 1977

Wood samples of stems, lignotubers, and roots of the majority of species of Penaeaceae were analyzed with respect to qualitative and quantitative features. Virtually no data have hitherto been presented on xylem features of this family, restricted to Cape Province, South Africa. Presence of vested pits in vessels, septate crystalliferous parenchyma in wood, intraxylary phloem, predominantly erect ray cells in the typically narrow, multiseriate rays and in the uniseriate rays, and amorphous deposits in ray cells place Penaeaceae securely in Myrtales and help to define that order. By comparison of ecological preferences of the species, as observed during field work, with quantitative analysis of conductive tissue, close correspondence of the wood structure to habit and habitat is demonstrated.

KEY WORDS:—Penaeaceae—wood—anatomy—phylogeny—ecology.

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INTRODUCTION

Wood anatomy of Penaeaceae has remained virtually undescribed, since the very scanty data offered by Metcalfe & Chalk (1950) are repeated from Solereder (1908), and no other accounts exist. The reason for this lack of information probably lies in the shrubby habit of most Penaeaceae. Most studies on wood anatomy of dicotyledons deal with arboreal species. Although some Penaeaceae, such as *Penaea cneorum*, can become small trees, most others, such as the abundant *P. mucronata*, are shrubs. Two species, *Brachysiphon rupestris* and *Sonderothamnus petraeus*, belong to a habitat form peculiarly characteristic of the Table Mountain Sandstone: diminutive subshrubs restricted to crevices in sandstone cliffs and outcroppings.

Another reason for the lack of studies on the wood anatomy of Penaeaceae is the fact that most species grow in highly restricted localities on the Table Mountain Sandstone and are endemic within Cape Province (Dahlgren, 1967a, 1971). The most wide-ranging genus, *Penaea*, extends eastward from the Cape Peninsula as far as the Port Elizabeth Division in Cape Province. None of the genera occurs in areas of South Africa other than Cape Province, and most species occur within a 200 km radius of Cape Town in the southwesternmost portion of Cape Province. During the field work of the senior author in Cape Province in 1973, the main focus was on species of Bruniaceae. Because Penaeaceae occur in many of the localities where Bruniaceae grow, the senior author found that a good collection of woods of Penaeaceae could easily be assembled. In addition, there is an inherent interest in wood anatomy of Penaeaceae with respect to confirming the systematic position of the family. The work of the senior author on woods of Onagraceae (Carlquist, 1975a) provided an impetus to see if Penaeaceae belong to Myrtales, as has been alleged by various authors.

The collection of woods of Penaeaceae covers all the genera except the monotypic *Glishrocolla*, and contains a majority of the species within the six other genera. All extremes in habits and habitats are represented. Thus, an unusually thorough selection of wood samples is available whereby to survey variation in wood anatomy in the family.

MATERIALS AND METHODS

Wood samples were all collected in the field. The importance of collection of wood samples by those who interpret wood anatomy is twofold.

Firstly, portions other than stems could be collected. There is relatively little information available on the wood anatomy of other plant parts. As shown in Table 1, lignotubers occur in some species of Penaeaceae, but not in others. Even within a single genus, lignotubers characterize some species (e.g., *Brachysiphon acutus*) but are absent in others (*B. fucatus*). Wood of roots was collected for a number of species, although not all (Table 1). In view of the potential differences in structure and function of wood of stems compared to that of lignotubers and roots (Carlquist, 1975b, 1976), information on these latter structures is necessary.

Secondly, if materials are collected in the field by the anatomist who is

studying the woods, correlations between ecology, habit, and anatomical data can be attempted.

For each species, samples of maximal diameter were collected. Portions of these samples have been retained in the wood collection at the Rancho Santa Ana Botanic Garden. Herbarium specimens documenting each collection were prepared. These vouchers are located in the Herbarium of the Rancho Santa Ana Botanic Garden; replicates have been distributed to other herbaria. Wood samples were dried. Sectioning was accomplished by means of the usual techniques; sections were stained with safranin. For purposes of demonstrating the presence of vestured pits, intense staining with safranin and counterstaining with fast green were employed. Macerations were prepared using Jeffrey's Fluid, followed by staining in safranin. Dimensions of vessel elements and tracheids were obtained, for each portion of each collection, by averaging 50 measurements. Averages for other quantitative features were derived from ten measurements. Data preparation work was done by the junior author.

Fortunately, the family Penaeaceae has been monographed in its entirety in a series of papers by Dahlgren (1967a, b, c, 1968, 1971). These comprehensive monographs are followed here and their contents are endorsed on the basis of observations by the senior author. Authors of names of taxa are cited in Table 1.

ANATOMICAL DESCRIPTIONS

Vessel elements

There is a marked range in Penaeaceae in means for vessel element length (377 to 1122 μm), vessel diameter (22 to 46 μm) and number of vessels per mm^2 of transection (56 to 340) (Table 1 and Plates 1 to 5). The last-named feature is mentioned in this context because there tends to be an inverse ratio between vessel diameter and number of vessels per mm^2 of transection (Carlquist, 1975b). This can be seen easily by comparing the transections (Plates 1A, 2A, 3A, C, 4A and 5A). Because these aspects seem to relate directly to the ecological nature of adaptation of woods in the family, they will be discussed in a later section.

Vessel elements are not notably thick-walled, and are relatively uniform throughout Penaeaceae. One can cite vessels angular in transection only in species with very narrow vessels, such as *Brachysiphon acutus* (Plate 1A) and *B. rupestris*. This is understandable, because narrow vessel elements, surrounded by only a few tracheids, would tend to be more angular than wide vessels surrounded by a large number of tracheids. Walls are uniformly thick, and not thickened at the angles, if angles occur.

Perforation plates are uniformly simple in the family. In *Penaea cneorum* subsp. *ruscifolia* (Carlquist 4539) occasional vessel elements were observed to have more than one perforation plate per end wall. Such instances are not to be considered multiperforate perforation plates, nor do other indications of vestigial scalariform or multiperforate perforation plates occur in Penaeaceae. The simple perforation plates in all Penaeaceae are bordered. Exceptionally wide borders were observed on perforation plates of vessel elements in the roots of *Saltera sarcocolla* (Carlquist 4500).

Table 1. Wood characteristics of Penaeaceae

Species	1. Collection number by S. Carlquist (RSA). 2. Portion of plant (S, stem; L, lignotuber; R, root; US, underground stem). 3. Mean number of vessels per mm ² as seen in transection. 4. Mean vessel diameter (μm). 5. Mean number of vessels per group. 6. Mean vessel element length (μm). 7. Mean tracheid length (μm). 8. Mean tracheid wall thickness (μm). 9. Mean multiseriate ray height (mm). 10. Mean uniseriate ray height (mm). 11. Ray histology (U, upright cells; S, square cells; P, procumbent cells as seen in radial section; the most abundant cell type or types are in upper case, infrequent occurrence indicated by lower case, and absence indicated by absence of letter). 12. Ratio of mean tracheid length to mean vessel-element length. 13. Ratio of mean vessel diameter to mean number of vessels per mm ² of transection. 14. Mean vessel-element length times mean vessel diameter divided by mean number of vessels per mm ² of transection.													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Brachysiphon acutus</i> (Thunb.) A. Juss.	4694	S	340	22	1.08	332	480	2.5	447	323	Usp	1.45	0.06	22
		L	154	32	1.16	308	377	3.1	1031	366	uSp	1.22	0.21	64
<i>B. fucatus</i> (L.) Gilg	4753	S	168	33	1.12	565	705	4.8	418	419	Usp	1.25	0.20	111
		S	190	38	1.24	508	694	4.0	634	466	Us	1.37	0.20	102
<i>B. rupestris</i> Sonder	5000	S	336	23	1.16	427	613	3.0	—	287	Us	1.44	0.07	29
		L	267	24	1.12	332	482	4.8	—	?	Us	1.45	0.09	30
<i>Endonema lateriflora</i> L.fil.) Gilg	4883	S	104	30	1.24	526	729	4.6	543	334	Usp	1.38	0.29	152
<i>E. retzioides</i> Sonder	4947	S	92	42	1.12	444	712	4.0	469	281	USp	1.59	0.46	203
		L	80	44	1.16	449	744	4.9	577	384	USp	1.66	0.55	247
<i>Penaea acutifolia</i> A. Juss.	4744	S	175	46	1.12	597	784	4.3	275	206	Us	1.31	0.26	157
		R				616	779					1.26		
<i>P. cneorum</i> Meerb. subsp. <i>cneorum</i>	4590	S	102	46	1.08	737	931	4.5	510	337	Usp	1.26	0.45	332
	4740	S	70	55	1.08	747	1004	6.4	420	246	UsP	1.34	0.79	587
<i>P. cneorum</i> subsp. <i>gigantea</i> R. Dahlgren	4737	S	80	45	1.08	491	636	3.9	—	487	Us	1.30	0.56	276
<i>P. cneorum</i> subsp. <i>ruscifolia</i> R. Dahlgren	4503	S	202	31	1.16	678	796	4.5	—	365	Us	1.17	0.15	104
	4539	S	79	45	1.12	483	643	4.3	622	213	UsP	1.33	0.57	275
<i>P. mucronata</i> L.	4975	S	146	44	1.12	458	601	4.4	—	285	Usp	1.31	0.30	138
<i>Saltera sarcocolla</i> (L.) Bullock	4500	S	74	35	1.08	885	1122	5.9	942	638	Usp	1.27	0.47	419
		S	77	33	1.08	899	1167	5.6	—	587	Us	1.30	0.43	385
		L	56	27	1.08	434	616	6.0	812	282	USP	1.42	0.47	209
		R	57	29	1.04	537	771	6.7	831	369	USP	1.44	0.51	273
	4575	S	106	37	1.12	562	760	4.6	569	406	Usp	1.35	0.35	196
		L	149	33	1.12	418	536	4.4	521	398	Usp	1.28	0.22	93
	4783	S	159	36	1.20	584	690	4.1	853	569	USP	1.18	0.23	132
		R	118	28	1.24	446	618	3.3	741	339	USP	1.39	0.24	106
<i>Sonderothamnus petraeus</i> (Barker) R. Dahlgren	4678	S	231	23	1.32	456	547	3.6	—	222	U	1.20	0.10	45
<i>Stylapteris ericoides</i> A. Juss. subsp. <i>ericoides</i>	4865	S	199	31	1.16	781	932	4.1	636	399	Usp	1.19	0.16	122
<i>S. fruticosus</i> (A. Juss.) R. Dahlgren	4600	S	220	27	1.04	515	643	3.0	791	348	Usp	1.25	0.12	63
		US	244	29	1.12	510	634	2.6	698	435	Usp	1.24	0.12	61

Lateral walls of vessel elements bear uniformly alternate pits where they face other vessels or tracheids (Plate 5C, D). The same is true for vessel-ray pitting, although occasional areas bear a few opposite pits in *Brachysiphon rupestris* (lignotuber), *Penaea cneorum* subsp. *cneorum* (Carlquist 4740, stem), *Saltera sarcocolla* (Carlquist 4500, root; Carlquist 4783, lignotuber and root) and *Stylapterus ericoides* subsp. *ericoides* (stem).

Pits on vessel walls are vested throughout the Penaeaceae. This vesturing is more conspicuous in some, such as *Brachysiphon acutus* (Plate 5C), less so in others, such as *Penaea cneorum* subsp. *cneorum* (Plate 5D). Deeply stained sections revealed small warts on the elliptical pit apertures in all species studied when examined at maximum magnifications. The vesturing is by no means as conspicuous as in some other myrtalean families, such as Onagraceae (Carlquist, 1975a). Light microscopy has revealed vested pits in the Oliniaceae (Mújica & Cutler, 1974), but SEM analysis as has been done by Butterfield & Meylan (1973) and Vliet (1975, 1976), should be applied when possible. Vessels are mostly solitary in Penaeaceae (Table 1 and Plates 1A, 2A, C, 3A, D, 4A and 5A). The degree of grouping does not increase with the number of vessels per mm² of transection (Table 1). A high proportion of solitary vessels characterizes the myrtalean families (Metcalf & Chalk, 1950), but a somewhat greater degree of grouping is found in some, such as Onagraceae (Carlquist, 1975a).

Tracheids

In Penaeaceae, pit apertures of imperforate elements are included within the outline of the border, and the imperforate elements can be said to be 'fully bordered' and therefore termed tracheids (Plate 4E). The only exception was found in *Endonema lateriflora*, where apertures are slightly longer than the diameter of the pit cavity, and imperforate elements would therefore qualify as fibre-tracheids.

Among myrtalean families, tracheids characterize Myrtaceae, Crypteroniaceae, and two subfamilies of Melastomaceae (Astronioideae and Memecyleae). Libriform fibres characterize Melastomataceae subfamily Melastomoideae, Combretaceae, Oliniaceae, Lythraceae, Punicaceae, Sonneratiaceae, and Onagraceae (Metcalf & Chalk, 1950; Mújica & Cutler, 1974; Vliet, 1975; Carlquist, 1975a). If the presence of borders on pits of imperforate elements is a more primitive expression than the absence of borders (Metcalf & Chalk, 1950; Carlquist, 1975b), Penaeaceae could be viewed as relatively primitive—conceding that wood of most members of the Myrtales (*Myrtus communis*, which has scalariform perforation plates on vessels would be an exception) is relatively specialized. The relatively long vessel elements of Penaeaceae would also fit this hypothesis; the vessel elements being, on average, much shorter in Onagraceae (Carlquist, 1975a). A similar sequence of vessel element lengths can be traced in the Asteraceae (Carlquist, 1966).

While longer than vessel elements they accompany in any given wood sample, tracheids are not substantially longer. The ratios of tracheid length to vessel element length for the Penaeaceae fall between 1.18 and 1.66 (Table 1). The average for the family as a whole is 1.29. This contrasts with the ratio 2.60 obtained for a sampling of dicotyledons with woods having simple perforation

plates and libriform fibres (Carlquist, 1975b). Despite the uniformly simple perforation plates of woods of Penaeaceae, this is a subsidiary indication for a moderate degree of specialization, if the theories (Carlquist, 1975b) of imperforate to vessel-element length ratios are correct. Ratios are notably higher in Onagraceae (Carlquist, 1975a), a family with libriform fibers rather than tracheids. The highest ratios in Penaeaceae occur in *Endonema*, where long wiry branches arising from a lignotuber may show correlation with greater strength of tracheids not only in their length, but in their wall thickness as well (Table 1; Plate 2A, B). Similarly, this habit occurs in *Saltera sarcocolla*, which also has relatively high ratios. The relatively long vessel elements and tracheids of *Penaea cneorum* (Table 1) may be related to the arboreal status of this species as well as to ecological factors, discussed later.

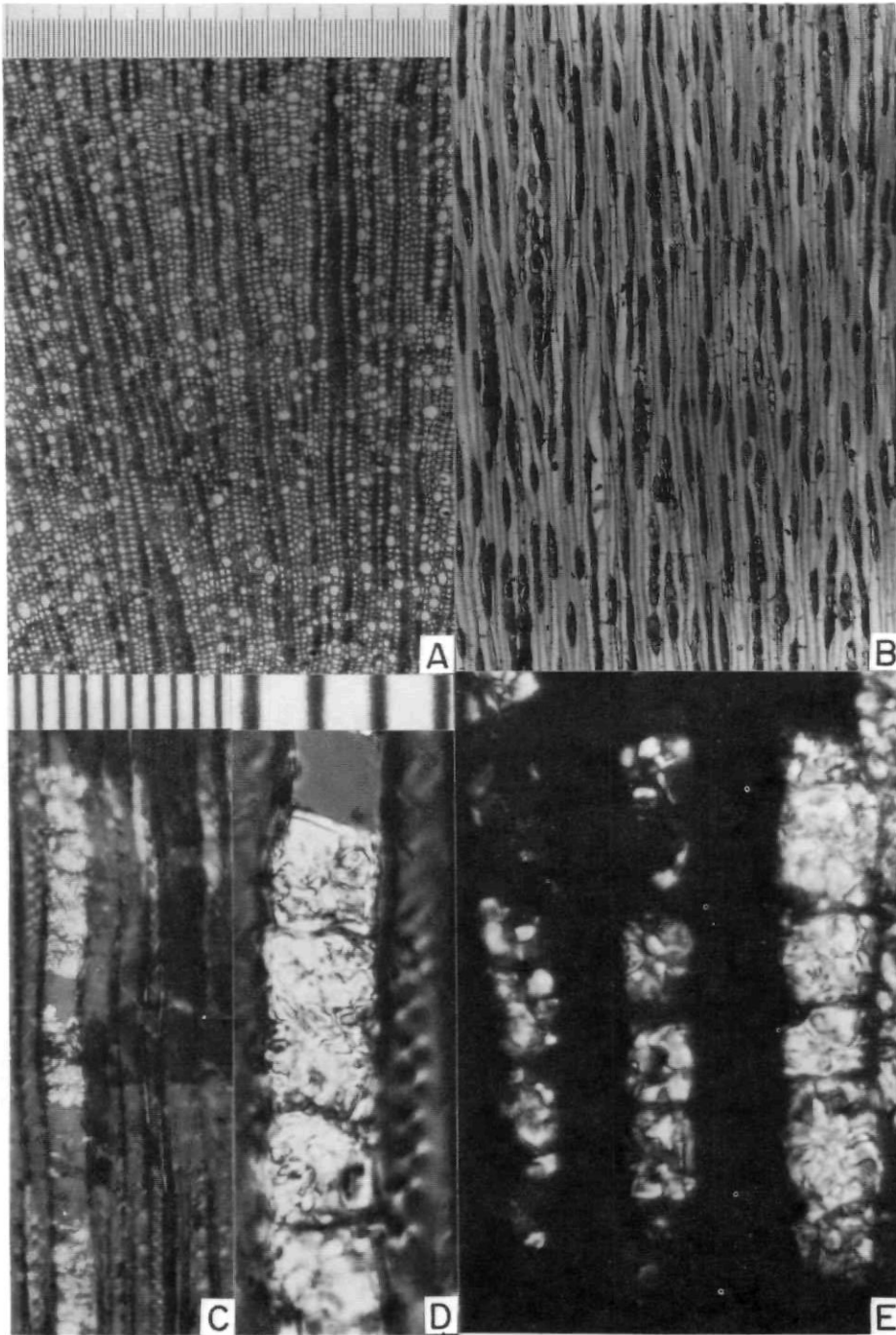
With respect to tracheid wall thickness, differences appear not only in data (Table 1), but in visual inspection of woods as well. The two *Stylapterus* species depicted in Plate 2 are pertinent in this regard. The thick-walled nature of tracheids in *Saltera sarcocolla* (Plate 4A, B) is easily visible. However, the tracheids of *Sonderothamnus petraeus* (Plate 5A, B) have thinner walls, but mean tracheid diameter is narrower, so that the lumina are, in fact, occluded. Thus, one must take into account diameter of the tracheids as well as their wall thickness in assessing mechanical strength.

Xylem rays

In Penaeaceae as a whole, uniseriate rays predominate over multiseriate rays, as can be seen in Plates 1B, 2B, D and 3B, E. Multiseriate rays can be said to be absent in some subspecies of *Penaea cneorum* (Table 1), *Sonderothamnus petraeus* (Plate 5B) and scarce or absent in stems of *Saltera sarcocolla* (Plate 4B). In stems, multiseriate rays are very rarely more than three cells in width, and biseriate rays are by far the most common of multiseriate rays. This accords of descriptions of rays in most myrtalean families (Metcalfe & Chalk, 1950; Mújica & Cutler, 1974; Carlquist, 1975a).

As shown in Table 1, there is a tendency for predominance of upright over procumbent cells in most Penaeaceae. However, procumbent cells do occur prominently in the multiseriate rays of the outer wood of stems of the small trees of *Penaea cneorum* and in the multiseriate rays of *Saltera sarcocolla*. In uniseriate rays, upright to square cells are found only. A predominance of upright cells in multiseriate and uniseriate rays, except for the outer wood of tree species, is characteristic of Myrtales (see discussion in Carlquist, 1975a; also Mújica & Cutler, 1974).

Plate 1. Sections of *Brachysiphon* stems. A-D. *B. acutus*, Carlquist 4594, sections of wood from stems. A. Transection, showing narrowness of vessels. B. Tangential section, showing abundance of uniseriate rays containing amorphous deposits. C. Radial section, showing a parenchyma strand with clustered crystals intact in most cells (left) and a portion of a ray (right), photographed with partially polarized light. D. Radial section, higher magnification, to show aggregation of crystals, under polarized light. E. *B. rupestris*, Carlquist 5000, radial section of bark to show clustered crystals in phloem parenchyma strands, photographed with polarized light. Magnifications indicated by photographs of stage micrometer enlarged at same scale as photomicrographs to which they relate. A, B, scale above A: finest divisions = 10 μ m. C, scale above C: divisions = 10 μ m. D, E, scale above D: divisions = 10 μ m.



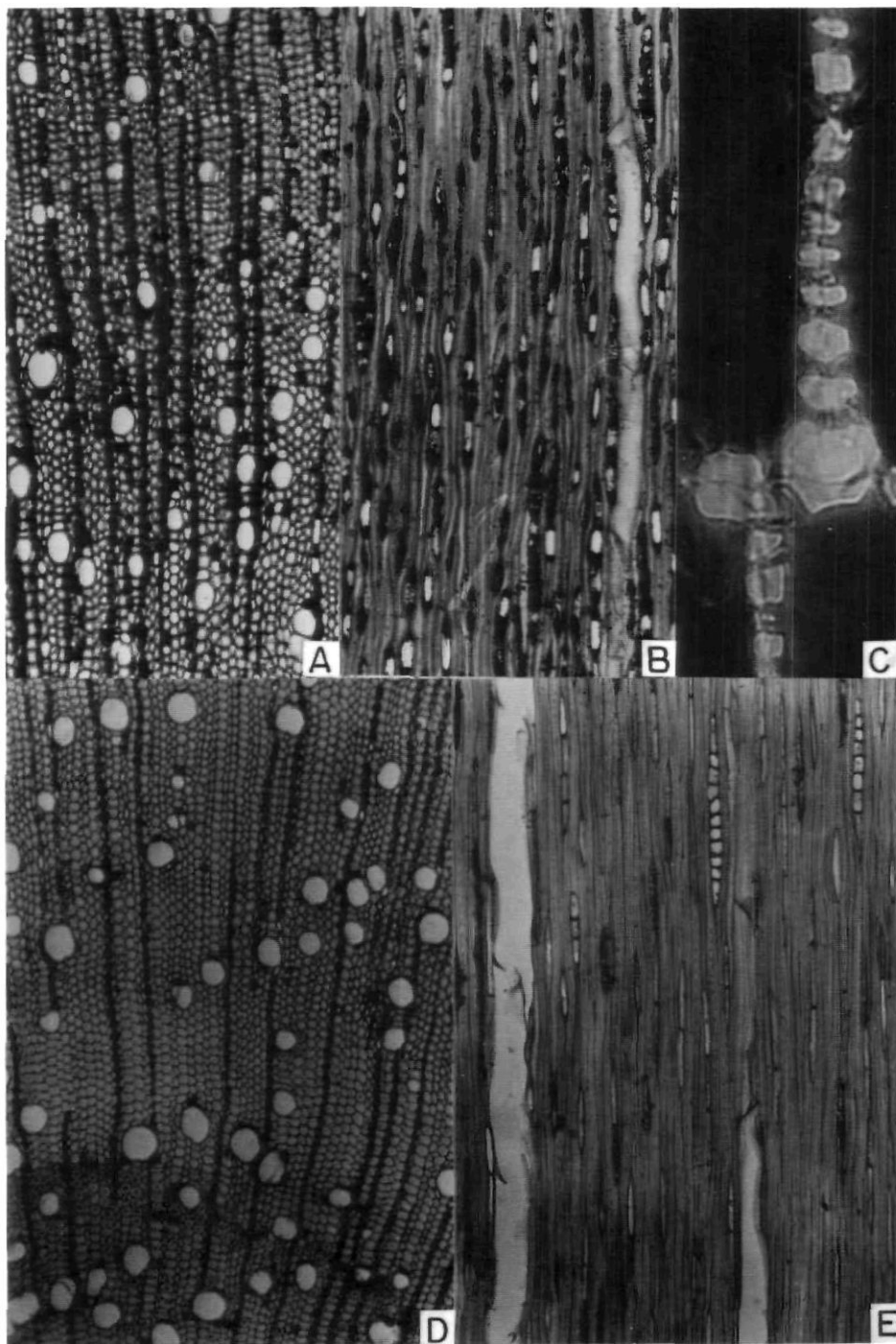


Plate 2. Stem wood sections of *Endonema* and *Penaea*. A-C. *Endonema retzioides*, Carlquist 4947. A. Transection, showing prominent amorphous deposits in rays and axial parenchyma. B. Tangential section; rays are abundant and large-celled. C. Portion of ray cell walls from radial section, showing thick secondary wall; some pits are slightly bordered. D-E. *Penaea cneorum* subsp. *cneorum*, Carlquist 4740. D. Transection, showing large vessels. E. Tangential section; note sparsity of rays. Magnification scale for A, B, D, E, above Plate 1A. Scale for C above Plate 1D.

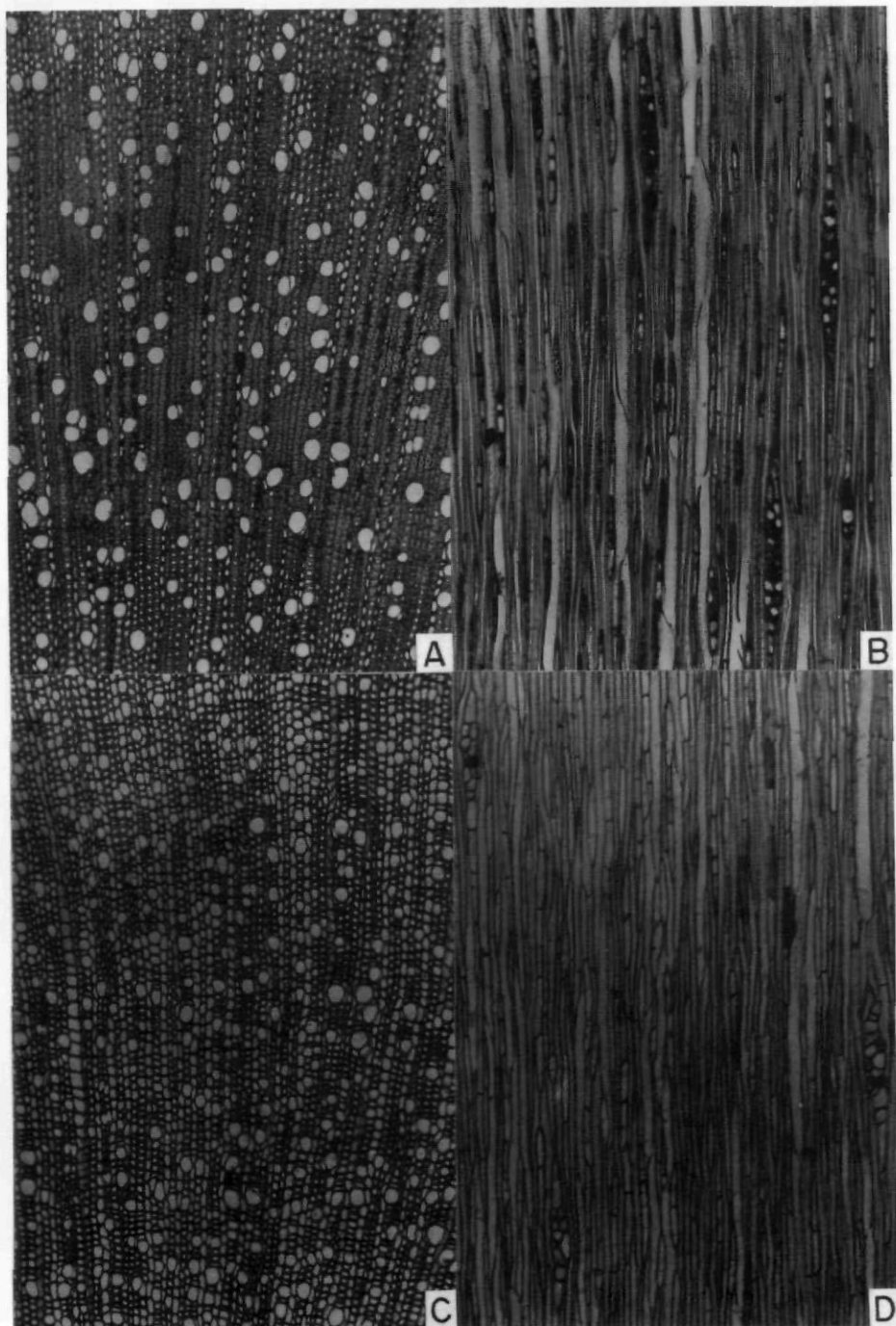


Plate 3. Stem wood structure of *Stylapterus*. A-B. *S. ericoides* subsp. *ericoides*, Carlquist 4865. A. Transection; tracheids are thick-walled. B. Tangential section; amorphous deposits prominent in rays. C-D. *S. fruticosus*, Carlquist 4600. C. Transection; vessels narrow, numerous. D. Tangential section; tracheids are thin-walled. Magnification scale for A-D above Plate 1A.

In lignotubers, multiseriate rays are more common, perhaps because of the persistence, during secondary growth, of unmodified primary rays, perhaps because these parenchyma zones provide centres for the initiation of buds when the above-ground stems are burnt—an explanation which seems justified for another South African genus, *Geissoloma* (Carlquist, 1976). A wide multiseriate ray (albeit poorly visible because polarized light was used in photographing it) is shown for a *Saltera sarcocolla* lignotuber in Plate 4D.

Ray cells in most Penaeaceae are moderately thick walled and lignified. Tangential walls tend to be thicker than radial walls. Notably thick tangential walls were observed in *Brachysiphon fucatus* and *Endonema retzioides* (Plate 3C). Notable thin ray cell walls characterize *Brachysiphon acutus* (Plate 2B), *Penaea cneorum* subsp. *cneorum* (Plate 3E), *Sonderothamnus petraeus* (Plate 5B) and *Stylapterus fruticulosus* (Plate 2D). Where ray cell walls are exceptionally thick, borders may be present on some pits (Plate 3C). Bordered pits on ray cells have been reported in another genus of Myrtales, *Metrosideros* (Sastrapadja & Lamoureux, 1969).

Axial parenchyma

Axial parenchyma is characteristically scanty and diffuse in distribution in Penaeaceae. A few parenchyma cells were observed to be aggregated in small groups in *Brachysiphon acutus* (stems), *Endonema retzioides* (lignotubers), and *Saltera sarcocolla* (lignotubers, Plate 4C). Diffuse distribution combined with some vasicentric parenchyma cells was observed in *Brachysiphon acutus* (lignotubers), *B. fucatus* (roots), *Endonema retzioides* (stem, Plate 3A), *Penaea cneorum* subsp. *cneorum* (stems, Plate 3D), *P. mucronata* (stems and lignotubers), *Saltera sarcocolla* (stems, Plate 4A), *Sonderothamnus petraeus* (stems, Plate 5A), and *Stylapterus fruticulosus* (Plate 3C). In some of these, axial parenchyma cells can readily be identified, because of their tendency, like that of ray cells, to accumulate the amorphous, dark-staining, gummy compounds.

Axial parenchyma strands in all species of Penaeaceae examined are composed of two to four, mostly three, cells. This does not apply to the parenchyma strands containing crystals, discussed below.

Growth rings

Growth rings are not marked in any of the Penaeaceae studied. This is not surprising in view of the highly mesic microclimates in which Penaeaceae typically grow, or, alternatively, the semi-succulence of lignotubers or underground stems in the family. Indistinct growth rings are illustrated here for *Stylapterus ericoides* subsp. *ericoides* (Plate 3A, near bottom) and *Penaea cneorum* subsp. *cneorum* (Plate 2D, near bottom). Such growth rings were also observed in *Brachysiphon rupestris* (stems), *Endonema lateriflora* (stems), *Penaea cneorum* subsp. *gigantea*, *P. cneorum* subsp. *ruscifolia* (stems), and *Saltera sarcocolla* (some stems, lignotubers, and roots). These growth rings take the form of slightly smaller vessels in latewood, larger vessels in earlywood. There does not appear to be an appreciable change in abundance of vessels in latewood compared to earlywood.

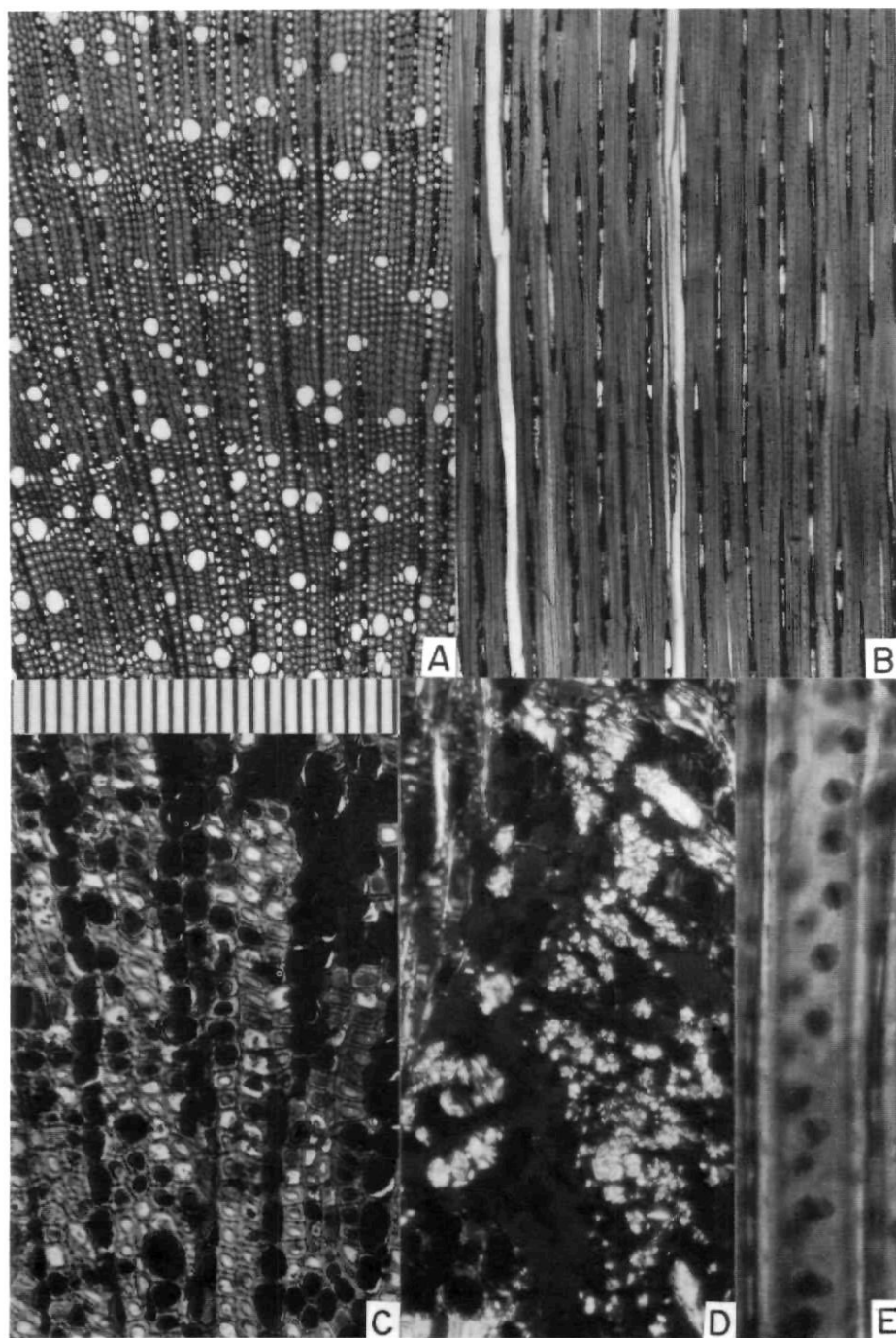


Plate 4. Wood sections of *Saltera sarcocolla*, Carlquist 4500. A. Stem wood transection; amorphous deposits in rays. B. Tangential section; fibres thick-walled. C. Transection of lignotuber wood; amorphous deposits abundant in rays and other cell types as well. D. Tangential section of lignotuber wood, showing large (probably primary) ray under polarized light. Most ray cells contain clustered crystals. E. Portion of tracheid from radial section, showing bordered pits. A, B, magnification scale above Plate 1A. C, D, scale above C. divisions = 10 μ m. E, scale above Plate 1D.

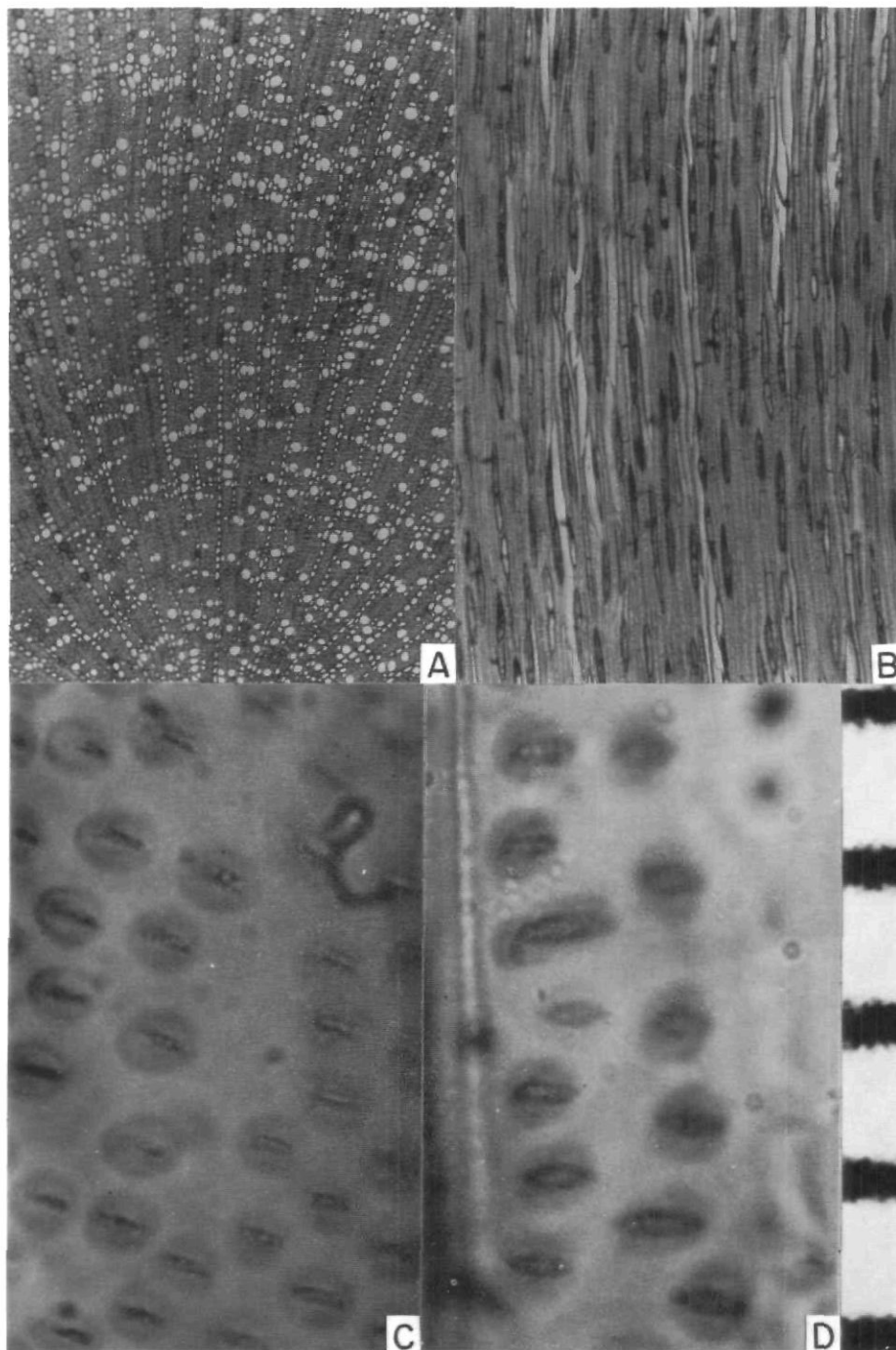


Plate 5. Stem wood sections of *Sonderothamnus*, *Brachysiphon*, and *Penaea*. A-B. *Sonderothamnus petraeus*, Carlquist 4678. A. Transection; vessels exceptionally narrow, numerous. B. Tangential section; rays numerous, tall. C. *Brachysiphon acutus*, Carlquist 469z. Portion of vessel wall from radial section, showing prominently vested pits. D. *Penaea cneorum* subsp. *cneorum*, Carlquist 4740. Portion of vessel wall from radial section, showing finely vested pits. Magnification scale for A, B, above Plate 1A. Scale for C, D, to right of D: divisions = 10 μ m.

Crystals

Only a few woods of Penaeaceae contain crystals, of which the most notable is that of *Brachysiphon acutus* (Plate 1C, D). A few axial parenchyma cells are sub-divided into a row of at least 10 cuboidal, crystal-bearing cells. These crystalliferous strands are appreciably wider than tracheids (Plate 1D), although of about the same length as tracheids. The crystals in each cell are numerous. Whether these form true druses or whether the crystals are dense could not be ascertained unequivocally. Cells in crystalliferous strands that appear to lack crystals (Plate 1C, D) are the result of loss of crystals during the sectioning process. A few crystalliferous axial parenchyma strands were also observed in stems of *Brachysiphon rupestris*, but not in any of the other Penaeaceae examined. However, in the large rays of lignotubers of *Saltera sarcocolla* (Plate 4D), numerous cells contain crystal aggregations.

If one examines phloem of Penaeaceae, as in *Brachysiphon rupestris* (Plate 1E), one can invariably find crystalliferous parenchyma strands of the type seen in the wood of *B. acutus*. Thus, the occurrence of chambered crystalliferous strands is not as rare in Penaeaceae as examination of wood alone would indicate—an important fact because of the diagnostic value of these strands in Myrtales. The crystalliferous strands of Penaeaceae are distinctive in that each chamber contains a cluster of crystals or druse rather than a single rhomboidal crystal, as in Punicaceae (Metcalf & Chalk, 1950).

Amorphous deposits

In all species of Penaeaceae examined, Plates 1 to 5, dark-staining amorphous deposits are present. These may be infrequent, as in *Stylapterus fruticulosus* (Plate 3D) or very abundant, as in the lignotuber of *Saltera sarcocolla* (Plate 4C). The primary sites of deposition are in the ray cells and the axial parenchyma (Plates 1A, B, 2A, D, 3A, B and 4A, B). When the secretion is abundant, the amorphous deposits spread into the vessels and even into tracheids (Plate 4C). The reddish tone of woods of Penaeaceae is probably the result of these deposits. The nature of this material has not been identified, but could be closely allied to the 'amorphous deposits' or 'gummy substances' mentioned by Metcalfe & Chalk (1950) and other authors for Myrtaceae, Lythraceae, Punicaceae, and other myrtalean families.

PHYLOGENETIC RELATIONSHIPS

The order Myrtales can be defined by: (1) the presence of intraxylary phloem adjacent to pith in stems; (2) the presence of crystalliferous strands in axial xylem; (3) the presence of vested pits in vessels; (4) the tendency for rays to be narrow multiseriate plus uniseriate, and for erect ray cells to be predominant; and (5) the presence of amorphous deposits in ray cells. If one takes into account the work of Metcalfe & Chalk (1950), Mújica & Cutler (1974), Vliet (1975, 1976), Carlquist (1975a), and the present data on Penaeaceae, the following families fall into Myrtales on the basis of the above criteria:

Myrtaceae	Penaeaceae
Combretaceae	Lythraceae
Melastomataceae	Sonneratiaceae
Crypteroniaceae	Punicaceae
Oliniaceae	Onagraceae

Some of these families could, and probably should be amalgamated (e.g., Lythraceae *sensu lato* including Sonneratiaceae and Punicaceae: Thorne, 1968). There seems little doubt that the order Myrtales is natural, and criteria other than those from xylem could be cited. The construction of interrelationships between the above families is a problematic exercise, although some families can be grouped more closely than others.

The families Rhizophoraceae and Lecythidaceae are often placed in Myrtales on account of details of floral morphology—chiefly a ‘floral diagram’ approach. These two families lack such key xylem features as vested pits and intraxylary phloem. Rhizophoraceae may prove, with further study, to be cornalean, and Lecythidaceae to belong to Theales, as Thorne (1968) suggests. The position of the family Thymeleaceae, which possesses intraxylary and interxylary phloem as well as vested pits in vessels (Metcalf & Chalk, 1950) is particularly troubling, for it does not yet fit convincingly into Myrtales, though other placements may be even less satisfying. Dahlgren & Rao (1969) have argued convincingly that Geissolomataceae should not be placed in Myrtales, and this is supported on the basis of wood anatomy (Carlquist, 1976).

ECOLOGICAL INTERPRETATIONS

Penaeaceae occupy a wide amplitude of ecological habitats which experience various degrees of drought as summer heat occurs. On the basis of the nature of vegetation, those plants which are restricted to rock crevices on cliffs or outcrops could be rated the most xeromorphic. Two rock crevice species are included in this study: *Brachysiphon rupestris* and *Sonderothamnus petraeus*. The former is smaller, 60–100 mm tall, with numerous narrow branches from a woody base; the latter, to 250 mm, has one to several branches from the woody base.

The next most xeric habitat occupied by Penaeaceae is probably the sand flats east and north of the Cape Peninsula. *Stylapterus fruticosus* is endemic to this region; it appears to have notably succulent bark on the massive underground stems.

Open slopes of either red soil, or soil intermixed with rocks and boulders of the Table Mountain Sandstone, are somewhat more mesic. Moisture may be retained under or in the shade of these boulders, especially on south-facing slopes. *Endonema lateriflora* and *E. retzioides* occupy south-facing (and therefore cooler) slopes in such habitats, as do *Brachysiphon acutus*, *B. fucatus*,

Penaea acutifolia, *P. mucronata*, and *Saltera sarcocolla*. Perhaps the most mesic habitats occupied by Penaeaceae are the river valleys or wet forest (e.g., Knysna) areas with red soil where large shrubs or trees *Penaea cneorum* grow. *Stylapteris ericoides* subsp. *ericoides* grows near streams, but in open areas on sand. For further ecological descriptions see Dahlgren (1967a, b, c, 1968, 1971).

Judging from the data of Table 1, the correlation of wood anatomy with habitat diversity appears rather close. The features in wood anatomy most directly related to ecology appear to be vessel diameter, vessel element length, and the number of vessels per mm² of transection. Shorter, narrower vessels can be cited as indicative of xeromorphy (Carlquist, 1975b). There is a rough inverse correlation between vessel diameter and number of vessels per mm² of transection, so that in general, more xeromorphic woods would be expected to have more numerous vessels per mm². One can speculate that short, narrow vessels may be more resistant to high water tensions in xylem (Carlquist, 1975b). More numerous vessels per mm² of transection would also have the advantage of 'redundancy' and therefore 'safety' if a portion of the vessels were disabled by air embolisms, for those not disabled could still conduct adequately (Martin H. Zimmermann, pers. comm.).

A simple formula adding average vessel diameter to average vessel element length for each species has been used as an index to mesomorphy or xeromorphy (Carlquist, 1975a). This simple index appears quite accurate as a predictor of the probable xeromorphy or mesomorphy of particular species, and is confirmed by field observations, as in *Dubautia* (Carlquist, 1974: 153). One can argue that if number of vessels per mm² is roughly an inverse of vessel diameter, the former measurement overlaps with the latter, and one or the other should be chosen if one is constructing an index. A relatively close correlation between these two measures was obtained previously (Carlquist, 1975b: 183).

However, vessel diameter is not by any means a close inverse of number of vessels per mm² in Penaeaceae as Table 1 indicates. For example, the stem of *Brachysiphon rupestris* has a very low ratio (0.06), whereas *Penaea cneorum* subsp. *cneorum* (Carlquist 4740) has a very high ratio (0.79). One might expect a modal value between 0.20 and 0.35, but the number of ratios above and below that range for the collections of Table 1 is quite considerable. A very large number of vessels per mm² of transection in a species would result in a low ratio, perhaps connoting Zimmermann's 'safety' hypothesis, and certainly also a high degree of xeromorphy. A very high ratio, as in *Penaea cneorum*, would indicate few vessels per unit area of transection, and therefore less 'safety' and greater mesomorphy. This ratio by itself is interesting, and so it has been included in Table 1. The range of these ratios shows that vessel diameter and number of vessel per unit transection can, in fact, be considered independently when comparing species.

Therefore, for the purposes of constructing a mesomorphy index for Penaeaceae, a ratio incorporating all three measurements has been devised:

$$\frac{\text{mean vessel diameter} \times \text{mean vessel element length}}{\text{mean number of vessels per mm}^2 \text{ transection}}$$

This index also appears in Table 1. It seems an accurate reflection of mesomorphy versus xeromorphy based on field observations by the senior author. However, there are some species where additional factors may result in ratios higher or lower than one would expect. For example, *Stylapteris ericoides* subsp. *ericoides* has a ratio indicating greater mesomorphy than *S. fruticosus*. Since *S. ericoides* subsp. *ericoides* grows along the wet margins of the Tulbagh River, one might have expected it to have a ratio as high as other riverine Penaeaceae, such as *P. cneorum*. One can suggest that not only is *S. ericoides* subsp. *ericoides* a small shrub, but it also represents a secondary entrant into the riparian habitat, derived from more xeromorphic ancestors, and that its relatively xeromorphic type of conducting tissue is not disadvantageous. On the other hand, *Saltera sarcocolla* appears to be more mesomorphic in wood anatomy than its occurrence on open slopes would at first suggest. However, it tends to occur principally on cool south-facing slopes; it has a lignotuber that could be regarded as a succulent buffer against drought; its habit (a few long, stout, sparsely branched stems attached to the lignotuber) features greater mechanical strength (and thereby both longer vessel elements as well as imperforate elements) than would characterize a much-branched shrub. Certain shrubs with long, sparsely-branched stems are often 'emergents' in the low *fynbos* scrub characteristic of the Table Mountain Sandstone, and these must contend with the great and almost constant wind pressure regime of the southwestern Cape.

A mesomorphy-xeromorphy index can thus be constructed and interpreted. Students of wood anatomy interested in potential functional aspects should be encouraged to assemble data on vessel diameter, vessel element length, and number of vessels per unit area of transection for other species from other environments to test the validity of such an index.

ACKNOWLEDGEMENTS

Appreciation is expressed to South African botanists, particularly Miss Elsie Esterhuysen, Miss Joan van Reenen, Dr J. Rourke, and Dr I. Williams for help during the senior author's field work in 1973. The use of facilities at the Kirstenbosch Botanic Garden and at the Bolus Herbarium of the University of Cape Town is gratefully acknowledged. Field studies and research were aided by a grant by the John Simon Guggenheim Memorial Foundation and National Science Foundation grants, GB-38901 and BMS 73-07055 A-1.

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