



# Comparative leaf anatomy of the Penaeaceae and its ecological implications

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The leaf anatomy of species representing all seven genera of the Penaeaceae was studied by light and scanning electron microscopy. Due to variability and inconsistency, leaf anatomical characters are not regarded as particularly useful for systematics within or among genera in this family. Across the family, a number of taxa exhibit a trend towards amphistomatous, isobilateral leaves, generally associated with increased leaf thickness and amount of palisade mesophyll. This trend is not apparent in closely related families, e.g. Alzateaceae, Crypteroniaceae, Oliniaceae and Rhynchochalcaceae. Most species are found in comparatively mesic habitats and it is difficult to postulate primary xeromorphic trends in leaf anatomy. The sclerophylly encountered across the family as a whole is likely to be related to paucity of soil nutrients rather than a response to water stress.

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**ADDITIONAL KEY WORDS:**— *Brachysiphon* – *Endonema* – *Glischrocolla* – *Penaea* – *Saltera* – *Sonderothamnus* – *Stylapterus*.

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## INTRODUCTION

This paper reports a descriptive study carried out as part of a larger project on the comparative systematic anatomy of the Myrtales, which will result in a volume of the second edition of *The anatomy of the dicotyledons* (eds D.F. Cutler, M. Gregory and W.C. Dickson).

The Penaeaceae is a small myrtalean family of seven genera (Dahlgren & Thorne, 1984; Dahlgren & Van Wyk, 1988) and 23 species are currently recognized (Rourke, 1995). They are all shrubs or shrublets, usually low, generally ericoid, and endemic to the Western Cape Province of South Africa, where they are characteristic of 'fynbos' vegetation (Cowling, 1992).

Dahlgren and Van Wyk (1988) have given a recent account of the systematics of the Penaeaceae, following revisions of the genera by Dahlgren (1967a–c, 1968, 1971). Since those revisions, two new species, *Penaea dahlgrenii* and *Brachysiphon microphyllum*, have been described by Rourke & McDonald (1989) and Rourke (1995), respectively.

Metcalf & Chalk (1950) described leaf anatomy in the family, their account (for five genera) leaning heavily on the earlier ones by Van Tieghem (1893) and Solereder (1899). Subsequently, Dahlgren (1967a–c, 1968, 1971) has published observations on leaf anatomy for most of the genera. Keating (1984) and Van der Merwe, Van der Walt & Marais (1994) have touched on aspects of leaf histology in certain members of the family. Carlquist & Debuhr (1977) studied wood anatomy in the Penaeaceae in some detail (12 spp. from six genera; *Glischrocolla* was not included). They interpreted variation in wood anatomical features in relation to ecological adaptation of taxa to successively drier habitats, especially on the basis of values of their 'mesomorphy index'.

## MATERIAL AND METHODS

Details of the leaf material examined, both fresh and dried, are listed in the Appendix. Dried material was obtained from sheets in the Kew Herbarium. Small samples (3–5 leaves) of apparently typical mature leaves were taken from parts of stems well away from inflorescences. Dried leaf samples were rehydrated by boiling them in water until they sank and regained the shape and texture of fresh material. Both fresh and rehydrated leaves were then fixed for 48 h in Formalin Acetic Acid, before being transferred to storage in 70% ethanol. On removal from storage, samples were thoroughly rinsed in several changes of tap water before further processing.

Whole leaves were cleared in 5% (w/v) NaOH solution, for periods varying from 2 to 10 days. After thorough rinsing in tap water they were treated with chloral hydrate until glassy, rinsed again, and veins and sclereids stained with Feulgen reagent.

Cuticular preparations were made by softening whole leaves for periods of 1–7 days in Jeffrey's Solution, followed by rinsing in tap water, and then careful removal of the cuticles from any remaining underlying material. The preparations were of both surfaces of whole leaves, except for the removal of basal and tip portions, and they were stained in Safranin (1% w/v in 50% ethanol) and Alcian Blue (1% w/v, aqueous).

Leaf transverse sections, 12–20  $\mu\text{m}$  thick, were cut half way along the lamina, using a 'Reichert OME' sliding microtome. The sections were cleared in 'Parozone' (diluted 50% with water) and thoroughly washed before staining in Safranin (1% w/v in 50% ethanol) and Alcian Blue (1% w/v, aqueous).

All prepared material for light microscopy was taken through an alcohol series (50%, 70%, 90% and 100% ethanol) and 'HistoClear', before being mounted in 'Euparal' to make permanent microscope slides. Some sections and cleared leaves were examined using Differential Interference Contrast.

Whole, or parts of leaves for examination by SEM were transferred through an alcohol series (70%, 90%, 100%, 100% ethanol; two minutes at each step) and then air-dried at room temperature, pressed between two microscope slides to prevent curling. Dried specimens were mounted on stubs using double-sided 'Sellotape', and coated with platinum for 6 or 8 minutes in an 'Emscope SC500' sputter coater. Specimens were examined in a Cambridge 'Stereoscan S240' SEM and photographed using Kodak Plus-X Pan 220 film.

All measurements in light microscopy were made using a calibrated eyepiece micrometer, with a 10 $\times$  or 40 $\times$  objective. Stomatal measurements were taken from single epidermal preparations of each surface, for each specimen. Those for overall dimensions (means, maxima and minima) result from observations on ten randomly chosen stomata. Measurements of rim width and aperture outline were based on five stomata. Values for aperture outline area were calculated from paired aperture outline length and width measurements, assuming an elliptical shape. For stomatal density the values of mean, maximum and minimum, were based on counts (40 $\times$  objective) of stomata in 30 randomly chosen fields of view (area 43 056  $\mu\text{m}^2$ ), avoiding midribs and margins, which were then multiplied by 22.9568, to give densities in  $\text{mm}^{-2}$ . Statistical analysis (correlation) was carried out using the data analysis tool of Microsoft Excel 5.

## OBSERVATIONS

### *Characteristics of the whole family*

#### *Leaf anatomy*

LEAVES: relatively small; sessile (except *Penaea dahlgrenii*), hence no description of petiole anatomy here;  $\pm$  coriaceous, opposite, entire, symmetrical, variable in shape from linear to broadly ovate; margins sometimes papillose.

#### *Leaf surface*

*Primary sculpturing.* VENATION: only the midveins distinct, sometimes poorly so, and only from the abaxial surface; clearing revealed a generally brochidodromous pattern (Hickey, 1979). HAIRS: none, except for some specimens of *Penaea mucronata*. The stout hairs, thought by Weberling (1963) to be reduced stipules, in the axils of the leaves are not considered here. EPIDERMAL CELLS: both surfaces, irregular, polygonal, with 4–6 straight or slightly wavy/curved sides (Figs 7, 8, 17, 18, 21), orientation random, largest diameter up to 50–60  $\mu\text{m}$  in adaxial cells, abaxial somewhat smaller; anticlinal cell walls appearing thick in surface view (Figs 7, 17, 21). STOMATA:

anomocytic (Figs 8, 17, 18); hypostomatous, amphistomatous, or sometimes intermediate (Table 1), usually level with the epidermis (rim slightly raised), or guard cells rarely slightly depressed (rim level with epidermis), broadly elliptical to almost circular (Figs 1, 2, 5, 8, 11, 16–18); continuously variable in size (Table 2), orientation  $\pm$  axial, guard cells without obvious polar thickenings or thin areas.

*Secondary sculpturing*: mostly striate, to varying degree (Figs 1, 5, 11).

*Tertiary sculpturing*: epicuticular wax usually absent or sparse.

#### *T.S. lamina*

**THICKNESS**: relatively thick (290–775  $\mu\text{m}$ ), variable (Table 1). **CUTICLE AND OUTER PERICLINAL WALL**: adaxial cuticle about as thick as outer periclinal wall (3.5–12.5  $\mu\text{m}$  combined), but with some variation (Table 1); outer periclinal wall  $\pm$  flat or gently convex in TS. **EPIDERMAL CELLS**: single layer on both surfaces, abaxial and adaxial often similar in size and shape, mostly more or less as tall as broad. **HYPODERMIS**: absent. **MESOPHYLL**: bifacial or isobilateral (Table 1). Palisade 1 or 2-layered; palisade cell length to width ratio (genus descriptions) and ratio of palisade to spongy mesophyll (Table 1) variable; spongy tissue of generally loosely-packed  $\pm$  irregularly-lobed cells. **VEINS**: embedded; surrounded by parenchymatous bundle sheaths, the latter lacking extensions. **MIDRIB BUNDLE**: circular or slightly flattened, surrounded by thick-walled parenchyma, and often collenchyma, sometimes forming an abaxial keel. **VASCULAR TISSUE OF MIDRIB**: circular or slightly flattened; vein embedded in  $\pm$  thick-walled parenchyma; the phloem usually lacking fibres, and either completely surrounding or adaxial and abaxial to the crescentiform xylem which consists of vessels and fibres. **MARGIN**: cuticle somewhat thicker than rest of lamina, epidermal cells often distinctly domed (papillose). **CRYSTALS**: cluster crystals (druses), frequently sub-epidermal and scattered through the spongy mesophyll (Figs 3, 9, 13, 14, 15). **IDIOBLASTS**: branched filiform sclereids (Figs 3, 4, 10, 13, 14, 19) and/or  $\pm$  branched tracheoidal cells (Figs 3, 4, 10, 14, 20; Table 1).

#### *Brachysiphon* A. Juss. (Figures 2–4)

A genus of four species, confined to the south-western Cape.

#### *Leaf anatomy*

**LEAVES**: variable in shape from elliptic to orbicular (see Dahlgren, 1968, for further details).

#### *Leaf surface*

*Primary sculpturing*. **STOMATA**: *B. acutus* hypostomatous, the rest amphistomatous; possibly larger in *B. fucatus* and *B. acutus* than in the rest (Table 2).

*Secondary sculpturing*: cuticular surface generally finely striate, tending to discontinuous or micropapillate in *B. rupestris* (Fig. 2).

TABLE 1. Results of observations on leaf anatomical characteristics of members of the Penaeaceae

Taxon	ID no. <sup>1</sup>	Sclereids <sup>2</sup>	Tracheoidal idioblasts <sup>2</sup>	Lamina thickness (µm) <sup>3</sup>	Palisade: spongy mesophyll ratio <sup>4</sup>	Stomatal distribution <sup>5</sup>	Leaf type <sup>6</sup>	Thickness of adax. cuticle + epidermal outer periclinal wall (µm) <sup>3</sup>
<i>Penaea mucronata</i>	00	1	1	340	0.4	H	B	5.8
<i>Penaea mucronata</i>	0	1	1	360	0.4	H+	B	8.0
<i>Penaea mucronata</i>	1	1	1	315	0.4	H	B	6.4
<i>Penaea mucronata</i>	2	1	1	315	0.5	H	B	8.5
<i>Penaea mucronata</i>	3	1	1	340	0.5	H	B	9.0
<i>Penaea mucronata</i>	4	1	1	290	0.7	H+	B	8.5
<i>P. cneorum</i> ssp. <i>cneorum</i>	5	1	1	305	1.7	A	B+	8.4
<i>P. cneorum</i> ssp. <i>cneorum</i>	6	1	1	340	2.7	H	B	7.0
<i>P. cneorum</i> ssp. <i>gigantea</i>	7	1	1	390	2.5	H+	B+	9.5
<i>P. cneorum</i> ssp. <i>ruscifolia</i>	8	1	1	330	0.5	A	B+	9.0
<i>P. cneorum</i> ssp. <i>lanceolata</i>	9	1	1	360	0.6	H+	B+	6.5
<i>P. acutifolia</i>	10	1	1	380	0.4	H+	B	8.0
<i>P. dahlgrenii</i>	11	1	1	340	3.0	A	I	8.0
<i>Stylapteris barbatus</i>	12	1	0	600	4.0	A	I	8.0
<i>S. micranthus</i>	13	1	0	480	1	A	I	7.0
<i>S. ericoides</i> ssp. <i>ericoides</i>	14	1	0	470	1.2	A	I	7.8
<i>S. fruticosus</i>	16	1	1	500	1.0	A	I	12.5
<i>S. fruticosus</i>	16	1	1	500	1.0	A	I	12.0
<i>S. ericifolius</i>	17	1	0	470	1.0	A	I	8.5
<i>Brachysiphon fucatus</i>	18	1	0	465	1.0	A	I	7.0
<i>Brachysiphon fucatus</i>	18A	1	0	420	1.0	A	I	9.0
<i>B. acutus</i>	20	1	0	465	0.5	H	B	12.0
<i>B. cf. rupestris</i>	21	1	0	605	1.0	A	I	7.0
<i>B. rupestris</i>	22	1	0	420	0.6	A	I	6.0
<i>B. mundii</i>	23	1	1	650	0.7	A	I	8.0
<i>Sonderothamnus petraeus</i>	24	1	0	560	2	A	I	7.3
<i>S. speciosus</i>	25	1	0	530	2	A	I	10.5
<i>Saltera sarcocolla</i>	26	1	1	775	1.0	A	I	15.5
<i>Saltera sarcocolla</i>	26A	1	0	725	1.0	A	I	9.0
<i>Saltera sarcocolla</i>	27	1	0	511	1.5	A	I	10.8
<i>Endonema laterifolia</i>	28	1	1	290	1	H	B	3.5
<i>E. retzioides</i>	29	0	1	280	0.5	H	B	15.0
<i>Glischmocola formosa</i>	30	0	1	510	0.33	H	B+	14.0

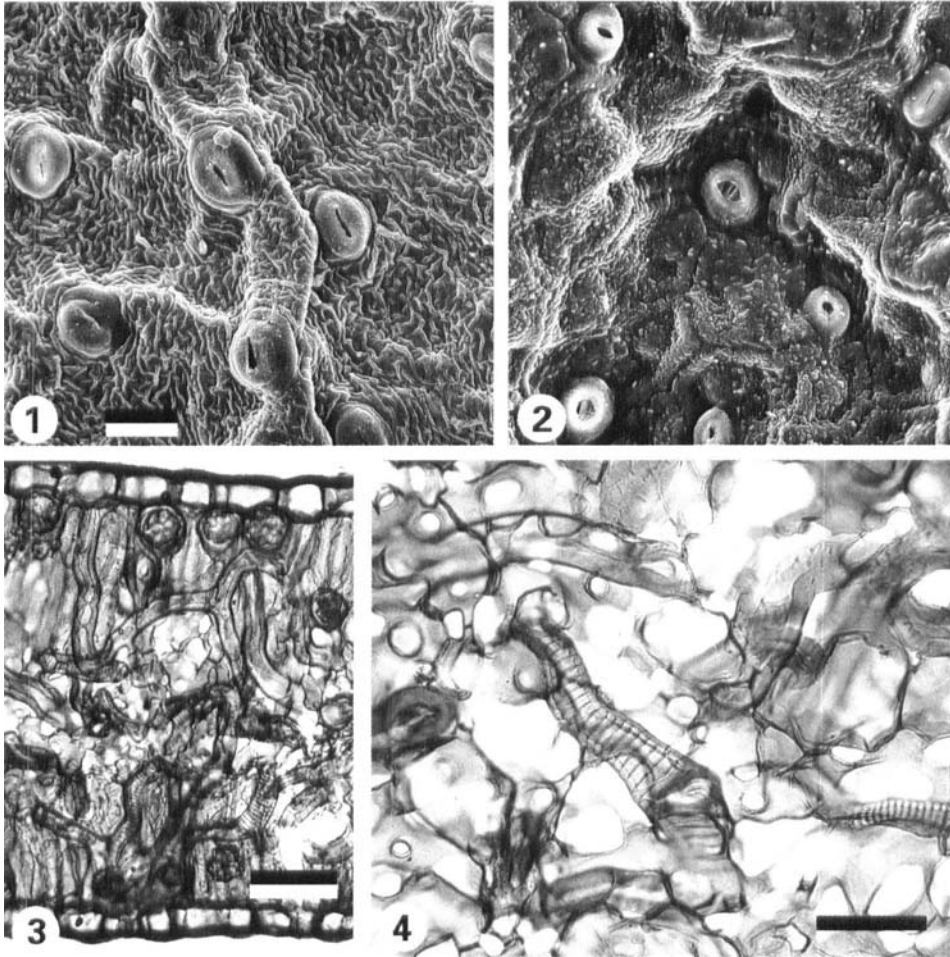
<sup>1</sup> See Appendix.<sup>2</sup> 1 = present (seen in both TS and cleared leaves); 0 = absent.<sup>3</sup> Average of measurements (usually 5) made in middle of lamina in TS.<sup>4</sup> From measurements of the height of each tissue in the middle of the lamina in TS.<sup>5</sup> From observations in TS and surface preparations: H = hypostomatous; A = amphistomatous; H+ = hypostomatous, but with stomata present on the adaxial surface at reduced density—half, or less than that on the abaxial surface.<sup>6</sup> From observations in TS: B = bifacial; I = isobilateral; B+ = predominantly bifacial, but with discontinuous palisade or palisade-like tissue on the abaxial side of the lamina.

TABLE 2. Results of measurements made on stomata of members of the Penaceae

Taxon	ID no.	Density (mm <sup>-2</sup> ) -abaxial	Density (mm <sup>-2</sup> ) -adaxial	Length (µm)	Width (µm)	Rim width (µm)	Aperture outline area (µm <sup>2</sup> )
<i>Penaea mucronata</i>	00	117-241-350	0	29-32.6-36	19-26-34	5	140.2
<i>Penaea mucronata</i>	0	117-219-380	0-14-58	29.3-32.6-36	22.5-24.5-27	6	146.6
<i>Penaea mucronata</i>	1	88-188-263	0	27-30.7-36	22.5-24-27	6.2	180.2
<i>Penaea mucronata</i>	2	146-247-351	0	27-30.6-31.5	22.5-24.6-27	6.8	110.9
<i>Penaea mucronata</i>	3	167-249-380	0	27-30.7-33.8	20.3-23.6-27	4.5	96.3
<i>Penaea mucronata</i>	4	117-220-351	0-17-58	27-30.3-32.6	22.5-24.8-27	5.5	146.0
<i>P. cneorum</i> ssp. <i>cneorum</i>	5	58-157-263	58-160-290	25-28-30	20-23-27	3.5	62.7
<i>P. cneorum</i> ssp. <i>cneorum</i>	6	117-215-292	0	27-34.2-40.5	20-22-25	6.75	97.4
<i>P. cneorum</i> ssp. <i>gigantea</i>	7	58-148-234	0-18-58	34-37-40	25-29-34	4.5	149.2
<i>P. cneorum</i> ssp. <i>ruscifolia</i>	8	88-163-292	58-127-204	29-33-36	20-24-27	4.0	120.2
<i>P. cneorum</i> ssp. <i>lanceolata</i>	9	102-175-248	0-74-146	29-34-38	0-27-29	4.7	97.7
<i>P. acutifolia</i>	10	102-221-292	44-116-204	25-28.5-31	22-24.7-27	4.5	47.5
<i>P. dahlgrenii</i>	11	29-115-190	29-113-204	25-32-38	23-27-31	5.65	97.7
<i>Sylaptenus barbatus</i>	12	0-100-175	58-107-190	29-31-34	27-29-31	5.5	64.8
<i>S. micranthus</i>	13	44-80-130	0-70-130	30-36.1-39	29-34.2-36	5.5	61.3
<i>S. ericoides</i> ssp. <i>ericoides</i>	14	73-102-175	29-138-204	32-33-34	25-29-32	5	190.8
<i>S. fruticosus</i>	15	73-131-190	102-166-219	29-34-36	27-30-32	3.5	70.7
<i>S. ericifolius</i>	17	29-92-161	29-128-175	28-30.4-33	22-24.7-27	—	127.6
<i>Brachysiphon fucatus</i>	18	29-83-190	0-97-204	38-41-43	31-35-38	5.75	223.8
<i>Brachysiphon fucatus</i>	18A	29-124-234	29-125-204	32-38-41	27-30.4-33	4	218.3
<i>B. acutus</i>	20	88-129-175	0	41-45-47	34-36-38	—	273.7
<i>B. cf. rupestris</i>	21	58-112-175	29-90-175	31-33-36	27-29-31	6.5	91.1
<i>B. rupestris</i>	22	0-88-175	29-72-131	29-35-38	25-33-36	4	33.0
<i>B. mundii</i>	23	0-64-102	0-82-131	1-32.3-34	23-26.6-32	4	136.0
<i>Sonderthamnus petraeus</i>	24	0-82-146	0-82-146	29-34.2-37	28-32.3-34	4	136.1
<i>S. speciosus</i>	25	73-130-190	29-128-219	32-38-42	28.5-34.2-37	—	—
<i>Saltera sarcocolla</i>	26	44-93-146	29-99-161	41-45.6-48	32-38-41	4	238.2
<i>Saltera sarcocolla</i>	26A	44-96-110	58-110-161	40.5-45.6-48	33-38-41	4	277.9
<i>Saltera sarcocolla</i>	27	29-85-131	29-89-146	31-38-41	29-34-35	7	190.8
<i>Endonema laterifolia</i>	28	146-295-380	0	34-36-38	27-29.5-32	4	201.4
<i>E. retzioides</i>	29	219-319-424	0	32-38-42	27-29-31	5.5	166.9
<i>Glichitocolla formosa</i>	30	161-233-292	0	38.5-43-46	33-36-38	6.5	204.2

Note: figures shown in bold type are mean values. Those not in bold represent the extremes of values recorded. See Material and methods for details of sampling.

<sup>1</sup> See Appendix.



Figures 1–4. *Glischrocolla formosa*: abaxial leaf surface with striations on epidermal cells, SEM. Scale bar = 25  $\mu\text{m}$ . Fig. 2. *Brachysiphon rupestris*: abaxial leaf surface with micropapillae on epidermal cells, SEM. Same scale as Fig. 1. Figs 3 & 4. *B. mundii*: Transverse section of leaf showing subepidermal druses and both tracheoidal idioblasts and sclereids. Scale bar for Fig. 3 = 100  $\mu\text{m}$ , for Fig. 4 = 50  $\mu\text{m}$ .

### *T.S. lamina*

**THICKNESS:** mostly up to *c.* 420–465  $\mu\text{m}$ , up to 600–650  $\mu\text{m}$  in *B. mundii* and one specimen of *B. rupestris* (J.J. Bos, 685). **CUTICLE AND OUTER PERICLINAL WALL:** cuticle (typically 2–5  $\mu\text{m}$ ) from as thick to twice as thick as the outer periclinal wall (typically 2–3  $\mu\text{m}$ ). **EPIDERMAL CELLS:** up to 30  $\mu\text{m}$  tall and up to 60  $\mu\text{m}$  wide on both surfaces; stomata level with surface or very slightly sunken, rims projecting. **MESOPHYLL:** bifacial with adaxial palisade in *B. acutus* and apparently so in one specimen of *B. rupestris* (H. Bolus 9827), the rest isobilateral. Palisade 1-layered (locally 2 layers, especially in the adaxial tissue of leaves with isobilateral arrangement); palisade cell length to width ratio 4 or 5:1. Ratio of palisade to spongy mesophyll 1:1 in isobilateral arrangement, 1:2 in bifacial. **MIDRIB BUNDLE:** abaxial support tissue (thick-walled parenchyma or collenchyma) present in *B. fucatus*, doubtful or absent in the others. **VASCULAR TISSUE OF MIDRIB:**  $\pm$  circular; the phloem abaxial to the xylem. **MARGIN:**

sometimes a few thick-walled, presumably supporting cells immediately beneath the epidermis in *B. fucatus*. CRYSTALS: cluster crystals (druses) usually sub-epidermal, but also concentrated around veins. IDIOBLASTS: branched filiform sclereids in all spp.:  $\pm$  branched tracheoidal cells only in *B. mundii* (Figs 3, 4), absent or indistinguishable from vein endings in the rest.

*Endonema* A. Juss.  
(Figures 5–9)

A genus of two species, confined to the southern part of Western Cape province.

*Leaf anatomy*

LEAVES: ovate to elliptic in *E. laterifolia*, linear in *E. retzioides*; margins papillose, strongly recurved in *E. retzioides*, not or barely so in *E. laterifolia*.

*Leaf surface*

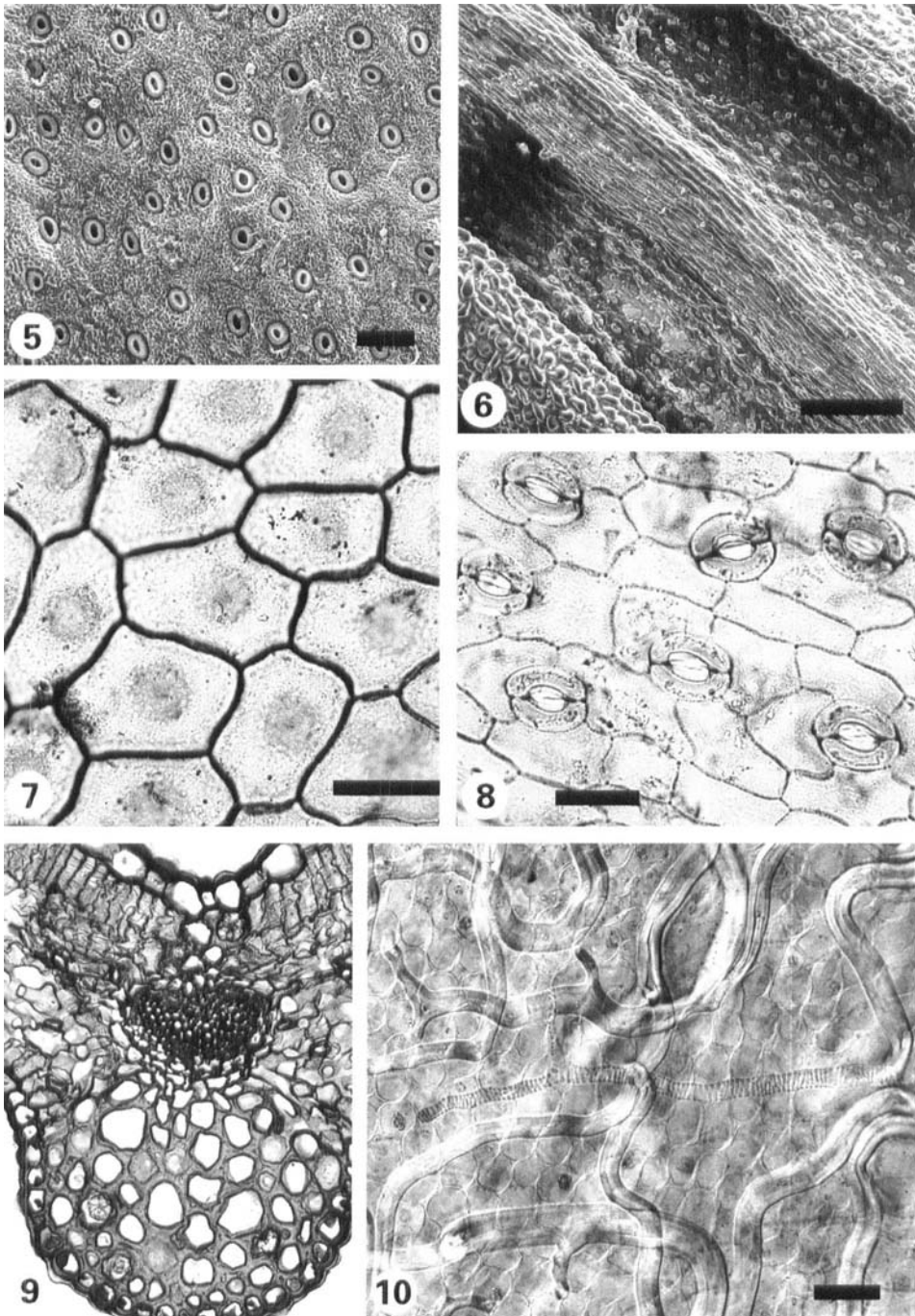
*Primary sculpturing.* EPIDERMAL CELLS: distinct domes or papillae on the adaxial surface of *E. retzioides*. STOMATA: hypostomatous, relatively dense in both spp. (Tables 1 and 2).

*Secondary sculpturing:* faint or lacking in *E. retzioides*; generally striate in *E. laterifolia*, heavily and irregularly folded on the abaxial surface (Fig. 5), less ornamented and with  $\pm$  parallel orientation on the adaxial.

*T.S. lamina*

THICKNESS: *c.* 250–325  $\mu\text{m}$ . CUTICLE AND OUTER PERICLINAL WALL: cuticle as thick, or almost as thick as outer periclinal wall in both spp., but both layers much thicker in *E. retzioides* (wall up to 9  $\mu\text{m}$ , cuticle 6–11  $\mu\text{m}$ ) than in *E. laterifolia* (wall and cuticle each 1.5–2  $\mu\text{m}$ ); outer periclinal wall convex in both spp., more so in *E. retzioides* (subpapilliform, Figs 7, 8). EPIDERMAL CELLS: in both species adaxial cells significantly taller (up to twice as tall) than abaxial, but proportionally taller on both surfaces in *E. retzioides*. MESOPHYLL: bifacial with adaxial palisade. Palisade 2-layered in *E. laterifolia*, 1-layered in *E. retzioides*, but locally with a second layer of cells, barely elongated and hardly distinguishable from spongy mesophyll; palisade cell length to width ratio up to 3:1. Ratio of palisade to spongy mesophyll 1:1 in *E. laterifolia*, 1:2 in *E. retzioides*; spongy tissue of generally loosely-packed  $\pm$  irregularly-lobed cells. MIDRIB BUNDLE: abaxial collenchyma forming a keel, slight in *E. laterifolia*, prominent in *E. retzioides* (Fig. 9), also adaxial collenchyma in *E. laterifolia*. VASCULAR TISSUE: phloem almost completely surrounding the xylem except for an adaxial gap (sub-concentric), scattered adaxial phloem fibres. MARGIN: strongly recurved in *E. retzioides* (Fig. 6). IDIOBLASTS: sclereids and tracheoidal cells in *E. laterifolia*, only tracheoidal cells in *E. retzioides*.





Figures 5–10. Fig. 5. *Endonema laterifolia*, abaxial surface SEM showing heavily and irregularly-folded striae on epidermal cells. Scale bar = 50  $\mu$ m. Fig. 6. *E. retzioides*, abaxial surface showing recurved leaf margins and keeled midrib. Scale bar = 250  $\mu$ m. Fig. 7. *E. retzioides*, adaxial surface, each epidermal cell domed (subpapilliform). Scale bar = 50  $\mu$ m. Fig. 8. *E. retzioides*, abaxial surface showing anomocytic stomata. Scale bar = 100  $\mu$ m. Fig. 9. *E. retzioides*, midrib showing collenchyma forming keel. Same scale as Fig. 8. Fig. 10. *Penaea cneorum*, showing a tracheoidal idioblast and dense sclereids in cleared leaf using Differential Interference Contrast. Scale bar = 50  $\mu$ m.

*Glischrocolla* (Endl.) A. DC  
(Figure 1)

Monotypic genus, confined to the southern part of Western Cape Province.

*Leaf anatomy*

LEAVES: flat or slightly keeled, rhombic-ovate or rhombic-elliptic; margins described by Dahlgren (1967a) as distinctly pale.

*Leaf surface*

*Primary sculpturing.* STOMATA: hypostomatous (Table 1).

*Secondary sculpturing:* generally striate on both surfaces, more pronounced ornamentation and random orientation on abaxial (Fig. 1).

*T.S. lamina*

THICKNESS: most *c.* 500  $\mu\text{m}$ , 600  $\mu\text{m}$  over midrib. CUTICLE AND OUTER PERICLINAL WALL: outer periclinal wall thicker (10–12  $\mu\text{m}$ ) than cuticle (2–4  $\mu\text{m}$ , up to 8–10  $\mu\text{m}$  at margins); cuticular ornamentation visible in TS. EPIDERMAL CELLS: adaxial cells on average somewhat larger, especially in width, than abaxial. MESOPHYLL: bifacial with 1-layered adaxial palisade, but abaxially with a sub-epidermal layer of upright cells at least twice as tall as broad, short palisade tending to become lobed (sub-palisade); palisade cell length to width ratio *c.* 4:1, ratio of palisade to spongy mesophyll 1:3. MIDRIB BUNDLE: abaxial collenchyma forming a pronounced keel. VASCULAR TISSUE: phloem generally abaxial (collateral) and lateral to the xylem, but also occasional scattered phloem tissue adaxial (not concentric). CRYSTALS: sub-epidermal cluster crystals (druses) concentrated near the margins and around midrib. IDIOBLASTS: tracheoidal cells restricted to abaxial mesophyll; sclereids absent.

*Penaea* L.  
(Figures 10–14)

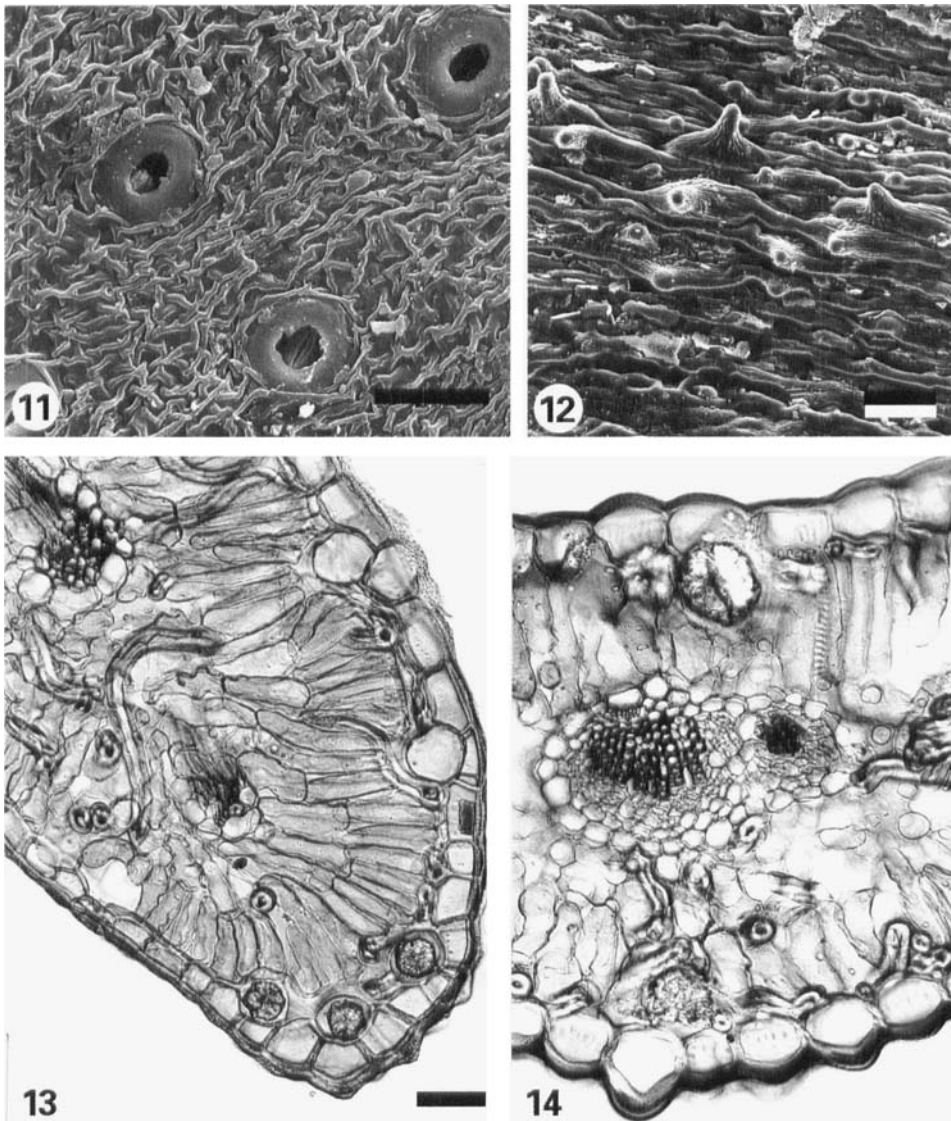
A genus of four species. Southern parts of the Western Cape Province (Dahlgren 1971).

*Leaf anatomy*

LEAVES: sessile, grasping at the base, except in *P. dahlgrenii*, which has definite petioles up to 1 mm long (Rourke & McDonald, 1989); usually  $\pm$  coriaceous, but more 'mesophytic' in some forms of *P. cneorum*, e.g. ssp. *gigantea*; variable in shape, especially within *P. cneorum* (Dahlgren, 1971) with the base rounded or obtuse and the apex pointed or acute to rounded or obtuse, more or less flat in most species, but characteristically recurved from the middle in *P. mucronata*; margins somewhat to barely papillose.

*Leaf surface*

*Primary sculpturing.* HAIRS: leaves glabrous, except for extended papillae arising from the abaxial epidermal cells overlying the midrib in three of the six samples of *P.*



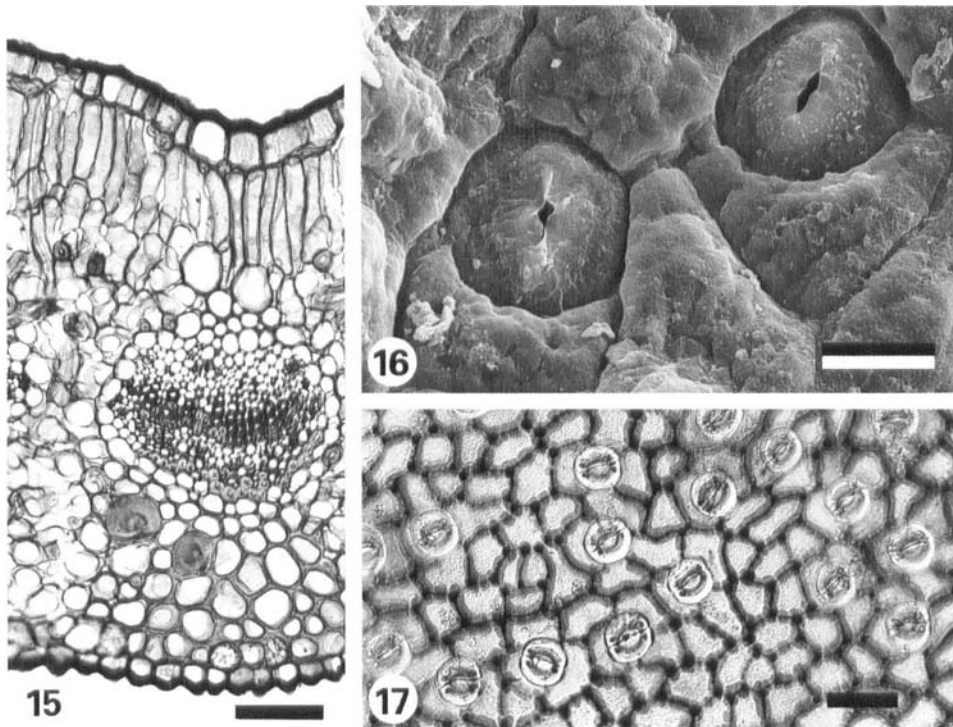
Figures 11–14. Fig. 11. *Pemaëa cneorum*, abaxial leaf surface showing striae on surface of epidermal cells. Scale bar = 20  $\mu\text{m}$ . Fig. 12. *P. mucronata*, abaxial midrib showing papillae. Scale bar = 50  $\mu\text{m}$ . Fig. 13. *P. mucronata*, leaf margin, showing subepidermal druses and sclereids. Scale bar = 50  $\mu\text{m}$ . Fig. 14. *P. dahlgrenii*, showing palisade on both sides of leaf, less well-defined here at midrib, large subepidermal druses, sclereids and one tracheoidal idioblast in adaxial palisade. Same scale as Fig. 13.

*mucronata* (Fig. 12). STOMATA: hypostomatous, or amphistomatous if present on adaxial surface, then usually at a lower density than abaxial, and quite sparse (Table 2).

*Secondary sculpturing*: generally striate, varying from faintly so in *P. dahlgrenii* to markedly so in *P. cneorum* ssp. *cneorum* (Fig. 11).

#### *T.S. lamina*

**THICKNESS**: most *c.* 300–360  $\mu\text{m}$  except close to midrib, up to 425  $\mu\text{m}$  in *P. cneorum* ssp. *gigantea*. **CUTICLE AND OUTER PERICLINAL WALL**: cuticle almost as thick as outer



Figures 15–17. Fig. 15. *Saltera sarcocolla*, TS midrib. Scale bar = 100  $\mu\text{m}$ . Fig. 16. *S. sarcocolla*, abaxial leaf surface. Scale bar = 20  $\mu\text{m}$ . Fig. 17. *Sonderothamnus speciosus*, abaxial leaf surface, epidermal cells with thick anticlinal walls. Differential Interference Contrast. Scale bar = 50  $\mu\text{m}$ .

periclinal wall in all spp., mean wall thickness (4.8  $\mu\text{m}$ , range 2–7  $\mu\text{m}$ ) and mean cuticle thickness (3  $\mu\text{m}$ , range 1.5–4.5  $\mu\text{m}$ ) in *P. mucronata* both close to the corresponding mean values for all the other spp. (4.5  $\mu\text{m}$ ; range 2–8  $\mu\text{m}$ ; 3.5  $\mu\text{m}$ , range 2–5  $\mu\text{m}$ , respectively). EPIDERMAL CELLS: abaxial and adaxial similar in size and shape, except that cells wider than tall more frequent in the adaxial, otherwise more or less as tall as broad. MESOPHYLL: bifacial with adaxial palisade; except *P. dahlgrenii*, isobilateral, and limited abaxial palisade near margins in *P. cneorum* (sub-isobilateral). Palisade 1-layered (locally 2 layers in *P. cneorum* ssp. *cneorum*), 1 layer to each face in *P. dahlgrenii*; palisade cell length to width ratio varying from 3:1 to 6:1 (sometimes up to 9:1 in *P. cneorum* ssp. *cneorum*). Ratio of palisade to spongy mesophyll from 1:1.5 to 1:2.5. MIDRIB BUNDLE: abaxial collenchyma absent in *P. dahlgrenii*, sometimes forming a slight keel in other species; small amount of adaxial collenchyma in *P. cneorum*. MARGIN: epidermal cells distinctly domed (papillose, Fig. 13). IDIOBLASTS: sclereids and tracheoidal cells present (Figs 10, 14).

*Saltera* Bullock  
(Figures 15, 16)

Monospecific genus, confined to the Western Cape Province of South Africa.

*Leaf anatomy*

LEAVES: broadly obovate to rhombic (Dahlgren, 1968, for further details); margins entire.

*Leaf surface*

*Primary sculpturing.* STOMATA: amphistomatous, mean density apparently constant between surfaces and between specimens (Table 2); elliptical to almost circular.

*Secondary sculpturing:* tuberculate to striate; sometimes only faintly sculptured (Fig. 16).

*Tertiary sculpturing:* sparse, epicuticular wax as scattered crystals or irregular flakes.

*T.S. lamina*

THICKNESS: mostly *c.* 690–775  $\mu\text{m}$ , except *c.* 510  $\mu\text{m}$  in Dahlgren & Strid 4994. CUTICLE AND OUTER PERICLINAL WALL: cuticle about half as thick as outer periclinal wall, mean wall thickness (3.5  $\mu\text{m}$ , range 3–5  $\mu\text{m}$ ) and mean cuticle thickness (8  $\mu\text{m}$ , range 4.5–12  $\mu\text{m}$ ); outer periclinal wall  $\pm$  flat or convex, distinctly so approaching the margins, cuticle thickest over cell junctions and over convex portions of outer periclinal walls. EPIDERMAL CELLS: abaxial and adaxial cells similar in shape, generally broader than tall, adaxial barely larger than abaxial. MESOPHYLL: isobilateral, adaxial palisade 1–2-layered, abaxial 1-layered; palisade cell length to width ratio varying from 3:1 to 6:1; ratio of palisade to spongy mesophyll 1–1.5:1; spongy tissue of generally loosely-packed sub-isodiametric or  $\pm$  irregularly-lobed cells. MIDRIB BUNDLE: abaxial collenchyma, also adaxial, but reduced (Fig. 15). VASCULAR TISSUE: the phloem generally abaxial (collateral) to the xylem, but also occasional scattered adaxial phloem tissue, phloem fibres well developed abaxially. IDIOBLASTS: branched sclereids present; also very thick-walled  $\pm$  isodiametric sclereids (stone cells) becoming more dense towards the leaf base (prominent in cleared leaves); tracheoidal cells present in one specimen, recorded as absent from the other two (possibly very sparse or indistinguishable from vein endings).

*Sonderothamnus* R. Dahlgren  
(Figure 17)

A genus of two species. Restricted to the southwest part of the Western Cape Province (Dahlgren, 1968).

*Leaf anatomy*

LEAVES: broadly lanceolate to ovate in *S. petraeus*, broadly circular-obovate in *S. speciosus*; margins entire, somewhat papillose (denticulate) towards the apex.

*Leaf surface*

*Primary sculpturing.* VENATION: apparently brochidodromous in cleared leaves, finer veins obscured by dense sclereids. STOMATA: amphistomatous (Table 1); orientation  $\pm$  axial, but random on adaxial surface in *S. speciosus*.

*Secondary sculpturing:* granular to striate (appears granular only in epidermal preparations, Fig. 17), orientation axial to random.

*Tertiary sculpturing:* very little, or no epicuticular wax on either surface in *S. petraeus*, amorphous wax on the adaxial surface in *S. speciosus*.

*T.S. lamina*

**THICKNESS:** up to 530–560  $\mu\text{m}$ . **CUTICLE AND OUTER PERICLINAL WALL:** cuticle *c.* twice as thick as outer periclinal wall in both spp., wall thickness 2–3.5  $\mu\text{m}$ , cuticle thickness 4.5–6.5  $\mu\text{m}$ ; outer periclinal wall  $\pm$  flat in TS. **MESOPHYLL:** isobilateral with 1–2 layers of palisade cells to each face; palisade cell length to width ratio varying from 3:1 to 6:1; ratio of palisade to spongy mesophyll 2:1. **MIDRIB BUNDLE:** circular, not distinct from other veins; surrounding thick-walled parenchyma apparently not extended to form any kind of supporting tissue, collenchyma absent. **VASCULAR TISSUE:**  $\pm$  circular; phloem abaxial (collateral) to the xylem, lacking fibres. **MARGIN:** acute in TS, epidermal cells not especially domed (papillose). **IDIOBLASTS:** branched sclereids present; tracheoidal cells absent.

*Stylapterus* A. Juss.  
(Figures 18–22)

A genus of up to eight species of ericoid shrubs, of which five were examined (Appendix). Endemic to the southwestern part of the Western Cape Province (Dahlgren, 1967c).

*Leaf anatomy*

**LEAVES:** variable in shape from broadly oblanceolate to ovate in *S. fruticosus* to linear or lanceolate in the other species; margins barely to definitely papillose; abaxial midrib grooves present in *S. barbatus*, *S. micranthus*, *S. ericoides* ssp. *ericoides* and a midrib keel in *S. ericifolius* (Fig. 22).

*Leaf surface*

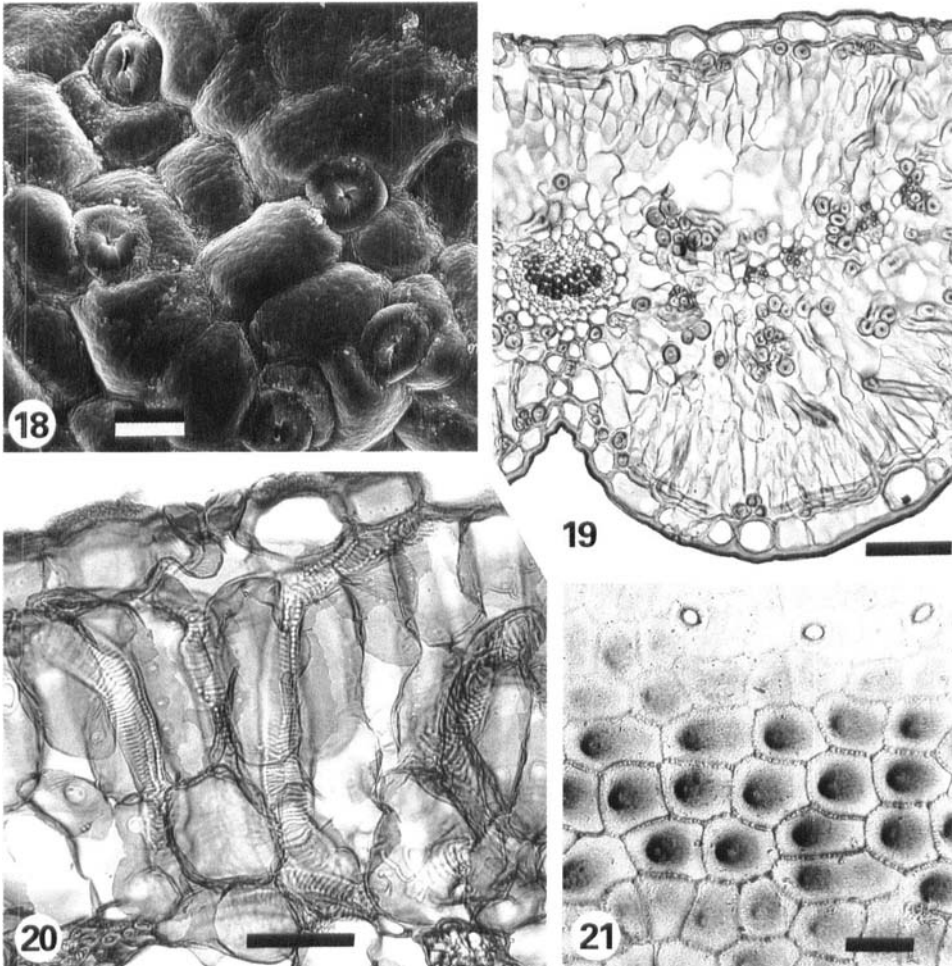
**Primary sculpturing.** **VENATION:** clearing revealed a brochidodromous pattern in the broader leaves of *S. fruticosus*, but this was usually less distinct in the narrow leaves of the other spp. **EPIDERMAL CELLS:** similar on both surfaces, domed (Fig. 21), largest diameter up to 80  $\mu\text{m}$ ; anticlinal walls thick, in grooves. **STOMATA:** amphistomatous with approximately equal densities on both surfaces and little variation in density among the spp. examined (Fig. 18, Table 2).

**Secondary sculpturing:** generally striate, parallel or reticulate.

**Tertiary sculpturing:** very little, or no epicuticular wax observed, except for one sample of *S. fruticosus* (Boucher & Shepherd 4341) with abundant small flat plates on the abaxial surface and scattered fine particles on the adaxial.

*T.S. lamina*

**THICKNESS:** *S. barbatus*, *S. micranthus*, *S. ericoides* ssp. *ericoides* variously and distinctively 'lobed' (Figs 19, 22) in TS, with the midrib regions (*c.* 230  $\mu\text{m}$  thick in *S. barbatus* and *S. ericoides* ssp. *ericoides* and 420  $\mu\text{m}$  in *S. micranthus*) forming a groove somewhat thinner than the rest of the lamina (*c.* 600  $\mu\text{m}$  in *S. barbatus*, *S. micranthus* and 470  $\mu\text{m}$  in *S. ericoides* ssp. *ericoides*). *S. fruticosus* *c.* 500  $\mu\text{m}$  overall and *S. ericifolius* thickest (470  $\mu\text{m}$ ) over the midrib (keel) with the much reduced lamina tapering towards the margins. **CUTICLE AND OUTER PERICLINAL WALL:** cuticle from about half as thick as outer periclinal wall to equally thick in individual species; mean wall thickness



Figures 18–21. *Stylapterus fruticosus*, adaxial surface with stomata. Scale bar = 25  $\mu\text{m}$ . Fig. 19. *S. micranthus*, TS showing grooved midrib, isobilateral arrangement and exclusively sclereid idioblasts. Scale bar = 100  $\mu\text{m}$ . Fig. 20. *S. fruticosus*, showing well-developed tracheoidal idioblasts in palisade. Scale bar = 50  $\mu\text{m}$ . Fig. 21. *S. ericifolius*, surface including papillate epidermal cells at leaf margin. Scale bar = 50  $\mu\text{m}$ .

5.5  $\mu\text{m}$  (range 4–8  $\mu\text{m}$ ) and mean cuticle thickness 3  $\mu\text{m}$  (range 1.5–6  $\mu\text{m}$ ). EPIDERMAL CELLS: abaxial and adaxial similar in size and shape, mostly broader than tall and moderately convex, becoming more so at the margins, likewise also away from the margins in *S. barbatus*. MESOPHYLL: isobilateral; palisade 1-layer (locally 2 layers) to each face, 2 layers to each face in *S. fruticosus*; palisade cell length to width ratio *c.* 5:1; ratio of palisade to spongy mesophyll 1:1 or greater with spongy tissue very reduced (almost none in *S. fruticosus*), spongy tissue of generally loosely-packed ovoid or  $\pm$  irregularly-lobed cells. MIDRIB BUNDLE: abaxial collenchyma in *S. barbatus* and *S. ericifolius*, absent in the others; palisade continuous above and below midvein in *S. fruticosus*. MARGIN: prominently domed (papillose) in *S. barbatus*, *S. ericoides* ssp. *ericoides* and *S. ericifolius* (Fig. 21). CRYSTALS: not seen in *S. ericoides* ssp. *ericoides*. IDIOBLASTS: branched sclereids present, tracheoidal cells recorded as absent in all

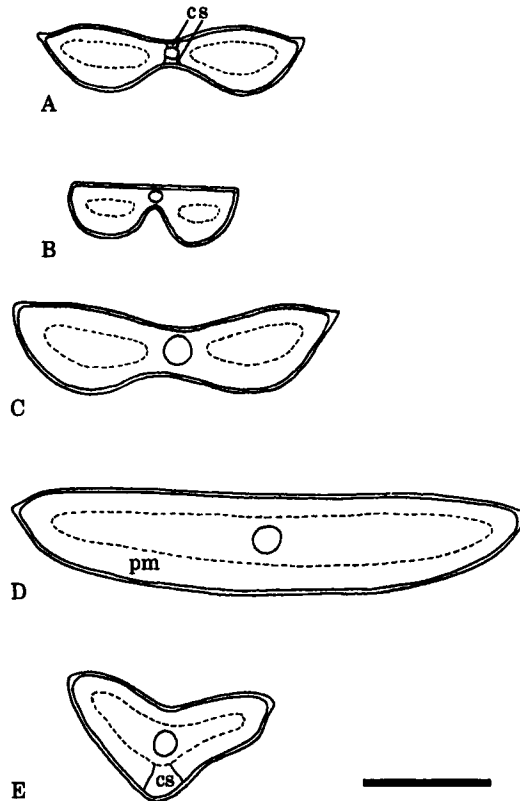


Figure 22. Variation in shape of *Stylapterus* leaves in TS. A, *S. barbatus*; B, *S. micranthus*; C, *S. ericoides* ssp. *ericoides*; D, *S. fruticosus*; E, *S. ericifolius*. Key: cs = collenchymatous tissue; pm = palisade mesophyll. Scale bar = 1 mm.

but *S. fruticosus*, where they were well developed (Fig. 20), but may be present in other species where they are very sparse and/or indistinguishable from vein endings.

#### DISCUSSION

The leaves of the Penaeaceae are all small—leptophyll or nanophyll, *sensu* Raunkiaer (1934). The plants have a generally 'ericoid' growth habit. Leaf shape varies from linear to broadly ovate and they are generally sessile, apart from the presence of very short petioles in *Penaea dahlgrenii* (Rourke & McDonald, 1989). In texture they are all more or less coriaceous and sclerophyllous (Turner, 1994).

#### *Leaf thickness*

The leaves are relatively thick (Table 1), varying from 280  $\mu\text{m}$  in *Endonema retzioides* to 775  $\mu\text{m}$  in one specimen of *Saltera sarcocolla*. The measurements on three specimens



of the latter are so variable they suggest that the total range of intra-specific variation might not be encountered in a limited amount of herbarium material. However, variation in leaf thickness among the six specimens of *P. mucronata*, both fresh and rehydrated is more limited. In all species leaf thickness was positively correlated ( $r$ , 0.519; df, 29;  $P < 0.01$ ) with mean length of stomatal apparatus (an indicator of stomatal size—see below); and negatively correlated with mean stomatal density of both leaf surfaces ( $r$ ,  $-0.477$ ; df, 29;  $P < 0.01$ ). The correlation between leaf thickness and the combined thickness of the adaxial cuticle plus epidermal outer periclinal wall was very weak, just failing to reach statistical significance at the five percent level ( $r$ , 0.3162; df, 30;  $0.1 > P > 0.05$ ). However, removal of a single, obvious outlier (*Endonema retzioides*) from the dataset strengthened the relationship considerably ( $r$ , 0.476; df, 29;  $P < 0.01$ ). So, excluding *E. retzioides*, there is a trend of increase in the combined thickness of adaxial cuticle and epidermal outer periclinal wall with increasing leaf thickness. Examination of Table 1 also suggests relationships between leaf thickness, leaf type (bifacial/isobilateral) and stomatal distribution (hypo/amphistomatous). Leaves thicker than about 500  $\mu\text{m}$  are isobilateral and amphistomatous (or occasionally intermediate) and never bifacial/hypostomatous, although several isobilateral/amphistomatous leaves do have thicknesses considerably less than 500  $\mu\text{m}$ . These relationships are confused by the association between leaf type and stomatal distribution described below. Also, the apparent partial resolution of the variation in leaf thickness along generic lines is similarly confused by this association; with *Endonema* averaging below 300  $\mu\text{m}$ , *Penaea* around 340  $\mu\text{m}$ , *Saltera* with considerable variation but averaging 670  $\mu\text{m}$  and the remaining genera between 500–550  $\mu\text{m}$ .

#### *Cuticle and epidermal cells*

The leaf surface of the Penaeaceae presents few taxonomically or diagnostically useful features. There is no discernible systematic pattern to the variation in the generally striate form of secondary sculpturing, which consists largely of differences in intensity (e.g. Figs 1, 5, 11), sometimes becoming micropapillate, e.g. *Brachysiphon rupestris* (Fig. 2). Appreciable epicuticular wax was observed on only the abaxial surface of *Stylapteris fruticosus*. Although it is possible that old herbarium material may have suffered damage leading to loss of surface features, this is not supported by observations in this study (the Appendix lists fresh and herbarium material). Apart from the rudimentary hairs seen in *Penaea mucronata* (Fig. 12), the leaves of all species are glabrous. These hairs could be the same as the ‘short, peg like hairs’ described by Dahlgren (1971: 7, 12) as covering the branchlets in *Penaea mucronata*.

The epidermal cells on both surfaces lack distinctive features in most species. In surface view, the only addition to a basic pattern of randomly orientated, irregular polygons, is in *Glischrocolla*, where adaxial cells are distinctly more angular than those on the abaxial surface. In TS, the adaxial epidermal cells of *Endonema retzioides* are domed or papillose. The adaxial cuticle in all species is relatively thick, and the adjoining epidermal outer periclinal cell wall approximately equally so; with the mean combined thickness of these two layers lying between 5.8  $\mu\text{m}$  in *Penaea mucronata* and 15.5  $\mu\text{m}$  in *Saltera sarcocolla* (Table 1). There is no apparent systematic trend in this variation, and intra-specific variation in both those species covers the majority of the total range in the family. As mentioned, the relation between mean lamina

thickness and combined cuticle and epidermal wall thickness is insignificant. Although the combined thickness appears positively correlated with stomatal length ( $r$ , 0.519; df, 28;  $P < 0.01$ ) the correlations with both stomatal density and ratio of palisade to spongy mesophyll were not significant ( $P > 0.1$ ), and there was no association between the combined thickness and leaf type.

### *Stomata*

The stomatal complexes are anomocytic throughout the family. They have a constant, oval to broadly oval shape; with the mean stomatal length (Table 2) strongly correlated with both mean width ( $r$ , 0.872; df, 29;  $P < 0.001$ ) and mean estimated aperture area ( $r$ , 0.758; df, 29;  $P < 0.001$ ). Mean stomatal length is thus an acceptable indicator of overall stomatal size; and varies approximately 1.5-fold across the family, from under 30  $\mu\text{m}$  to around 46  $\mu\text{m}$ . *Glischrocolla formosa* has comparatively large stomata, while the smallest ones occur within *Penaea*. Otherwise, there is no clear association between guard cell size and genus. The range of stomatal length recorded within *Brachysiphon* is almost as large as that for the whole family. Stomatal length is not related to stomatal distribution or leaf type. However, there is a weak, but significant negative correlation between stomatal length and mean stomatal density (over both surfaces) ( $r$ ,  $-0.366$ ; df, 29;  $P < 0.05$ ). Mean stomatal density (averaged over both surfaces) is also negatively correlated with mean lamina thickness (see also association with leaf type, below); and it varies more than two-fold in the family, from 73  $\text{mm}^{-2}$  in *Brachysiphon mundii* to 168.5  $\text{mm}^{-2}$  in *Penaea acutifolia*. Such variation in stomatal density needs to be interpreted with care in a broad family survey such as this, e.g. Poole *et al.* (1996) found a similar level of variation within individual leaves of *Alnus glutinosa*. Dahlgren (1971) noted the variability in stomatal density on the adaxial surfaces among population groups of *Penaea cneorum* in particular. Stomatal density is not strongly associated with genus. While, on average, values in *Stylapterus*, *Brachysiphon* and *Saltera* may appear lower than the rest, there is much overlap for individual species and few degrees of freedom for proper statistical contrasts. It is likely that variation in mean stomatal density is less important than the distribution of leaf thickness and type. There is no difference in stomatal density between species with hypostomatous leaves and those with amphistomatous leaves. This supports a similar finding by Kelly & Beerling (1995), who studied a wide variety of herbaceous species from woodland margins.

### *Mesophyll*

Leaf type (bifacial or isobilateral) is a character with systematic value at generic level within the Penaeaceae. All species of *Stylapterus*, *Sonderothamnus* and *Saltera* have isobilateral leaves, and all but one species of *Brachysiphon* (*B. acutus*) are likewise. On the other hand both species of *Endonema* and all but one species of *Penaea* (*P. dahlgrenii*) have bifacial leaves. In *Glischrocolla formosa*, and some species of *Penaea* the arrangement of the mesophyll is basically bifacial with the addition of discontinuous palisade on the abaxial side, tending to an intermediate condition. A tendency for the palisade to be in two layers rather than one is mainly seen in species with an isobilateral arrangement, and usually on the adaxial side (see genus descriptions). Combining

the frequencies of H+ and B+ (Table 1) with those for hypostomatous and bifacial respectively, in a  $2 \times 2$  table gives  $\chi^2_1 = 24.89$  ( $P < 0.001$ ). Of the 16 taxa with isobilateral leaves, none is hypostomatous or intermediate; and of 11 taxa with strictly bifacial leaves, eight are hypostomatous and three intermediate (H+ in Table 1). Thus, the type of stomatal distribution correlates well with leaf type. The ratio of palisade to spongy mesophyll is quite variable (Table 1) across the family. It does not correlate with any of the other features, except that the highest ratios are in species with isobilateral leaves, though other examples of the latter type show ratios well inside the range (lower) for bifacial leaves.

#### *Vascular tissue*

Venation appears to be universally brochidodromous, but becomes less so in linear leaves. The midrib is visible to the naked eye in only some taxa. Internally the veins are quite uniform, embedded and surrounded by parenchymatous bundle sheaths without obvious extensions, although the midrib frequently has collenchyma on the abaxial side. The vascular tissue is quite unvaried across the family and relatively unspecialized. The phloem either completely surrounds, or is adaxial and abaxial to the xylem, and usually lacks fibres.

#### *Crystals and idioblasts*

Cluster crystals (druses) appear ubiquitous in the family, usually in a sub-epidermal location, as well as in the spongy mesophyll close to the veins.

In addition to the isodiametric sclereids (stone cells) seen only in *Slatera sarcocolla*, the two kinds of branched idioblasts (thick-walled sclereids and annular or spirally thickened tracheoidal cells), have long been known as a distinctive feature of leaf anatomy in the Penaeaceae (Van Tieghem, 1893; Rao, 1965, 1991; Rao & Das, 1976). Van Tieghem (1893) published a key to the genera relying heavily on the presence of either or both types. However, the results of the present study cast some doubt on the reliability of these characters. While our observations for *Penaea*, *Glischrocolla* and *Sonderothamnus* agree with earlier work (Van Tieghem, 1893; Dahlgren, 1967a, 1968, 1971), there are inconsistencies in the other four genera. In *Endonema* we failed to find sclereids in *E. retzioides*, whereas the genus is described by both Van Tieghem (1893) and Dahlgren (1967b) as possessing both kinds of idioblast. *Brachysiphon* was said to have only thick-walled sclereids (Van Tieghem, 1893; Dahlgren, 1968), but *B. mundii* clearly showed both kinds (Figs 3, 4), a species not examined by Dahlgren (1968). Similar variability appears within the monospecific genus *Saltera*, where all three specimens of *S. sarcocolla* examined have thick-walled sclereids, but only one has tracheoidal cells. This is in contrast to the observations of Van Tieghem (1893) and Dahlgren (1968) who reported both types as a constant feature of this taxon. According to Van Tieghem (1893), *Stylapterus* has only tracheoidal cells, but Dahlgren (1971) believed *Stylapterus* to be similar to *Penaea* in possessing both types, although the thick-walled type may be sparse and difficult to find in *S. fruticulosus*, in particular. In contrast to previous workers, we had no difficulty in finding the thick-walled cells in every specimen examined, including the two specimens of *S. fruticulosus*. The latter species was the only one in which we

could clearly see tracheoidal cells (both specimens). Dahlgren (1971) noted the variable frequency of tracheoidal cells in *Stylapterus* in particular, as well as the need for a special study of their importance and function. Although they have been generally classified as sclereids, previous authors (Van Tieghem, 1893; Rao, 1965) have suggested that they are connected to the leaf vascular tracheids and are involved in water transport or storage. Dahlgren (1971) was able to see the connection with the main vascular system in a specimen of *S. fruticosus*, but we have been unable to do so. In most instances these tracheoidal cells are easily distinguished from the tracheary elements of fine veinlets, being noticeably larger than the latter and not organized in bundles (Figs 3, 4, 10, 20). It is conceivable that the so-called tracheoidal idioblasts or sclereids could be a form of enlarged and much extended vein endings, and where significant enlargement has not taken place misidentification could occur. An alternative, though perhaps less likely hypothesis is that the tracheoidal cells are actually sclereids with thin walls having annular or spiral thickening, possibly related to the more conventional thick-walled type by developmental arrest.

#### *General remarks*

We support the view of Dahlgren (1968) that, due to variability and inconsistency, leaf anatomical characters have no significant role in the systematics or diagnostics of the Penaeaceae. This is in contrast to Keating's (1984) conviction of the value of leaf histological studies to the diagnostics and clarification of evolutionary relationships in the Myrtales as a whole. He was aware of the limited sampling of genera in his analysis, since only two species, *Endonema laterifolia* and *Penaea mucronata*, represented the Penaeaceae. Our study includes every genus and most of the recognized species, and, for example, records the frequent occurrence of amphistomatous and isobilateral leaves in the family, two features not observed by Keating (1984). While care must be taken in interpreting the correlations of characters described above, these two associated characters form a major part of the main trend in the variation in leaf anatomy of the family. Isobilateral and/or amphistomatous leaves are known in the Myrtales (Keating, 1984), but are not common. They appear to be absent from the Alzateaceae, Crypteroniaceae, Oliniaceae and Rhynchocalycaceae (Mújica & Cutler, 1974; Keating, 1984; Mentinck & Baas, 1992), families purported to be the closest relatives of the Penaeaceae (Dahlgren & Van Wyk, 1988). Alongside the trend towards isobilateral and amphistomatous leaves, is one of increasing leaf thickness. The association between the two trends is imperfect, whereby the thickest leaves are exclusively isobilateral and amphistomatous, but some isobilateral amphistomatous leaves are thinner, in the range occupied by bifacial hypostomatous leaves. As leaves get thicker, the amount of palisade mesophyll tends to increase, the thickness of the adaxial cuticle plus epidermal outer periclinal cell wall increases, and mean stomatal density decreases; and stomatal size may increase slightly with reduction in density.

The above combination of features may constitute an 'adaptive character syndrome' (Rury & Dickison, 1984). Most have been regarded, especially when encountered together, as xeromorphic adaptations (Fahn & Cutler, 1992). Increase in palisade tissue, possibly leading to increased leaf thickness is thought to improve gas exchange efficiency under conditions where water supply is short (Parkhurst, 1978). Amphistomatous leaves are frequently associated with plants growing under

dry conditions, but the primary relationship is probably with increased leaf thickness, again for reasons concerned with optimized gas exchange under water stress (Parkhurst, 1978). Tracheoidal idioblasts may improve the efficiency of water movement or may be used for water storage (Fahn & Cutler, 1992: 92–95). While the thick-walled sclereids could have a role in preventing mesophyll tissue from collapsing under water deficit, Heide-Jorgensen (1990) has suggested that the sclereids in the xeromorphic leaves of *Hakea suaveolens* serve for water transport as well as support. However, a direct relationship between cuticle thickness and resistance to water diffusion now seems unlikely (Riederer, 1991), with thick cuticles probably having a much more general structural and protective role (Kerstiens, 1996). From field measurements of total leaf conductance, *Penaea mucronata*, in fact appears to behave as a mesophyte (Miller, Miller & Miller, 1984). The family favours mainly moist, mesic habitats (Rourke, 1995), with the exception of *Brachysiphon microphyllus*, a xeromorphic species which inhabits rock cracks in the arid interior of the south western Cape, outside the present distribution of the rest of the family. Though not examined here, the description and drawings of leaf morphology suggest rather thick, narrow leaves, somewhat similar in cross section to species of *Stylapterus* (Fig. 22), presumably amphistomatous and with isobilateral mesophyll. However, in another recently described species, *Penaea dahlgrenii* (Rourke & McDonald, 1989), the last two characters appear not to be primarily xeromorphic, as the species inhabits perennially moist sites.

Carlquist & Debuhr (1977) proposed that variation in xylem anatomy in the Penaeaceae shows a xeromorphic trend, with species from the most xeric sites, including cracks in rock faces, having the lowest values of their calculated 'mesomorphy index'; e.g. *Brachysiphon rupestris*, *Sonderothamnus petraeus* and *Stylapterus fruticulosus*. The leaves of these three species are no more xeromorphic than their congeners, though all have quite thick, amphistomatous, isobilateral leaves (Table 1). However, a number of other species from more mesic habitats with higher mesomorphy index values have the same leaf anatomical features, e.g. *Saltera sarcocolla*. Both species of *Endonema* grow in more mesic habitats (Dahlgren, 1967b), and *E. retzioides* has a rather higher xylem mesomorphy index than *E. laterifolia*. Nevertheless, the former species has leaf characters that might be regarded as xeromorphic (Fahn & Cutler, 1992), i.e. reduced leaf area (narrow leaves), strongly recurved margins, and conspicuously convex (domed) adaxial epidermal outer cell walls in TS. According to Dahlgren (1967c), all the species of *Stylapterus* inhabit relatively mesic sites, whereas Carlquist & Debuhr (1977) regard *S. fruticulosus*, with its low mesomorphy index as coming from quite xeric ones. However, all the species have thick, amphistomatous, isobilateral leaves, and *S. fruticulosus* shows the least reduction in cross sectional shape in the genus (Fig. 22D). *S. ericoides* ssp. *ericoides* (Fig. 22C) has leaves much reduced in cross-sectional shape together with a relatively low mesomorphy index, yet it apparently inhabits the most mesic sites.

It is clearly difficult to identify a definite trend in leaf xeromorphic characteristics that correlates closely to the one proposed for xylem anatomy. Although it has been suggested (Van der Merwe *et al.*, 1994) that many fynbos species exhibit leaf adaptations typical of xerophytes, it is likely that the general sclerophylly in the Penaeaceae and other fynbos taxa is primarily protective (Turner, 1994), and related to ensuring long leaf lifespans in species growing slowly on the nutrient poor soils, rather than an adaptation to summer drought (Stock, van der Heyden & Lewis, 1992). Nevertheless, the current distribution of Penaeaceae is relictual

(D.J. McDonald, pers. comm.), and may not reflect the past habitats and climate which they encountered.

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## APPENDIX: DETAILS OF SPECIMENS EXAMINED

Taxon	ID no.	Dried (D)/ Fresh (F)	Collector/Number	Site/Remarks (from Herbarium sheet, etc.)
<i>Penaea mucronata</i> L.	00	F	NBI Kirstenbosch	Kirstenbosch Estate
<i>Penaea mucronata</i> L.	0	F	NBI Kirstenbosch	Kalk Bay
<i>Penaea mucronata</i> L.	1	D	National Herbarium, Pretoria 269	Cape Flats (c. sea level)
<i>Penaea mucronata</i> L.	2	D	Parker 3693	Upper Laurens River valley (360 m)
<i>Penaea mucronata</i> L.	3	D	R.J. Rodin 3208	900 m; 0.6 m plant
<i>Penaea mucronata</i> L.	4	D	J.P.H. Acocks 22982	150 m; 2 m plant, by swampy stream
<i>P. cneorum</i> ssp. <i>cneorum</i> Meerb.	5	D	S. Carlquist 4539	45 m; 4.5 m plant
<i>P. cneorum</i> ssp. <i>cneorum</i> Meerb.	6	D	Fourcade 358	Humansdorp Flats, Racheibosch (210 m)
<i>P. cneorum</i> ssp. <i>gigantea</i> R. Dahlgren	7	D	Dahlgren & Strid 2925	380 m; plant 2-4 m tall
<i>P. cneorum</i> ssp. <i>ruscifolia</i> R. Dahlgren	8	D	I. Williams 2307	30 m; up to 4 m tall; damp places near streams
<i>P. cneorum</i> ssp. <i>lancoolata</i> R. Dahlgren	9	D	Dahlgren & Strid 3063	780 m; part burnt area on sloping ground; plants 45-70 cm tall
<i>P. acutifolia</i> A. Juss.	10	D	Dahlgren & Strid 2927	530 m; plants 40-60 cm
<i>P. dahlgrenii</i> Rourke	11	D	Bijl	700 m; streamside; plants 0.5-1.5 m tall
<i>Syplapteris barbatus</i> A. Juss.	12	D	Dahlgren & Strid 4168	1250 m; sandy soil, slightly moist
<i>S. mucronatus</i> R. Dahlgren	13	D	Esterhuysen 35659	360-400 m; 0.3-0.6 m tall
<i>S. ericoides</i> A. Juss. ssp. <i>ericoides</i>	14	D	Dahlgren & Strid 3836	280-300 m; in coarse white sand along streamlet; 0.8-0.9 m
<i>S. frutescens</i> (L. fil.) A. Juss.	15	D	Dahlgren & Strid 2420	Among <i>Erica</i> ; 0.3 m
<i>S. frutescens</i> (L. fil.) A. Juss.	16	D	Boucher & Shepherd 4341	180 m; on well-drained sandy soil; 1.5 m tall
<i>S. ericifolius</i> (A. Juss.) R. Dahlgren	17	D	H.C. Taylor 10031	450 m; by stream; up to 0.75 m tall

Continued



## APPENDIX—Continued

Taxon	ID no.	Dried (D)/ Fresh (F)	Collector/Number	Site/Remarks (from Herbarium sheet, etc.)
<i>Brachysiphon ficatus</i> (L.) Gilp.	18	D	H. Bolus 362	550 m
<i>Brachysiphon ficatus</i> (L.) Gilp.	18A	F	NBI Kirstenbosch	
<i>B. acutus</i> A. Juss.	20	D	Carlquist 4959	
<i>B. cf. rupestris</i> Sond.	21	D	J.J. Bos 685	800 m; cracked rock faces
<i>B. rupestris</i> Sond.	22	D	H. Bolus 9827	100–200 m; larger leaves cf. above
<i>B. mundii</i> Sond.	23	D	Burgers 1683	90 m; steep N-facing slopes on limestone bedrock
<i>Sonderothamnus petraeus</i> (Barker) R. Dahlgren	24	D	Dahlgren & Strid 3519	N-facing rock fissures; little soil, lichens on stem
<i>S. speciosus</i> (Sond.) R. Dahlgren	25	D	E.R. Orchard 218	250 m; open sandy crest with rocks
<i>Saltera sarcocolla</i> (L.) Bull.	26	D	Dahlgren & Strid 3586	390 m; shrubs 0.7–1 m tall
<i>Saltera sarcocolla</i> (L.) Bull.	26A	F	NBI Kirstenbosch	
<i>Saltera sarcocolla</i> (L.) Bull.	27	D	Dahlgren & Strid 4994	In sand & stones; shrubs up to 0.5 m
<i>Endonema laterifolia</i> (L. fil.) Gilg.	28	D	E. Esterhuysen 5064	S-facing slopes
<i>E. retzioides</i> Sond.	29	D	P. Goldblatt 2063	SE-facing slope
<i>Glossocolla formosa</i> (Thunb.) R. Dahlgren	30	D	J.P. Rourke 1046	In moist peaty soil on SE-facing ledge; up to 1 m tall