

COMPARATIVE ANATOMY AND SYSTEMATICS OF
TWELVE WOODY AUSTRALASIAN GENERA
OF THE SAXIFRAGACEAE

By

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TABLE OF CONTENTS

SECTION	PAGE
ACKNOWLEDGEMENTS.....	ii
LIST OF TABLES.....	v
LIST OF FIGURES.....	vi
KEY TO TISSUES: NODES AND PETIOLES.....	xiv
ABSTRACT.....	xv
INTRODUCTION.....	1
Systematics of the Saxifragaceae.....	1
Anatomical Work on the Saxifragaceae.....	3
Anatomical Work on New Zealand Genera.....	6
Anatomical Work on the Cunoniaceae.....	9
Rationale for the Present Study.....	10
MATERIALS AND METHODS.....	14
RESULTS.....	19
<u>Tetracarpaea</u> Hook.	19
<u>Ixerba</u> A. Cunn.	31
<u>Bauera</u> Banks	43
<u>Anopterus</u> Labill.	59
<u>Cuttsia</u> F. v. Muell.	73
<u>Abrophyllum</u> Hook. f.	85
<u>Carpodetus</u> J. R. & G. Forst.	95
<u>Corokia</u> A. Cunn.	110
<u>Argophyllum</u> J. R. & G. Forst.	127
<u>Donatia</u> J. R. & G. Forst.	141
<u>Anodopetalum</u> A. Cunn.	150
<u>Aphanopetalum</u> Endl.	160
DISCUSSION.....	168
Anatomy of Twelve Australasian Genera.....	168
Relationships of <u>Ixerba</u>	173
Relationships of <u>Anopterus</u>	176
Relationships of <u>Cuttsia</u> and <u>Abrophyllum</u>	179
Relationships of <u>Carpodetus</u>	181
Relationships of <u>Corokia</u> and <u>Argophyllum</u>	185
Relationships Among the Escallonioideae.....	190

Possible Delimitation of the Escallonioideae.....	193
Relationships of <u>Tetracarpaea</u>	195
Relationships of <u>Bauera</u>	198
Relationships of <u>Anodopetalum</u>	202
Relationships of <u>Aphanopetalum</u>	204
Relationships of <u>Donatia</u>	206
Australasian Genera and Geological History.....	209
CONCLUSIONS.....	211
SUMMARY.....	220
APPENDIX.....	221
LITERATURE CITED.....	229
BIOGRAPHICAL SKETCH.....	240

LIST OF TABLES

TABLE	PAGE
Table 1. Twelve Australasian genera classified according to Adolph Engler.....	13
Table 2. Woody saxifragaceous species from Australasia examined anatomically.....	18
Table 3. Anatomical features of eleven Australasian woody saxifragaceous genera.....	169
Table 4. Specimens of Australasian woody Saxifragaceae examined anatomically.....	222

LIST OF FIGURES

FIGURE	PAGE
Figure 1. Leaf of <u>Tetracarpaea tasmaniaca</u>	26
Figure 2. Vein ending of <u>T. tasmaniaca</u>	26
Figure 3. Transverse sections of a node and petiole of <u>T. tasmaniaca</u>	26
Figure 4. Transverse section of a leaf of <u>T. tasmaniaca</u>	28
Figure 5. Transverse section of the abaxial epidermis of a leaf of <u>T. tasmaniaca</u>	28
Figure 6. Transverse section of a leaf of <u>T. tasmaniaca</u>	28
Figure 7. Marginal tooth of a leaf of <u>T. tasmaniaca</u>	28
Figure 8. Transverse section of the secondary xylem of <u>T. tasmaniaca</u>	30
Figure 9. Radial section of the secondary xylem of <u>T. tasmaniaca</u>	30
Figure 10. Secondary xylem of <u>T. tasmaniaca</u>	30
Figure 11. Tangential section of the secondary xylem of <u>T. tasmaniaca</u>	30
Figure 12. Radial section of the secondary xylem of <u>T. tasmaniaca</u>	30
Figure 13. Leaf of <u>Ixerba brexioides</u>	38
Figure 14. Vein ending of <u>I. brexioides</u>	38
Figure 15. Transverse sections of a node and petiole of <u>I. brexioides</u>	38
Figure 16. Transverse section of a leaf of <u>I. brexioides</u>	40
Figure 17. Optically anisotropic crystalloid from a leaf of <u>I. brexioides</u>	40

Figure 18. Transverse section of the midvein of a leaf of <u>I. brexioides</u>	40
Figure 19. Paradermal section of the abaxial epidermis of a leaf of <u>I. brexioides</u>	40
Figure 20. Transverse section of the abaxial epidermis of a leaf of <u>I. brexioides</u>	40
Figure 21. Marginal crenation of a leaf of <u>I. brexioides</u>	42
Figure 22. Paradermal section of a marginal crenation of a leaf of <u>I. brexioides</u>	42
Figure 23. Transverse section of the secondary xylem of <u>I. brexioides</u>	42
Figure 24. Radial section of the secondary xylem of <u>I. brexioides</u>	42
Figure 25. Tangential section of the secondary xylem of <u>I. brexioides</u>	42
Figure 26. Radial section of the secondary xylem of <u>I. brexioides</u>	42
Figure 27. Leaf of <u>Bauera rubioides</u>	52
Figure 28. Diversity of leaf shapes in <u>B. capitata</u>	52
Figure 29. Vein ending of <u>B. rubioides</u>	52
Figure 30. Diagrammatic representation of a node and the nodal pattern of <u>B. rubioides</u>	54
Figure 31. Transverse section of a leaf of <u>B. capitata</u>	56
Figure 32. Transverse section of a leaf of <u>B. capitata</u> showing prismatic crystals near a vascular bundle.....	56
Figure 33. Transverse section of a leaf of <u>B. sessiliflora</u>	56
Figure 34. Transverse section of a leaf of <u>B. sessiliflora</u>	56
Figure 35. Paradermal section of the abaxial epidermis of a leaf of <u>B. rubioides</u>	56
Figure 36. Transverse section of the abaxial epidermis of a leaf of <u>B. capitata</u>	56

Figure 37. Marginal serration of a leaf of <u>B. rubioides</u>	56
Figure 38. Transverse section of a leaf of <u>B. capitata</u>	56
Figure 39. Transverse section of the secondary xylem of <u>B. rubioides</u>	58
Figure 40. Radial section of the secondary xylem of <u>B. rubioides</u>	58
Figure 41. Radial section of the secondary xylem of <u>B. sessiliflora</u>	58
Figure 42. Tangential section of the secondary xylem of <u>B. sessiliflora</u>	58
Figure 43. Leaf of <u>Anopterus glandulosus</u>	68
Figure 44. Vein ending of <u>A. glandulosus</u>	68
Figure 45. Transverse section of a node of <u>A. glandulosus</u>	68
Figure 46. Transverse sections of a petiole of <u>A. glandulosus</u>	68
Figure 47. Transverse sections of a petiole of <u>A. macleayanus</u>	68
Figure 48. Transverse section of a leaf of <u>A. glandulosus</u>	70
Figure 49. Transverse section of the midvein of a leaf of <u>A. glandulosus</u>	70
Figure 50. Transverse section of the midvein of a leaf of <u>A. macleayanus</u>	70
Figure 51. Transverse section of the abaxial epidermis of a leaf of <u>A. glandulosus</u>	70
Figure 52. Marginal crenation of a leaf of <u>A. glandulosus</u>	70
Figure 53. Paradermal section of a marginal crenation of a leaf of <u>A. glandulosus</u>	70
Figure 54. Transverse section of the secondary xylem of <u>A. glandulosus</u>	72
Figure 55. Radial section of the secondary xylem of <u>A. glandulosus</u>	72

Figure 56. Tangential section of the secondary xylem of <u>A. glandulosus</u>	72
Figure 57. Radial section of the secondary xylem of <u>A. glandulosus</u>	72
Figure 58. Leaf of <u>Cuttsia viburnea</u>	80
Figure 59. Vein ending of <u>C. viburnea</u>	80
Figure 60. Transverse sections of a node and petiole of <u>C. viburnea</u>	80
Figure 61. Transverse section of a leaf of <u>C. viburnea</u>	82
Figure 62. Crystal sand in the spongy mesophyll layer of a leaf of <u>C. viburnea</u>	82
Figure 63. Transverse section of the midvein of a leaf of <u>C. viburnea</u>	82
Figure 64. Paradermal section of the abaxial epidermis of a leaf of <u>C. viburnea</u>	82
Figure 65. Marginal serration of a leaf of <u>C. viburnea</u>	82
Figure 66. Transverse section of the secondary xylem of <u>C. viburnea</u>	84
Figure 67. Radial section of the secondary xylem of <u>C. viburnea</u>	84
Figure 68. Tangential section of the secondary xylem of <u>C. viburnea</u>	84
Figure 69. Radial section of the secondary xylem of <u>C. viburnea</u>	84
Figure 70. Leaf of <u>Abrophyllum ornans</u>	92
Figure 71. Vein ending of <u>A. ornans</u>	92
Figure 72. Transverse sections of a node and petiole of <u>A. ornans</u>	92
Figure 73. Transverse section of a leaf of <u>A. ornans</u>	94
Figure 74. Transverse section of a midvein of a leaf of <u>A. ornans</u>	94
Figure 75. Transverse section of the abaxial epidermis of a leaf of <u>A. ornans</u>	94

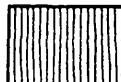
Figure 76. Transverse section of the secondary xylem of <u>A. ornans</u>	94
Figure 77. Radial section of the secondary xylem of <u>A. ornans</u>	94
Figure 78. Tangential section of the secondary xylem of <u>A. ornans</u>	94
Figure 79. Leaf of <u>Carpodetus serratus</u>	105
Figure 80. Domatium in the axil of a secondary vein of <u>C. serratus</u>	105
Figure 81. Vein ending of <u>C. serratus</u>	105
Figure 82. Transverse sections of a node and petiole of <u>C. serratus</u>	105
Figure 83. Transverse section of a leaf of <u>C. serratus</u>	107
Figure 84. Transverse section of a leaf of <u>C. serratus</u>	107
Figure 85. Transverse section of a midvein of a leaf of <u>C. serratus</u>	107
Figure 86. Marginal serration of a leaf of <u>C. serratus</u>	107
Figure 87. Transverse section of the secondary xylem of <u>C. serratus</u>	109
Figure 88. Transverse section of the secondary xylem of <u>C. major</u>	109
Figure 89. Radial section of the secondary xylem of of <u>C. arboreus</u>	109
Figure 90. Tangential section of the secondary xylem of <u>C. serratus</u>	109
Figure 91. Leaf of <u>Corokia macrocarpa</u>	120
Figure 92. Leaf of <u>C. carpodetoides</u>	120
Figure 93. Vein ending of <u>C. macrocarpa</u>	120
Figure 94. Transverse sections of a node and petiole of <u>C. macrocarpa</u>	120
Figure 95. Transverse sections of a node and petiole of <u>C. virgata</u>	122

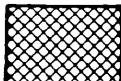
Figure 96. Transverse section of a leaf of <u>C. carpodetoides</u>	122
Figure 97. Transverse section of a midvein of a leaf of <u>C. virgata</u>	122
Figure 98. Transverse section of a midvein of a leaf of <u>C. macrocarpa</u>	122
Figure 99. Transverse section of a leaf of <u>C. macrocarpa</u>	124
Figure 100. Paradermal section of the abaxial epidermis of a leaf of <u>C. macrocarpa</u>	124
Figure 101. Transverse section of the abaxial epidermis of a leaf of <u>C. virgata</u>	124
Figure 102. Multicellular, T-shaped trichome of <u>C. macrocarpa</u>	124
Figure 103. Multicellular, T-shaped trichome of <u>C. virgata</u>	124
Figure 104. Multicellular, T-shaped trichome of <u>C. macrocarpa</u>	124
Figure 105. Pitting between the terminal cell and the uppermost stalk cell of a T-shaped trichome of <u>C. macrocarpa</u>	124
Figure 106. Transverse section of the secondary xylem of <u>C. buddleiooides</u>	126
Figure 107. Transverse section of the secondary xylem of <u>C. collenettei</u>	126
Figure 108. Radial section of the secondary xylem of <u>C. collenettei</u>	126
Figure 109. Tangential section of the secondary xylem of <u>C. whiteana</u>	126
Figure 110. Leaf of <u>Argophyllum cryptophlebum</u>	136
Figure 111. Vein ending of <u>A. nullumense</u>	136
Figure 112. Transverse sections of a node and petiole of <u>A. nullumense</u>	136
Figure 113. Transverse section of a leaf of <u>A. nullumense</u>	138
Figure 114. Transverse section of the midvein of a leaf of <u>A. nullumense</u>	138

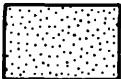
Figure 115. Transverse section of the abaxial epidermis of a leaf of <u>A. nullumense</u>	138
Figure 116. Pitting between the terminal cell and uppermost stalk cell of a T-shaped trichome of <u>A. cryptophlebum</u>	138
Figure 117. Marginal serration of a leaf of <u>A. cryptophlebum</u>	138
Figure 118. Transverse section of the secondary xylem of <u>A. nullumense</u>	140
Figure 119. Radial section of the secondary xylem of <u>A. ellipticum</u>	140
Figure 120. Tangential section of the secondary xylem of <u>A. ellipticum</u>	140
Figure 121. Radial section of the secondary xylem of <u>A. ellipticum</u>	140
Figure 122. Leaves of <u>Donatia novae-zelandiae</u>	147
Figure 123. Portion of a lamina of <u>D. novae-zelandiae</u>	147
Figure 124. Unilacunar, one-trace nodal pattern of <u>D. novae-zelandiae</u>	147
Figure 125. Transverse section of a leaf of <u>D. novae-zelandiae</u>	147
Figure 126. Portion of lamina of <u>D. novae-zelandiae</u> proximal to the leaf apex.....	147
Figure 127. Lignified parenchyma cells abaxial to vascular bundles in leaves of <u>D. novae-zelandiae</u>	149
Figure 128. Paradermal section of a leaf of <u>D. novae-zelandiae</u>	149
Figure 129. Transverse section of the abaxial epidermis of a leaf of <u>D. novae-zelandiae</u>	149
Figure 130. Multicellular, uniseriate trichome of <u>D. novae-zelandiae</u>	149
Figure 131. Transverse section of a stem of <u>D. novae-zelandiae</u>	149
Figure 132. Radial section of the secondary xylem of <u>D. novae-zelandiae</u>	149

Figure 133. Leaf of <u>Anodopetalum biglandulosum</u>	157
Figure 134. Vein ending of <u>A. biglandulosum</u>	157
Figure 135. Transverse sections of a node and petiole of <u>A. biglandulosum</u>	157
Figure 136. Transverse section of a leaf of <u>A. biglandulosum</u>	159
Figure 137. Transverse section of a midvein of a leaf of <u>A. biglandulosum</u>	159
Figure 138. Marginal crenation of a leaf of <u>A. biglandulosum</u>	159
Figure 139. Transverse section of the secondary xylem of <u>A. biglandulosum</u>	159
Figure 140. Radial section of the secondary xylem of <u>A. biglandulosum</u>	159
Figure 141. Tangential section of the secondary xylem of <u>A. biglandulosum</u>	159
Figure 142. Leaf of <u>Aphanopetalum resinosum</u>	165
Figure 143. Transverse section of a stem and petiole of <u>A. resinosum</u>	165
Figure 144. Transverse section of the avascular stipules of <u>A. resinosum</u>	165
Figure 145. Vein ending of <u>A. resinosum</u>	165
Figure 146. Transverse sections of a node and petiole of <u>A. resinosum</u>	167
Figure 147. Transverse section of a leaf of <u>A. resinosum</u>	167
Figure 148. Transverse section of a midvein of a leaf of <u>A. resinosum</u>	167
Figure 149. Marginal serration of a leaf of <u>A. resinosum</u>	167

Key to Tissues Nodes and Petioles

Sclerenchyma  Xylem 

Lignified
Parenchyma  Collenchyma 

Cork  Phloem 

From Metcalfe and Chalk (1950) with minor modification

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Vegetative anatomical data are provided for twelve woody saxifrageous genera from Australasia. These data are used, where possible, to determine the taxonomic position of these plants. The twelve genera are Tetracarpaea, Ixerba, Bauera, Anopterus, Cuttsia, Abrophyllum, Carpodetus, Argophyllum, Corokia, Donatia, Anodopetalum and Aphano-petalum. Typically these taxa possess dorsiventral leaves with uniseriate epidermides and anomocytic stomatal apparatuses. The nodal pattern is either unilacunar, one-trace or trilacunar, three-trace. The wood possesses angular, solitary pores, long vessel elements with oblique, scalariform perforation plates, tracheids with spiral thickenings and sparse axial parenchyma. Cuttsia, Abrophyllum, Carpodetus, Ixerba, Anopterus, Corokia and Argophyllum possess most or all of eleven anatomical features of an archetypical woody

saxifrage. While wood anatomy is similar among Tetracarpaea, Bauera and an archetypical woody saxifrage, leaf anatomy is distinctive for each group. Donatia, Anodopetalum and Aphanopetalum possess few anatomical features of an archetypical woody saxifrage. Ixerba is anatomically isolated from the Brexioideae, but is similar to Anopterus in the Escallonioideae. Cuttsia and Abrophyllum are very similar anatomically and closely related. Anatomical data do not support the maintenance of the tribe Argophylleae of the Escallonioideae which includes Carpodetus, Corokia and Argophyllum. Carpodetus is more similar anatomically to Cuttsia and Abrophyllum than to Corokia and Argophyllum. Corokia and Argophyllum are very similar anatomically and probably closely related, but their taxonomic position remains obscure. Anatomical data support the union of the genus Argyrocallymma with Carpodetus, and the union of the genus Colmeiroa with Corokia. Tetracarpaea and Bauera are anatomically distinctive and isolated genera and may deserve familial status. Tetracarpaea is more closely allied to the Saxifragaceae based upon its wood anatomy, while Bauera is more closely allied to the Cunoniaceae because of its opposite leaves and foliaceous stipules. The nodal, leaf and wood anatomy of Anodopetalum is more similar to that of the Cunoniaceae than to that of the Saxifragaceae. Aphanopetalum and Donatia are readily distinguishable and isolated from the Saxifragaceae, but their taxonomic positions remain obscure. Donatia should probably be placed in its own family, but Aphanopetalum remains an enigma.

INTRODUCTION

Systematics of the Saxifragaceae

Although the family *Saxifragaceae*, *sensu lato*, is cosmopolitan, most species occur in temperate regions. The family contains trees, shrubs, vines, and herbs, and approximately 40 genera contain woody species. The taxonomic problems in the *Saxifragaceae* are numerous and well known (e.g., Cronquist, 1968; Dahlgren, 1975; Stern, 1974b; Takhtajan, 1980; Thorne, 1976, 1983), and occur at almost every taxonomic level.

According to Engler (1928), the family consists of 15 subfamilies, 80 genera and approximately 1200 species. Thorne (1976, 1983) and Schulze-Menz (1964) also recognize a single large family that consists of 13-17 subfamilies and 78 to 80 genera. Other taxonomists have divided this group of plants into either a few families (Cronquist, 1968, 1981; Hutchinson, 1967) or many families (Airy Shaw in Willis, 1973; Dahlgren, 1975, 1980, 1983; Takhtajan 1966, 1980, 1983). These smaller families usually correspond to Engler's (1928) subfamilies (Takhtajan, 1980), but may be much more inclusive (Cronquist, 1981).

Despite these differing opinions concerning the number of families, most taxonomists agree that the *Saxifragaceae* belong to the order Rosales (Engler, 1928; Schulze-Menz,

1964; Cronquist, 1981; Thorne, 1983), or the roughly equivalent order Saxifragales (Takhtajan, 1980). Dahlgren (1975, 1980, 1983), however, deviated from this consensus and split the various families into two superorders (Rosiflorae and Corniflorae) distributed among three orders (Cunoniales, Saxifragales, and Cornales). Hutchinson (1967) divided Saxifragaceae along herbaceous and ligneous lines, and placed the corresponding genera into his Saxifragales and Cunoniales, respectively.

In addition to these largely unresolved taxonomic problems, the placement and delimitation of several genera is questionable. Bauera, for example, has been placed in the Saxifragaceae (Engler, 1928), the monogeneric Baueraceae (Hutchinson, 1967), and the Cunoniaceae (Cronquist, 1981). Aphanopetalum is another genus often placed in the Cunoniaceae, but its affinities are questionable (Dickison, 1980b). Donatia is also enigmatic. Engler (1890) originally placed this genus in the Saxifragaceae, but later (1928) was uncertain of its affinities. Other taxonomists have placed Donatia in the Stylidiaceae (Mildbraed, 1907; Thorne, 1976, 1983; Dahlgren, 1975, 1980, 1983) or in the monogeneric Donatiaceae (Cronquist, 1981). Another bewildering genus, Corokia, has been shuttled among the Saxifragaceae (Engler, 1928), Escalloniaceae (Takhtajan, 1980), Cornaceae (Cronquist, 1981), and Corokiaceae (Dahlgren, 1983). In addition, Corokia carpodetoides was originally the basis of a separate genus, Colmeiroa (Engler, 1928), although Smith

(1958) more recently has combined this genus with Corokia. Similarly, the genus Argyrocallymma, endemic to New Guinea, has been reduced to a section of the genus Carpodetus (Engler, 1928; Reeder, 1946; Schlechter, 1914). Hydrangea also has been divided into two sections, Hydrangea and Cornidia (McClintock, 1957), and each of these sections has at times been elevated to the generic level (Small and Rydberg, 1905).

Anatomical Work on the Saxifragaceae

Early anatomical studies of the Saxifragaceae are those of Thouvenin (1890) and Holle (1893). These workers noted that, despite their anatomical heterogeneity, the woody saxifrageous genera typically share the following characteristics: scalariform perforation plates, three vascular traces at the base of a petiole, and a stomatal apparatus without subsidiary cells. In addition, trichomes vary from simple, unicellular to branched, multicellular or glandular, multicellular types. Prismatic crystals, druses, raphides, or crystal sand also occur.

Thouvenin (1890) recorded anatomical descriptions of stems and leaves for Ixerba, Bauera, Anopterus, Abrophyllum, and Donatia along with other mostly herbaceous Saxifragaceae. He concluded that the escallonioid and brexioid genera (i.e., Ixerba, Anopterus, and Abrophyllum) were a central group and all other tribes should be arranged around them. Donatia and two other genera of the herbaceous tribe Saxifrageae were thought to provide a link to Brexieae

(through Rousseia) because these genera possess secretory cells in the internal portions of the cortex.

Holle (1893) emphasized the anatomy of stem, leaf, and cork of various herbaceous and woody saxifrages including Bauera, Anopterus, Abrophyllum, Argophyllum, Carpodetus, and Anodopetalum. Within all of these genera, cork originates subepidermally. Holle grouped Argophyllum and Abrophyllum together because they lacked crystals. He also placed Carpodetus and Anopterus relatively close together because they possess druses and simple hairs. Anodopetalum and Bauera were isolated from the other four genera and separated from one another because the former has both simple crystals and druses, while the latter only has simple crystals.

Zemann (1907) elaborated on the anatomy of Argophyllum in her monograph of the genus. She divided Argophyllum into two sections, Brachycalyx and Dolichocalyx, based upon the length of the calyx relative to the corolla. Zemann also noted that the leaves of species in section Brachycalyx either possess a bi- to triseriate hypodermis or palisade cells that are very short and square in transection, whereas the leaves of species in section Dolichocalyx lack a hypodermis and possess columnar palisade cells.

In his systematic anatomical summary of the dicotyledons, Solereder (1908) considered all of the above genera to be saxifragaceous. He also included the monotypic genus Colmeiroa among the Saxifragaceae, and noted that according to Engler, this genus possesses two-armed trichomes.

Watari (1939) investigated the leaf anatomy of some Saxifragaceae, including Ixerba, Bauera, Corokia, and Carpodetus. Except for Bauera, these genera possess penninerved, simple leaves, trilacunar nodal patterns and bifacial petioles. Bauera possesses palmately compound leaves, unilacunar nodal patterns and bifacial petioles. In addition, the foliar vascular bundles of these genera exhibit radial rows of xylary elements and fairly regular to irregular starch sheaths adjacent to the pericycle (Watari, 1939). Swamy (1954) studied nodal and petiolar vasculature of the Escallonioidae and reported unilacunar, one-trace nodal patterns in Abrophyllum and Tetracarpaea and trilacunar, three-trace nodal patterns in Ixerba, Anopterus, Cuttsia, Argophyllum, Corokia and Carpodetus. A pentalacunar nodal pattern was noted for Argophyllum laxum. Swamy (1954) indicated that the petiole patterns were similar among certain groups of genera with unilacunar and trilacunar nodal configurations.

As part of a comparative study of the wood anatomy of the Moraceae and alleged allies, Tippo (1938) briefly described the wood of the Hydrangeaceae, Grossulariaceae, sensu stricto, and Escalloniaceae based upon a few species from each family. All three families are characterized by mostly solitary, angular, thin-walled, small-diameter pores. Vessel elements are medium to long and have predominantly scalariform perforation plates. Imperforate elements are mostly tracheids and fiber-tracheids and axial parenchyma is sparse. Xylem rays are heterogeneous with sheath cells

usually present. He concluded that a close relationship exists between the Escalloniaceae and Grossulariaceae, and somewhat less affinity occurs between the Escalloniaceae and Hydrangeaceae. Also, the family Escalloniaceae is the most advanced of these three families.

Metcalfe and Chalk (1950), in their survey of the vegetative anatomy of the dicotyledons, did the last broad treatment of the anatomy of the Saxifragaceae. Based upon their anatomical summaries, they placed Bauera in the Saxifragaceae, sensu stricto, Anopterus, Abrophyllum, Argophyllum, and Carpodetus in the Escalloniaceae, Corokia in the Cornaceae, Anodopetalum in the Cunoniaceae, and Donatia in the Styliadiaceae.

Anatomical Work on New Zealand Genera

Certain studies of the woody plants of New Zealand include the genera Carpodetus, Ixerba, and Corokia (Brook, 1951; Butterfield and Meylan, 1976; Meylan and Butterfield, 1978; Morrison, 1953; Ohtani, Meylan and Butterfield, 1983; Patel, 1973a, 1973b; Robinson and Grigor, 1963; Sampson and McLean, 1965). Some of these studies have provided systematic conclusions based upon anatomical data (Brook, 1951; Patel, 1973a, 1973b). Brook (1951) studied the vegetative anatomy of the endemic Carpodetus serratus and supported its placement in the Escalloniaceae because of its wide rays, vessel elements with scalariform perforation plates, and large bordered pits in the wood fibers. Patel (1973b) investigated the wood anatomy of the

Escalloniaceae, including Carpodetus serratus and the monotypic Ixerba brexioides. Both species possess narrow, angular pores, and vessel elements with scalariform perforation plates. Xylem ray tissue is heterogenous type II. The wood of Carpodetus, however, possesses some very wide rays, whereas the wood of Ixerba possesses only narrow rays. Patel (1973b) concluded that both genera belonged in the Escalloniaceae, although Ixerba was less primitive than Carpodetus.

Although Corokia is widely distributed in the South Pacific Islands, its center of diversity is New Zealand (Allan, 1961). In his study of the Cornaceae Sertorius (1893) described the leaf and stem anatomy of two species of Corokia. He noted, as have other workers (Eyde, 1966; Weiss, 1890), the distinctive, multicellular, T-shaped trichomes in this genus. Sertorius further described the leaves of Corokia with their uni- to biseriate palisade mesophylls, uniseriate epidermides, and sclerenchymatous bundle sheaths surrounding the vascular bundles. He characterized Corokia wood as fine-textured, consisting of numerous, thick-walled fibers bearing circular-bordered or simple pits and solitary, narrow, angular pores. Vessel perforations are scalariform with 10-20 thin bars per plate.

Later studies of the wood anatomy of the Cornaceae (Adams, 1949; Li and Chao, 1954; Patel, 1973a) also have provided descriptions of some species of Corokia. Adams (1949) placed this genus in the Cornaceae near Cornus. While Li

and Chao (1954) acknowledged some affinity between Corokia and Cornus, they also noted a close similarity between the wood of Corokia and the wood of Saxifragaceae. Patel (1973a) noted septate fiber-tracheids in the wood of Corokia, and concluded that affinities with either the Cornaceae or the Escalloniaceae were unsatisfactory for this problematic genus. Descriptions of the distribution and development of anomocytic stomatal patterns on the leaves and flowers of Corokia also have been made (Bhatnagar, 1973; Kapil and Bhatnagar, 1974).

Eyde (1966) excluded Corokia from the Cornaceae based upon floral morphology and anatomy. He argued for an affinity between Corokia and Argophyllum based upon floral anatomy and the presence of multicellular, T-shaped trichomes and septate fiber-tracheids in both genera. Although both genera are included in Engler's (1928) Saxifragaceae, subfamily Escallonioideae, Eyde questioned the validity of this taxonomic arrangement.

Another genus that occurs in New Zealand is Donatia. Mildbraed (1907) used vegetative and reproductive anatomical characteristics and traditional morphological characters to include Donatia in the Stylidiaceae within its own subfamily, Donatioideae. Data from floral anatomy (Carolin, 1960) and embryology (Philipson and Philipson, 1973) also support inclusion of Donatia in the Stylidiaceae, although Carolin discussed the possibility that this family may be closer to the Saxifragaceae rather than the Campanulaceae to which it is often allied (Cronquist, 1981). Other work on

the vegetative anatomy of Donatia (Chandler, 1911; Rapson, 1953) has revealed multicellular, uniseriate trichomes, tannin cells, a lignified endodermis, vessel elements with scalariform perforation plates and sclerenchyma associated with the foliar veins. Based upon these data, these workers support the separation of the Donatiaceae from the Stylidiaceae, although they emphasize that a close taxonomic relationship exists between these two families. Both studies also rejected any saxifragaceous affinities for Donatia. Carlquist (1969), however, has noted morphological similarities between Donatia and the Saxifragaceae.

Anatomical Work on the Cunoniaceae

The family Cunoniaceae is usually regarded as a close relative of the Saxifragaceae (Cronquist, 1981; Engler, 1928; Thorne, 1983). Recent comparative floral and vegetative anatomical studies in the Cunoniaceae (Dickison, 1975c, 1975d, 1980a, 1980b) support the inclusion of Anodopetalum in this family but are inconclusive regarding the placement of Bauera and Aphanopetalum. Dickison (1980a) and earlier workers (Dadswell and Eckersley, 1935; Ingle and Dadswell, 1956) place Anodopetalum among the advanced members of the Cunoniaceae because the wood has numerous vessels commonly distributed in multiples with vessel elements connected by mostly simple perforation plates and opposite to alternate intervacular pitting. Fiber-tracheids, weakly heterogenous xylem ray tissue and aggregated axial parenchyma also are present.

Dickison (1980a, 1980b) studied the nodal and wood anatomy of Bauera sessiliflora. The presence of unilacunar, one-trace nodes and lack of interpetiolar stipules made an affinity to the Cunoniaceae doubtful. Nevertheless, he noted that the wood anatomy is not inconsistent with that found in other advanced cunoniaceous woods. Based upon floral anatomy, Dickison (1975b) supported the inclusion of Bauera in the Saxifragaceae, whereas Bensel and Palser (1975c) favored a placement in the Cunoniaceae. These workers have emphasized the need for further critical study of Bauera. Carey (1938) reported a brief anatomical description of the leaves of Bauera rubioides from two different habitats, and characterized this species as sclerophyllous.

Based upon study of leaf and nodal anatomy in Aphano-petalum, Dickison (1975c, 1980b) found no affinity of this genus to the Cunoniaceae because of its unilacunar, one-trace nodes, lack of stipules, leaf epidermal cells with undulate anticlinal walls, and its scrambling viny habit. He offered no other taxonomic placement for this genus.

Rationale for the Present Study

The Saxifragaceae, sensu lato, are certainly in need of systematic study. Stern (1974b) asserted that our failure to sort out plants assigned to Saxifragaceae has given rise to various classification schemes typically based upon similar, morphological data which emphasize floral morphology. He stated that solutions to the taxonomic problems will develop only from analysis of new data and novel methods of

interpreting old data rather than from reworking old data using time-worn procedures. He suggested intensive studies in plant anatomy as one means of securing new data. The application of comparative anatomical data to the solution of taxonomic and phylogenetic problems in plants is well-known (Bailey, 1944; Carlquist, 1961; Metcalfe and Chalk, 1950, 1979, 1983; Stern, Brizicky, and Eyde, 1969). Details of vegetative anatomy, particularly wood anatomy, have been shown to be especially useful in taxonomic and phylogenetic interpretations of various plant groups without bias or preconception from earlier classification systems (Dickison, 1975a; Stern, 1978b; Tippo, 1938). A recent application of the comparative anatomical method in the Saxifragaceae is a study of Hydrangea (Stern, 1978a).

The purpose of this work is to provide vegetative anatomical and morphological data, especially wood anatomy, for twelve woody saxifrageous genera that occur in Australia, New Zealand, New Guinea, New Caledonia and some smaller South Pacific islands, and to use these data, where possible, to determine the taxonomic position and evolutionary relationships of these plants. Although various anatomical studies of the Saxifragaceae have been done, a comparative, systematic study of the vegetative anatomy of these twelve genera is lacking. The generic level has been chosen as the unit of study to avoid any bias from previous classification systems. The twelve genera are listed in Table 1 according to Engler's (1928) classification system.

This system is presented as a convenient point of reference because it is still the most comprehensive treatment of the Saxifragaceae. Because of the relatively similar geological history of the above Australasian land masses (Raven and Axelrod, 1972), these 12 genera may have undergone similar evolutionary influences and thus may exhibit many anatomical similarities. The present anatomical study should provide new perspectives to aid in delineating taxonomic affinities between and among these plants from the antipodes.

Table 1. Twelve Australasian genera
classified according to Engler (1928).
Distribution information in parentheses:
A, Australia; NC, New Caledonia; NG, New
Guinea; NZ, New Zealand; PI, Other Pacific
Islands; SA, South America; T, Tasmania.

SAXIFRAGACEAE

Subfamily Tetracarpaeoideae

Tribe Tetracarpaeae
Tetracarpaea (T)

Subfamily Brexioideae

Tribe Brexieae
Ixerba (NZ)

Subfamily Baueroideae

Tribe Bauereae
Bauera (A,T)

Subfamily Escallonioideae

Tribe Anoptereae
Anopterus (A,T)

Tribe Cuttsieae
Cuttsia (A)
Abrophyllum (A)

Tribe Argophylleae
Argophyllum (A,NC)
Corokia (A,NZ,PI)
Carpodetus (NG,NZ)

Incertae sedis: Donatia (NZ,SA,T)

CUNONIACEAE

Tribe Spiraeanthemeae
Aphanopetalum (A)

Tribe Cunonieae
Anodopetalum (T)

MATERIALS AND METHODS

Preserved leaves, stems and wood, and dried wood of twelve woody saxifrageous genera from Australasia were used in this study (Table 2). Only dried leaf and stem material of Corokia carpodetoides was available for study. These plant materials are part of an extensive collection of specimens of woody Saxifragaceae gathered through collection, correspondence and exchange by Professor William Louis Stern since the late 1960's. Collection information for individual specimens is included in the appendix (Table 4). The authorities for the names of the species studied are listed in Table 2.

Standard microtechnical methods were used and are similar to those followed by Stern, Sweitzer and Phipps (1970), so that direct comparisons could be made between the present study and recent studies of the woody Saxifragaceae (Stern, 1974a, 1978a; Stern, Sweitzer and Phipps, 1970; Styer and Stern, 1979a, 1979b). Dried wood specimens were boiled in water to eliminate air in the tissue, and the blocks were stored in a 50:50 mixture of 95% ethanol and glycerin. Fluid-preserved wood specimens were washed in water and kept in the same storage solution. Transverse, radial, and tangential sections of unembedded wood samples of each specimen were made with a sliding microtome.

Similar sections were prepared from a few celloidin-embedded wood samples. Sections were stained with Heidenhain's iron alum hematoxylin and counterstained with safranin (Johansen, 1940). Because ammoniacal iron alum dissolves oxalate crystals (Metcalfe, 1983), a few sections were dehydrated and mounted without staining. Wood slivers were macerated using Jeffrey's fluid (50:50 mixture of 10% nitric acid and 10% chromic acid) and stained with safranin (Johansen, 1940). Wood sections and macerations were mounted on glass slides with Canada balsam or Permount.

Dried leaves and stems were boiled in water to reconstitute the tissues, fixed in a formalin-acetic acid-alcohol solution and stored in 70% ethanol. Fluid-preserved leaves and stems also were stored in 70% ethanol. Leaves were cleared using 5% NaOH, washed in distilled water and bleached with a saturated aqueous solution of chloral hydrate (Arnott, 1959). Fully cleared leaves were washed in distilled water, stained with safranin, dehydrated and mounted on glass slides with Permount. Transverse and paradermal sections of paraffin-embedded leaves were cut on a rotary microtome, affixed to a glass slide with a modified Haupt's adhesive (Bissing, 1974), stained with iron alum hematoxylin and safranin and mounted with Canada balsam. A few leaf sections were mounted unstained to detect crystals.

Freehand sections were cut of at least two nodes from a stem and at the proximal (point of attachment to stem), median (a midpoint on petiole), and distal (near lamina) portions of at least two petioles. These sections were

treated with an aqueous phloroglucinol solution followed by concentrated HCl to demonstrate lignified regions. The nodal regions of the stems and petioles of some specimens also were cleared and stained using the above clearing procedure. Species with very short nodes and small petioles were embedded in paraffin and sectioned with a rotary microtome. These sections were treated similarly to the paraffin-embedded leaf sections.

Anatomical analyses of leaves, including vascular architecture, cell and tissue types, trichomes and surface features (i.e., stomata, hydathodes, etc.), followed the terminology used by Hickey (1979), Metcalfe (1979), Theobald, Krahulik and Rollins (1979), and Wilkinson (1979). Although developmental studies were not performed, the term biserrate epidermis was used to describe both the outermost cell layer and the subjacent cell layer in leaves where these two layers occur to be consistent with the terminology of other recent studies of the woody Saxifragaceae (Stern, 1974a, 1978a; Stern, Sweitzer and Phipps, 1970; Styer and Stern, 1979a, 1979b). Measurements were made of both the long and short axes (length and width) of ten pairs of guard cells for each specimen. The nodal patterns and vasculature of the petiole were diagrammed and described following the summaries by Howard (1979a, 1979b).

Characterization of the wood followed the diagnostic features set forth by Tippo (1941) and the terminology advocated by the Committee on Nomenclature, International Association of Wood Anatomists in the Multilingual Glossary

of Terms Used in Wood Anatomy (1964). The only exception is the use of the term marginal parenchyma in place of either terminal or initial axial parenchyma. The following measurements were made for each specimen: 1) pore distributions were percentages based upon counts taken from ten 0.2 mm² microscopic fields; 2) tangential vessel diameters were determined from 50 measurements taken from cross sections; 3) wall thicknesses were based upon measurements of ten vessels and ten imperforate tracheary elements taken from cross sections; 4) lengths of cells were based upon measurements from end to end of 50 vessel elements and 50 imperforate tracheary elements taken from macerated wood; 5) number of bars per perforation plate were counted from thirty scalariform perforation plates; 6) end-wall angles of vessel elements, relative to the vertical axis of the cell, were measured for ten cells from tangential sections using an ocular goniometer; 7) vertical diameters of intervacular pits were determined from ten pits viewed in radial section; 8) length and width of xylem rays were measured from ten rays viewed in tangential section. Unless noted otherwise, the measurements reported below represent an average for all the species examined in a genus.

Table 2. Woody saxifragaceous species from Australasia
examined anatomically: d, dried material;
p, fluid-preserved material.

SPECIES	WOOD	LEAVES
<u>Abrophyllum ornans</u> Hook. f.	d p	p
<u>Anodopetalum biglandulosum</u> A. Cunn.	p	p
<u>Anopterus glandulosus</u> Labill.	d p	p
<u>Anopterus macleayanus</u> F.v. Muell.	d p	p
<u>Aphanopetalum resinosum</u> Endl.		p
<u>Argophyllum cryptophlebum</u> Zemann	p	p
<u>Argophyllum ellipticum</u> Labill.	d	
<u>Argophyllum nullumense</u> R.T. Baker	p	p
<u>Bauera capitata</u> Seringe		p
<u>Bauera rubioides</u> Andr.	d p	p
<u>Bauera sessiliflora</u> F.v. Muell.	d p	p
<u>Carpodetus</u> sp.	p	p
<u>Carpodetus arboreus</u> (K. Schum. et Lauterb.) Schltr.	d	
<u>Carpodetus major</u> Schltr.	d	
<u>Carpodetus serratus</u> J.R. & G. Forst.	d p	p
<u>Corokia buddleioides</u> A. Cunn.	d	
<u>Corokia carpodetoides</u> (F.v. Muell.) L.S. Smith		d
<u>Corokia collenettei</u> Riley	d	
<u>Corokia macrocarpa</u> Kirk		p
<u>Corokia virgata</u> Turrill		p
<u>Corokia whiteana</u> L.S. Smith	d	
<u>Cuttsia viburnea</u> F.v. Muell.	d p	p
<u>Donatia novae-zelandiae</u> Hook. f.	p	p
<u>Ixerba brexioides</u> A. Cunn.	d p	p
<u>Tetracarpaea tasmaniaca</u> Hook.	p	p

RESULTS

Tetracarpaea Hook.

Introduction

The monotypic genus Tetracarpaea was described from specimens of T. tasmaniaca and placed in the Cunoniaceae by William J. Hooker in 1840. The generic name refers to its distinctive four carpellate apocarpous gynoecium (Hooker, 1840). The genus is endemic to and occurs throughout most of Tasmania, but is absent from the east and northwest floristic zones of the island (Mosley, 1974b). Plants of T. tasmaniaca are small, erect bushy shrubs that commonly grow in subalpine habitats and may attain a height of approximately one foot (Bentham, 1864). These plants bear small, exstipulate, alternate or scattered leaves and four-merous, hypogynous, flowers arranged in racemes.

Joseph D. Hooker (1865) positioned Tetracarpaea in his tribe Escalloniaeae, while Bentham (1864) placed this genus in his tribe Cunonieae. Both tribes are included in their order Saxifrageae (= the modern family Saxifragaceae [Stearn, 1965]). Engler (1890) placed Tetracarpaea in his inclusive rosalean family Saxifragaceae, first within the subfamily Escallonioideae, but later (1928) in its own subfamily, Tetracarpaeoideae. Schulze-Menz (1964) and Thorne (1976, 1983) have supported the later Englerian

treatment, but other workers have diverged from this view. Hutchinson (1967) included Tetracarpaea in the Escalloniaceae of his Cunoniales, while Cronquist (1981) placed it in his larger rosalean family, Grossulariaceae. Takhtajan (1966, 1980) placed this genus in his Saxifragales, initially (1966) in the monotypic Tetracarpaeaceae, but recently (1980, 1983) in his Escalloniaceae. Airy Shaw (in Willis, 1973) and Dahlgren (1975, 1980, 1983) also considered this genus to form the basis of a monotypic family, and Dahlgren has tentatively placed Tetracarpaea in his Cornales.

Observations

Tetracarpaea possesses small, ovate, serrate, alternate leaves. The small teeth of the leaf margin are rounded. The petiole is very short and almost indistinguishable because the lamina tapers gradually toward the point of attachment of leaf to stem. Venation is simple craspedodromous with a prominent midrib and conspicuous secondary veins that terminate at the leaf margin (Fig. 1). Vein areole development is incomplete to lacking. The veinlets are usually straight and tapered, but may be somewhat forked (Fig. 2). Vein endings consist of two to four tracheids with helical thickenings (Fig. 2). Infrequently these tracheids are accompanied by fiber-tracheids with thicker walls and oval bordered pits.

The nodal pattern is unilacunar, one-trace, and a single collateral vascular bundle enters the base of a

petiole (Fig. 3). Two collateral bundles separate from the midvein near the base of a petiole, and a third bundle splits from the midvein at a midpoint in a petiole. A median section of a petiole, therefore, shows four collateral bundles (Fig. 3). The outermost two bundles represent the first two bundles that diverge from the midvein. The larger of the two, central bundles represents the petiolar midvein, while the smaller bundle represents the third bundle to diverge from the midvein. All four bundles enter the lamina distally (Fig. 3).

Leaves are dorsiventral with a well-differentiated, triseriate palisade layer and a lacunose spongy mesophyll layer (Fig. 4). The cells of the innermost layer of the palisade layer are sometimes shorter than the other typically columnar cells of this layer, but are distinct from the cells of the spongy mesophyll. The spongy mesophyll has more cell layers but is approximately the same thickness as the palisade layer (Fig. 4). The spongy mesophyll cells have various shapes and sizes and are loosely arranged with numerous, large intercellular spaces. The two cell layers adjacent to the abaxial epidermis are more tightly arranged and have smaller and fewer intercellular spaces than the remainder of the spongy mesophyll (Figs. 4 & 5). Druses commonly occur in the cells of the spongy mesophyll (Fig. 6).

The small, arc-shaped vascular bundles of a leaf are collateral (Fig. 4). Very little secondary growth is visible within these bundles. Although bundle sheaths and

bundle sheath extensions are lacking, thick-walled abaxial fibers are present adjacent to the primary phloem of the midvein (Fig. 4).

Both the adaxial and abaxial epidermal layers are uniserial and composed of variously-shaped cells with evenly-thickened walls (Fig. 4). In surface view these cells also are variously-shaped (polygonal to elongate), and possess curved, evenly thickened, anticlinal walls. Both epidermal layers lack trichomes and are covered by a very thick cuticle (approximately 10 μm ; Fig. 5).

Abundant stomata are restricted to the abaxial epidermis, and the stomatal apparatus is anomocytic. In surface view the guard-cell pair possesses an almost circular outline, while the individual guard cells are reniform. Guard-cell pairs average 30 μm in length and 26 μm in width (length/width ratio 1.15). In transection the guard cells are oval to circular and each cell bears a prominent, cuticular horn that represents the outer ledge overarching a stoma (Fig. 5).

In cleared leaves the marginal teeth have a tumid appearance indicating the presence of hydathodes. A prominent vein extends nearly to the tooth apex (Fig. 7), but water pores associated with functional hydathodes are not distinguishable. Apical cells of the leaf teeth stain lighter in cleared leaves than surrounding cells which may indicate thinner cell walls (Fig. 7). The densely stained cytoplasm of these cells in paradermal sections of uncleared leaves may signify that this tissue is glandular.

Tetracarpaea wood is diffuse porous with poorly discernible growth rings (Fig. 8). The wood is very fine-textured with numerous angular pores (range 180-445/mm², $\bar{x}=309$) that have extremely small tangential diameters (range 11.7-23.4 μm , $\bar{x}=16$) and walls 2.1-4.2 μm ($\bar{x}=2.8$) thick. Pores are predominately solitary (80%) with radial multiples (3%) and clusters (17%) of two to three pores resulting mostly from overlapping vessel element end walls. Rarely clusters of four or five pores are observed. Vessels are difficult to distinguish from axial parenchyma in slide Aw 27721 because the parenchyma is devoid of contents, and the slide has been stained with safranin only. Thus, counts of the number of pores per field are greatly inflated in this specimen. Vessel elements are of medium length (range 213-455 μm , $\bar{x}=354$), and very fine spiral thickenings are present in some of these cells. Vessel element end walls are oblique, and end-wall angles range from 0-22° ($\bar{x}=10$). Perforation plates are exclusively scalariform, possess 5 to 18 bars per plate ($\bar{x}=8$), and the perforations are completely bordered (Fig. 9). Scalariform perforation plate bars are thick and may be branched in various ways to form a reticulate pattern. Occasionally two scalariform perforation plates occur in a vessel element end wall. Scalariform, transitional to opposite intervacular pitting is confined mostly to overlapping end walls of contiguous vessel elements (Fig. 9). Pit diameter is minute and ranges from 3.2-4.2 μm ($\bar{x}=3.3$).

Tracheids bear circular-bordered pits with oval apertures that extend slightly beyond the margins of the pit border (Fig. 9). The diameter of these pits is similar to that of the intervacular pits. Tracheids are extremely short (range 325-520 μm , $\bar{x} = 396$). Tracheid walls are relatively thick and range from 2.1-6.3 μm ($\bar{x} = 4$). Very fine spiral thickenings are present in some of these cells (Fig. 10).

Axial parenchyma is sparse and apotracheal diffuse or diffuse-in-aggregates. Vessel to axial parenchyma pitting is scalariform. No ergastic substances are noted in these cells.

Although the xylem ray system consists of homocellular uniseriate rays of upright cells and heterocellular uni- and biseriate rays, uniseriate rays predominate. Most heterocellular rays are biseriate (Fig. 11), although these rays are two cells wide for only 1-4 cells of their length. Ray height ranges from 1-17 cells (.07-.75 mm) for homocellular rays and from 7-31 cells (.28-1.22 mm) for heterocellular rays. Ray cells contain dark brown deposits and numerous starch grains (Figs. 9 & 11). Perforated ray cells are infrequent (Fig. 12), while sheath cells and crystals are absent. Vessel to ray parenchyma pitting is opposite to alternate. No fusion of rays is noted.

Figure 1. Leaf of Tetracarpaea tasmannica. X10. Note simple craspedodromous venation.

Figure 2. Vein ending of T. tasmannica. X175.

Figure 3. Transverse sections of a node (a) and proximal (b), median (c) and distal (d) sections of a petiole of T. tasmannica. X30.

Details: t, tracheids.

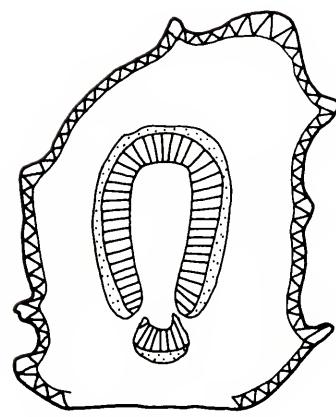
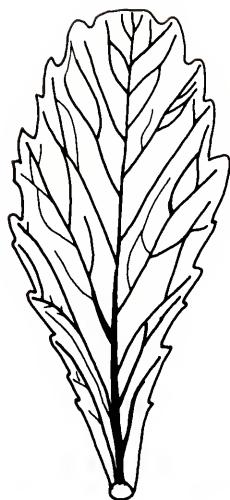
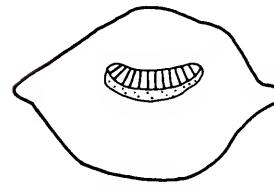
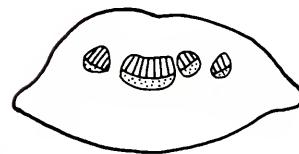
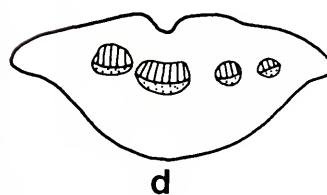
**a****b****c****d**

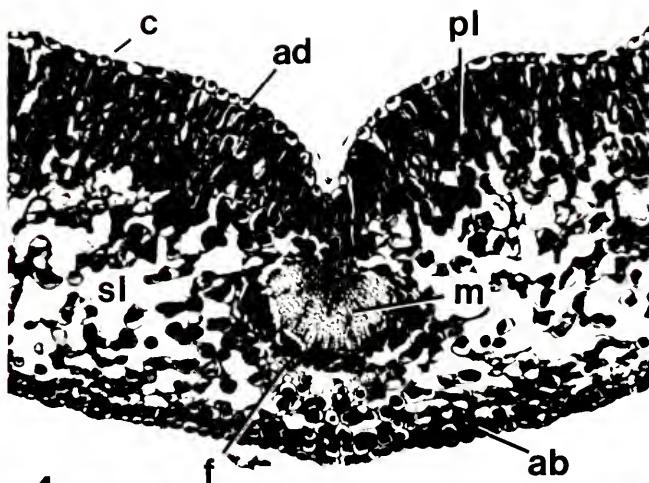
Figure 4. Transverse section of a leaf of Tetracarpaea tasmannica. X110. Note fibers abaxial to the midvein.

Figure 5. Transverse section of the abaxial epidermis of a leaf of T. tasmannica. X700. Note the guard-cell pair with prominent cuticular horns (arrows).

Figure 6. Transverse section of a leaf of T. tasmannica. X437. Note druses in the spongy mesophyll.

Figure 7. Marginal tooth of a leaf of T. tasmannica. X110.

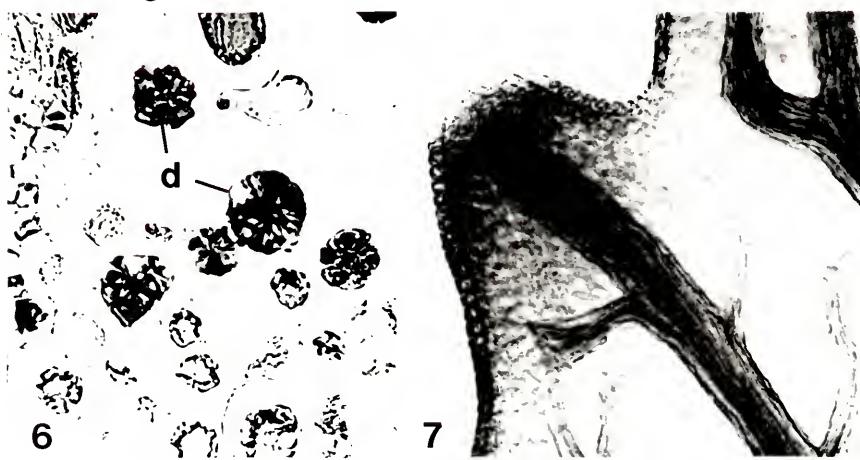
Details: ab, abaxial epidermis; ad, adaxial epidermis; c, cuticle; d, druses; f, fibers; gc, guard cell; m, midvein; pl, palisade layer; sl, spongy mesophyll layer.



4



5



6

7

Figure 8. Transverse section of the secondary xylem of Tetracarpaea tasmannica. X175. Note solitary, angular pores.

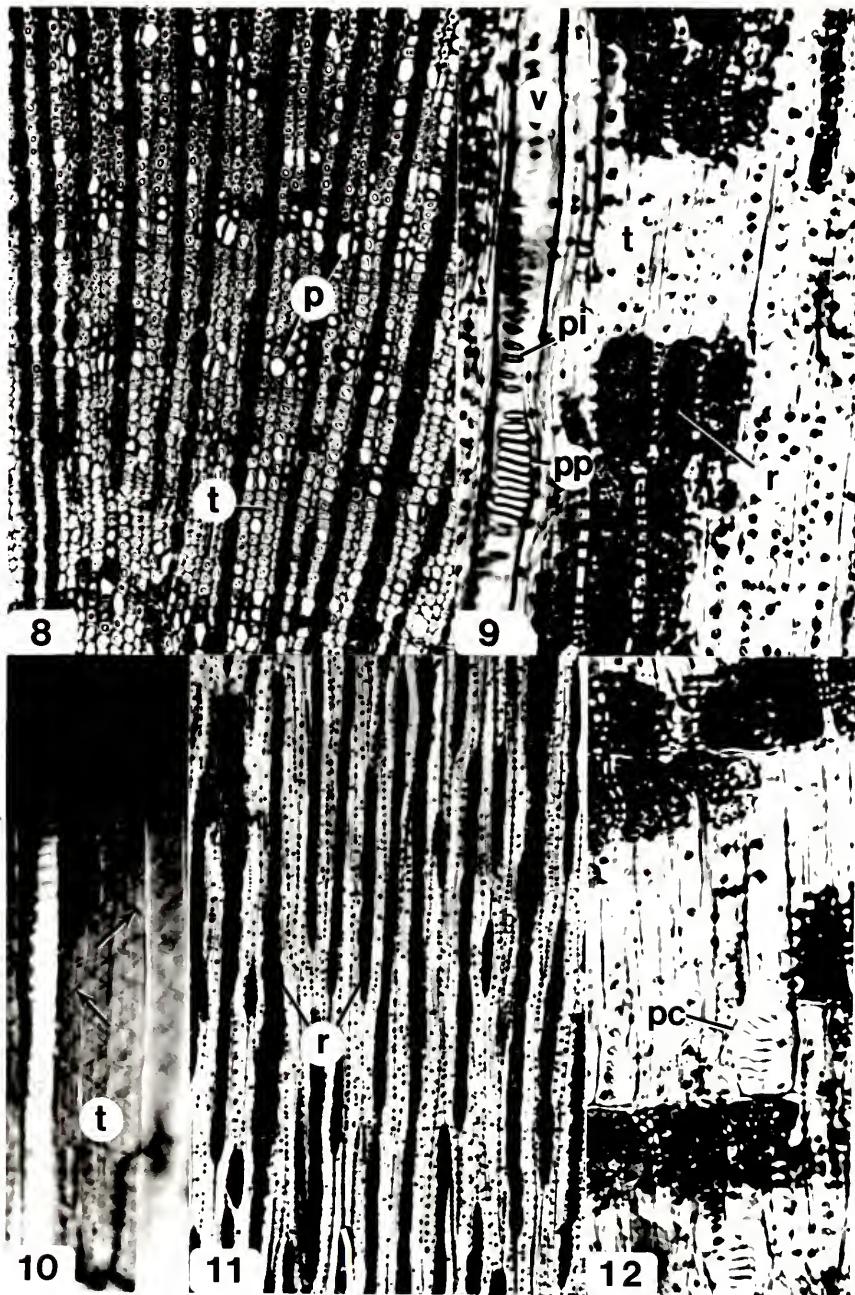
Figure 9. Radial section of the secondary xylem of T. tasmannica. X437.

Figure 10. Secondary xylem of T. tasmannica. X 700. Note tracheids with spiral thickenings (arrows).

Figure 11. Tangential section of the secondary xylem of T. tasmannica. X175. Note uni- and biserrate rays.

Figure 12. Radial section of the secondary xylem of T. tasmannica. X437. Note perforated ray cell with scalariform perforation plate.

Details: p, pores; pi, pits; pc, perforated ray cell; pp, perforation plate; r, ray parenchyma; t, tracheids; v, vessel element.



Ixerba A. Cunn.Introduction

The monotypic genus Ixerba was described by A. Cunningham (1839) from specimens collected in Wangaroa, New Zealand. He based the generic name on an anagram of Brexia Thouars to emphasize an affinity which he believed to exist between the two genera. Ixerba brexioides is endemic to North Island, New Zealand and occurs throughout Auckland and northern Hawke's Bay Districts in hilly lowland and montane forests (Allan, 1961; Cheeseman, 1914, 1925). Plants of Ixerba are small trees with linear, opposite, alternate, or whorled, exstipulate leaves (Allan, 1961; Cheeseman, 1925). The five-merous, hypogynous, flowers are arranged in panicles, and the fruit is a capsule.

Various taxonomists have agreed with Cunningham's view that Ixerba and Brexia are closely related and have placed these genera in the subfamily Brexioideae of the Saxifragaceae (Engler, 1928; Schulze-Menz, 1964; Thorne, 1976) or the Brexiaceae (Airy Shaw in Willis, 1973; Dahlgren, 1975, 1980, 1983; Takhtajan, 1966). Hooker (1865), however, included Ixerba in the tribe Escalloniaceae of the Saxifragaceae, and Engler (1890) originally placed it in the Escallonioideae of the Saxifragaceae. Recently, Thorne (1983) has changed his placement of Ixerba to the Escallonioideae. Hutchinson (1967) and Takhtajan (1980, 1983) have advocated a position in the Escalloniaceae for Ixerba, while Cronquist (1981) placed it in his Grossulariaceae.

Observations

Ixerba possesses narrowly oblong to elliptic, alternate, opposite or whorled leaves that bear blunt, widely-spaced crenations. Venation is semicraspedodromous with a prominent midrib and conspicuous secondary veins that branch to extend near the leaf margin and arch distally to join with superadjacent secondary veins (Fig. 13). Vein areole development is incomplete. Veinlets vary, from simple and straight to once, twice, or three times branched (Fig. 14). The vein endings may be branched or unbranched and tapered, and are composed of helically thickened tracheids that may be elongate, curved, forked, or irregularly shaped (Fig. 14). These tracheids often possess protuberances which are characterized by helical thickenings that differ in orientation from the thickenings in the remainder of the cell. Parenchymatous bundle-sheath cells and thick-walled fibers are associated with the vascular tissues in most vein endings.

The nodal pattern is trilacunar, three-trace, and three collateral bundles enter a petiole (Fig. 15). These bundles fuse laterally to produce a single, large flattened bundle in the center of the petiole in median and distal sections (Fig. 15). In some petioles a median section reveals that one lateral bundle fuses with the central bundle before the other lateral bundle. In these latter petioles the large flattened bundle is only visible in more distal sections of the petiole. A very small collateral bundle splits from

each end of the large central petiolar bundle. These small accessory bundles occur lateral to the central bundle (Fig. 15).

Leaves of Ixerba are dorsiventral with a well-developed, bi- to triseriate palisade layer and a highly lacunose spongy mesophyll layer (Fig. 16). The two uppermost layers of palisade cells are typically columnar and tightly appressed, while the cells of the innermost layer are highly variable in shape, often widely-spaced, and intergrade with the adjacent spongy mesophyll cells (Fig. 16). The cells of the spongy mesophyll are highly variable in shape and size and separated by numerous, large intercellular spaces. One or two large, yellowish, optically anisotropic, crystalloid inclusions occur in most cells of the palisade and spongy layers and both epidermides (Figs. 16 & 17). These inclusions probably are not calcium oxalate crystals because they did not dissolve in ammoniacal iron alum.

All vascular bundles of a leaf are collateral and surrounded by a bundle sheath. The large, flattened, arc-shaped, midvein, with well-developed secondary growth, is almost completely surrounded by thick-walled, lignified parenchyma cells (Fig. 18). This large bundle also possesses adaxial and abaxial bundle sheath extensions composed of parenchyma and collenchyma cells. The smaller vascular bundles (secondary and minor veins) exhibit no secondary growth, have a few sclerenchyma cells adjacent to the

primary vascular tissues, are surrounded by a parenchymatous bundle sheath and lack bundle sheath extensions (Fig. 16).

Both the adaxial and abaxial epidermal layers are uniserrate, and consist of mostly square to rectangular cells in transection (Fig. 16). The outer periclinal walls of all epidermal cells are slightly thickened. In surface view the epidermal cells are square to polyhedral with straight anticlinal walls. The cuticle is very thick (>5 um), and trichomes are absent.

Abundant stomata are restricted to the abaxial epidermis, and the stomatal apparatus is anomocytic (Fig. 19). In surface view guard cells are reniform, and guard-cell pairs are virtually circular in outline with an average length of 36 um and a width of 34 um (length/width ratio 1.06). In transection guard cells are oval, and each cell bears a small, thin, cuticular horn that represents the outer ledge overarching a stoma (Fig. 20).

Marginal crenations of Ixerba leaves contain glands that are characterized by thick-walled parenchyma cells arranged in regular files (Fig. 21). In paradermal sections of uncleared leaves, the cytoplasm of these cells is very dense and stains very darkly (Fig. 22). Each crenation is supplied by an arc of vascular tissue that is derived from the union of two secondary or tertiary veins (Fig. 21).

Wood of Ixerba is diffuse porous and exhibits distinct growth rings (Fig. 23). The wood is fine-textured with very numerous angular pores (range 70-235/mm², $\bar{x} = 114$) that possess thin radial walls (range 1.1-3.7 um, $\bar{x} = 1.9$) and

very small tangential diameters (range 25-55 μm , $\bar{x}=41$). The pores are predominantly solitary (76%), although radial multiples of two pores (2%) and clusters of two to five pores (22%) mostly due to overlapping end walls of vessel elements do occur. Vessel elements are long and range from 617-1600 μm ($\bar{x}=1149$). Vessel elements possess oblique end walls with angles ranging from 2-18° ($\bar{x}=8$) and lack spiral thickenings. Perforation plates are exclusively scalariform with 16-71 thin bars per plate ($\bar{x}=40$) (Fig. 24). One specimen (Aw H-20087) of Ixerba was distinct from all the others because of its exceptionally long vessel elements (range 1117-1942 μm , $\bar{x}=1498$) and very numerous bars per scalariform perforation plate (range 47-111, $\bar{x}=71$). Although perforations typically lack borders, perforations with borders at the ends or rarely with complete borders may be found in the narrowest vessel elements. Intervascular pitting is extremely rare and confined to overlapping vessel element end walls. When present, round to oval pits with small diameters (range 3.7-5.3 μm , $\bar{x}=4.5$) typically occur in uniseriate files (Fig. 24).

Tracheids bear circular-bordered pits with oval inner apertures that may be included within or extend beyond the margins of the pit border (Fig. 24). The diameter of these pits is similar to that of the intervacular pits. Tracheids are medium to moderately long (range 867-2084 μm , $\bar{x}=1438$), with relatively thin radial walls (range 2.6-8.9 μm , $\bar{x}=4.7$), and fine or coarse spiral thickenings occasionally are present.

Axial parenchyma is sparse and predominantly apotracheal diffuse and paratracheal scanty, although diffuse-in-aggregates parenchyma may also occur. Vessel to axial parenchyma pitting is mostly transitional or opposite, rarely alternate. No ergastic substances are noted in these cells.

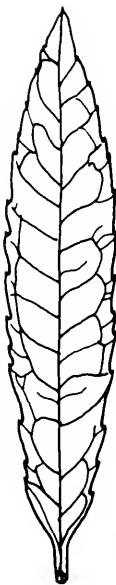
The xylem ray system predominantly is composed of homocellular, uniseriate rays of upright cells and heterocellular, bi- and multiseriate rays (Fig. 25). Most heterocellular rays are biseriate, although some may be uniseriate. Ray height ranges from 1-15 cells (.06-1.03 mm) for homocellular rays, 8-27 cells (.25-1.18 mm) for heterocellular uniseriate rays, and 6-52 cells (.25-2.00 mm) for heterocellular bi- and multiseriate rays. Heterocellular rays range from 2-4 cells (26-70 μm) wide. Very few ray cells contain dark brown deposits, and crystals are absent. Sheath cells are absent, while perforated ray cells with scalariform or reticulate perforation plates commonly occur in some specimens (Fig. 26). The pitting between vessels and ray parenchyma and vessels and axial parenchyma is mostly transitional to opposite. All types of rays may be fused end-to-end.

Figure 13. Leaf of Ixerba brexioides. X1. Note marginal crenations and semicraspedodromous venation.

Figure 14. Vein ending of I. brexioides. X175.

Figure 15. Transverse sections of a node (a) and the proximal (b), median (c) and distal (d) sections of a petiole of I. brexioides.

Details: f, fibers; t, tracheids.

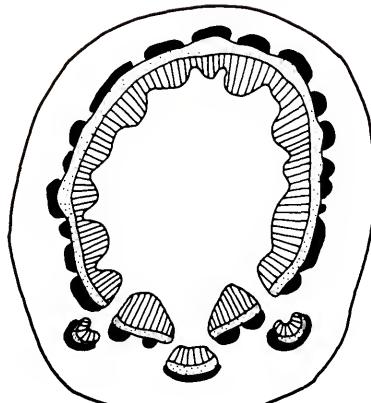


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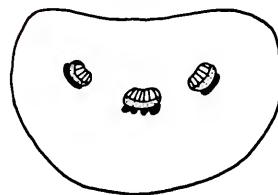


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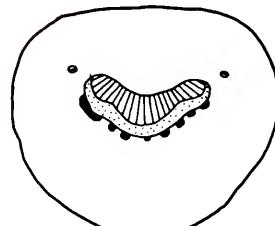
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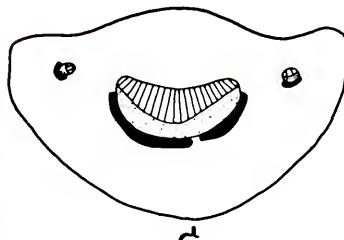
a



b



c



d

Figure 16. Transverse section of a leaf of Ixerba brexioides. X175.

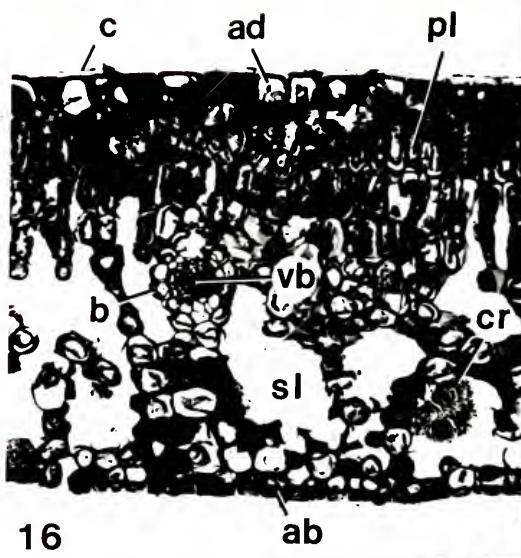
Figure 17. Optically anisotropic crystalloid from a leaf of I. brexioides. X700.

Figure 18. Transverse section of the midvein of a leaf of I. brexioides. X110.

Figure 19. Paradermal section of the abaxial epidermis of a leaf of I. brexioides. X437. Note anomocytic stomatal apparatus.

Figure 20. Transverse section of the abaxial epidermis of a leaf of I. brexioides. X700. Note the guard cells with small cuticular horns (arrows).

Details: ab, abaxial epidermis; ad, adaxial epidermis; b, bundle sheath; be, abaxial bundle sheath extension; be', adaxial bundle sheath extension; c, cuticle; cr, crystalloid; gc, guard cells; lp, lignified parenchyma; pl, palisade layer; sl, spongy mesophyll layer ; st, stoma; vb, vascular bundle.



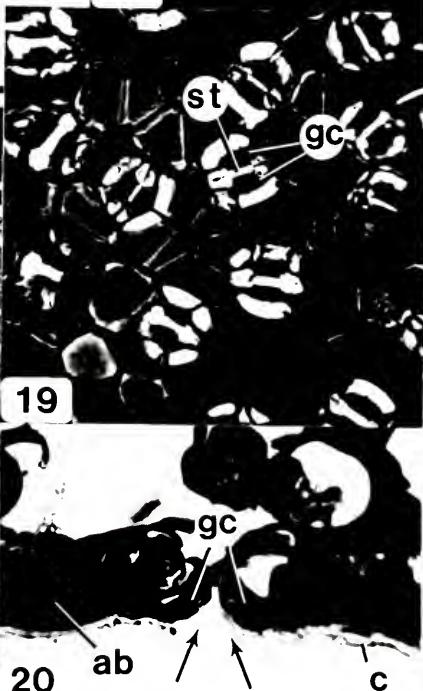
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Figure 21. Marginal crenation of a leaf of Ixerba brexioides. X110. Note the arc of vascular tissue.

Figure 22. Paradermal section of a marginal crenation of a leaf of I. brexioides. X110. Note apical gland.

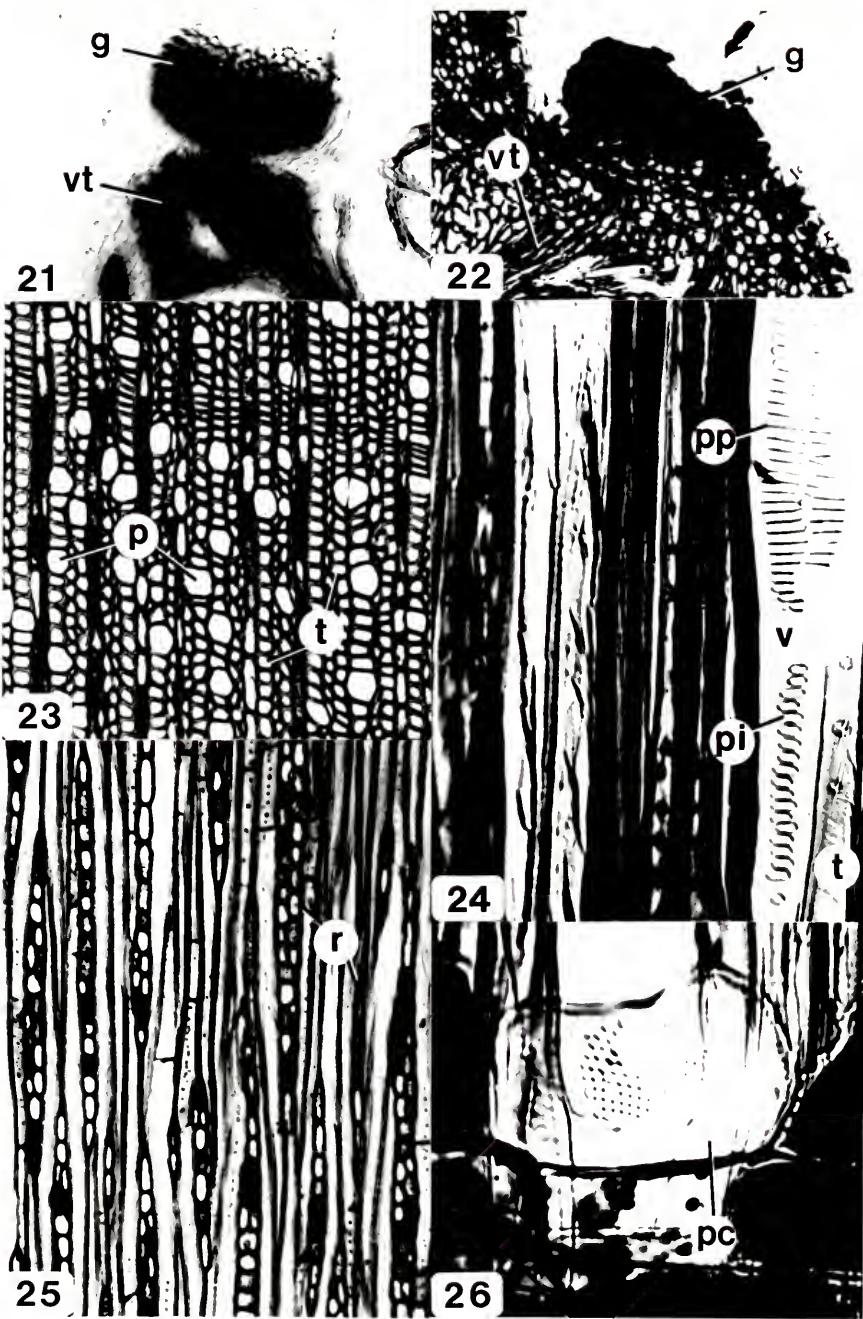
Figure 23. Transverse section of the secondary xylem of I. brexioides. X110. Note solitary, angular pores.

Figure 24. Radial section of the secondary xylem of I. brexioides. X437.

Figure 25. Tangential section of the secondary xylem of I. brexioides. X110. Note uni- and biserate rays.

Figure 26. Radial section of the secondary xylem of I. brexioides. X437. Note the perforated ray cell with scalariform perforation plate.

Details: g, gland; p, pore; pc, perforated ray cell; pi, pits; pp, perforation plate; r, ray parenchyma; t, tracheid; v, vessel element; vt, vascular tissue.



Bauera BanksIntroduction

The genus Bauera was named by Sir Joseph Banks and described from specimens of B. rubioides in 1801 (Bailey, 1900; Bentham, 1864; Black, 1924; Burbidge, 1963; Willis, 1972). The generic name commemorates the botanical artists Francis and Ferdinand Bauer (Bailey, 1900; Black, 1924). The three species of this genus are endemic to southeastern Australia and Tasmania. Bauera rubioides, the most widespread species, occurs in wet places throughout Tasmania, eastern Victoria, eastern New South Wales and southeastern Queensland (Black, 1924; Bailey, 1900; Bentham, 1864; Willis, 1972). This species is rare on Kangaroo Island in South Australia (Mosley, 1974a). Bauera capitata occurs in southeastern New South Wales and Fraser's Island off the coast of southeastern Queensland (Bailey, 1900; Bentham, 1864). Bauera sessiliflora is restricted to the Grampian Mountain range in western Victoria. Plants of Bauera are either prostrate or upright shrubs up to 2 m tall. All species of Bauera reportedly bear opposite, sessile, exstipulate, three-foliolate leaves which give the appearance of a whorl of six leaves (Bailey, 1900; Bentham, 1864). Although flowers may have four to ten sepals and petals, most flowers have five to nine sepals and petals (Bailey, 1900; Bentham, 1864; Dickison, 1975b). Each flower possesses a few to many stamens and contains a

superior to half-inferior, bicarpellate, syncarpous gynoecium that ripens into a capsule. Bauera is commonly grown as a greenhouse shrub (Bailey, 1944; Bailey and Bailey, 1976; Syngle, 1974).

Although Hooker (1865) considered Bauera an anomalous genus within the Saxifragaceae, Bentham (1864) placed it in the tribe Cunonieae of the Saxifragaceae. Two recent workers (Cronquist, 1981; Takhtajan, 1980, 1983) have placed this genus in the Cunoniaceae, and have aligned this family within either the order Grossulariales or Saxifragales, respectively. Other systematists have placed Bauera in the monogeneric subfamily Baueroideae of the Saxifragaceae (Engler, 1890, 1928; Schulze-Menz 1964; Thorne, 1976), and included this family in the Rosales. Thorne (1983), however, recently has placed this genus in the monogeneric family Baueraceae, as have other workers (Airy Shaw in Willis, 1973; Dahlgren, 1975, 1980, 1983; Hutchinson, 1967), and they all place the Baueraceae among the Cunoniales.

Wood, nodes and leaves of B. rubioides and B. sessiliflora, and nodes and leaves of B. capitata were available for study (Table 2). Unless noted otherwise, data apply to all species examined.

Observations

Bauera typically possesses simple, opposite, petiolate leaves, although B. rubioides may have whorled leaves. Each leaf is accompanied laterally by two large stipules that are

morphologically and anatomically similar to the leaves. Each stipule is attached to the stem by a very short stalk. Leaves of B. rubioides and B. sessiliflora are elliptic or ovate with entire to obscurely toothed margins (Fig. 27). Leaves of B. capitata may be elliptic or two- to three-lobed (Fig. 28). Venation is semicraspedodromous to brochidodromous in B. rubioides and B. sessiliflora with a prominent midvein and conspicuous secondary veins that either extend to the leaf margin and/or form arches with superadjacent secondary veins (Fig. 27). Venation is mixed craspedodromous in B. capitata with some secondary veins that extend to the leaf margin and others that arch distally to join with superadjacent secondary veins (Fig. 28). Vein areole development is incomplete in B. sessiliflora and lacking in both B. rubioides and B. capitata. Veinlets typically are forked or branched. Most tracheids of a vein ending are elongate and slender with helical thickenings, while the terminal tracheids of a vein ending usually are shorter, larger in diameter and thicker-walled than the elongate tracheids (Fig. 29). The terminal tracheids have reticulate wall thickenings and may possess short protuberances.

The nodal pattern is unilacunar, one-trace, and this leaf trace quickly splits twice to form three traces, each of which is a collateral bundle (Fig. 30). The median trace enters a leaf, and each of the lateral traces enters a lateral, foliaceous stipule. These bundles traverse the length of a short petiole or stipular stalk (Fig. 30). At

approximately the same level as the trifurcation of the leaf trace in the stem, two branch traces arise and quickly fuse to form a cylindrical stele in the branch opposite a simple leaf (Fig. 30).

Leaves of Bauera are dorsiventral with a well-differentiated, uni- to biseriate palisade layer and a highly lacunose spongy mesophyll layer (Fig. 31). The palisade cells typically are elongate and columnar, but may be short and oval in transection. These cells may be tightly appressed or loosely arranged with small intercellular spaces. The cells of the spongy mesophyll have various shapes and sizes and are separated by numerous, large intercellular spaces. Prismatic crystals are common in the spongy mesophyll cells, especially near a vascular bundle (Fig. 32).

The oval or round vascular bundles of Bauera leaves are collateral, and only the midvein exhibits a small amount of secondary growth. Although bundle sheaths and bundle sheath extensions are absent, thick-walled fibers commonly occur adjacent to the primary vascular tissues of each bundle (Fig. 31).

The abaxial epidermis in all species is exclusively uniseriate and composed of very narrow, thick-walled cells in transection. The adaxial epidermis is uniseriate (B. capitata and B. rubicoides) or biseriate (B. rubicoides and B. sessiliflora). In the latter species the cells of the outermost layer of the adaxial epidermis resemble those of the abaxial epidermis, while the cells of the innermost layer are composed of very large, thin-walled cells

(Fig. 33). These latter cells are very delicate and often become distorted and disintegrate when sectioned (Fig. 34). In surface view the cells of both the abaxial epidermis and the outermost layer of the adaxial epidermis are variously shaped and possess sinuous or curved anticlinal walls. Although the cuticle is thin (<5 um) in all three species, it is slightly thicker on the abaxial surface of a leaf.

Numerous stomata are restricted to the abaxial epidermis. The stomatal apparatus is anomocytic, although the three or four subsidiary cells which surround a guard-cell pair are smaller than the other epidermal cells (Fig. 35). In surface view individual guard cells are reniform, and guard-cell pairs are elliptic to circular in outline (Fig. 35). Guard-cell-pair length averages 32 um and width averages 29 um (length/width ratio 1.10). In transection guard cells are oval, and each cell bears a large cuticular horn that represents the outer ledge overarching a stoma (Fig. 36). Unicellular, thick-walled, lignified trichomes with tapered ends are abundant on both epidermal layers and along the margins of leaves of B. rubicoides and B. sessili-flora, but are sparse on the leaves of B. capitata (Fig. 37). The base of each trichome is surrounded by a ring of epidermal cells which are much larger than the surrounding epidermal cells (Figs. 33 & 34). One or two adaxial epidermal cells along most of the margin of the leaves of B. capitata are expanded into a ridge which appears as an elongate or clavate protrusion in transection (Fig. 38).

The apex and marginal teeth of a leaf possess thick-walled cells with darkly staining cytoplasm that resemble glandular cells (Fig. 37).

Although the wood of the two species of Bauera studied is very similar, B. sessiliflora has longer vessel elements and tracheids and taller rays than B. rubiooides. Distinct growth layers occur in the wood of both species. The wood of B. rubiooides is diffuse porous while the wood of B. sessiliflora is ring porous (Fig. 39). Both species possess very numerous pores, with ranges of 270-385/mm² ($\bar{x}=325$) for B. rubiooides and 185-320/mm² ($\bar{x}=257$) for B. sessiliflora. Both species have thin-walled (range 1.1-4.2 um, $\bar{x}=2.0$) angular pores with very small tangential diameters (range 18-57 um, $\bar{x}=37$). Pores are predominantly solitary (84%), although true radial multiples (3%) and clusters (13%) do occur. Vessel elements are medium length, however, those of B. sessiliflora (range 234-780 um, $\bar{x}=523$) are longer than those of B. rubiooides (range 208-579 um, $\bar{x}=383$). Vessel element end walls vary from transverse to oblique, with end-wall angles that range from 22-90° ($\bar{x}=39$). Perforation plates are typically simple, however scalariform perforation plates with 1-5 thin bars may occur in both species (Fig. 40). All perforations lack borders. Very fine spiral thickenings rarely occur in the vessel elements of B. sessiliflora only. Intervascular pitting usually is scalariform or transitional in both species, although opposite or alternate patterns rarely occur.

(Fig. 40). The diameter of the elongate or oval pits is minute (range 3.2-7.4 μm , $\bar{x} = 4.7$).

Tracheids of both species bear circular-bordered pits with oval inner apertures that are included within the pit border (Fig. 41). The diameter of these pits is similar to that of the intervacular pits. The tracheids of both species are very short, although those of B. sessiliflora are longer (range 436-956 μm , $\bar{x} = 721$) than those of B. rubicoides (range 312-650 μm , $\bar{x} = 484$). These tracheids have relatively thin radial walls (range 2.6-5.3 μm , $x = 3.7$) and fine spiral thickenings.

Axial parenchyma is sparse and either apotracheal diffuse or paratracheal scanty. Vessel to axial parenchyma pitting is not visible in the material examined. Dark brown deposits commonly occur in these cells.

The xylem ray system is composed mostly of homocellular, uniseriate rays of upright or square cells and a few heterocellular, bi- and multiseriate rays (Fig. 42). Homocellular, biserrate and heterocellular, uniseriate rays are rare. The homocellular rays are slightly taller in B. sessiliflora (1-14 cells, 0.11-0.81 mm) than in B. rubicoides (1-6 cells, 0.04-0.31 mm). Although heterocellular rays also are taller in B. sessiliflora (18-84 cells, 0.50-1.89 mm) than in B. rubicoides (19-61 cells, 0.32-0.98 mm), the width of these rays is similar in both species (2-7 cells, 18-75 μm). Dark brown deposits commonly occur in the ray cells of both species (Fig. 40). Sheath cells are absent, while perforated ray cells with simple or foraminated

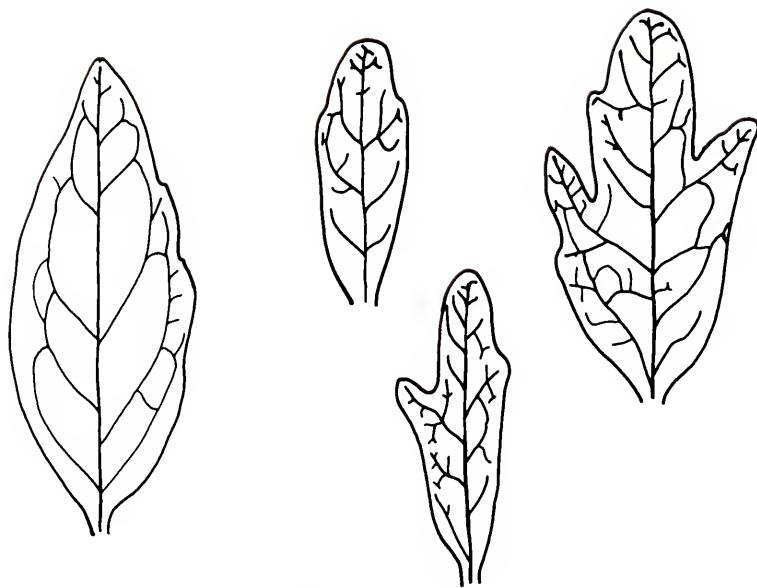
perforation plates are occasionally present (Fig. 41). Vessel to ray parenchyma pitting is scalariform to fenestri-form. Both homocellular and heterocellular rays may be fused end-to-end.

Figure 27. Leaf of Bauera rubicoides. X10. Note semicraspedodromous to brochidodromous venation.

Figure 28. Diversity of leaf shapes in B. capitata. X10.

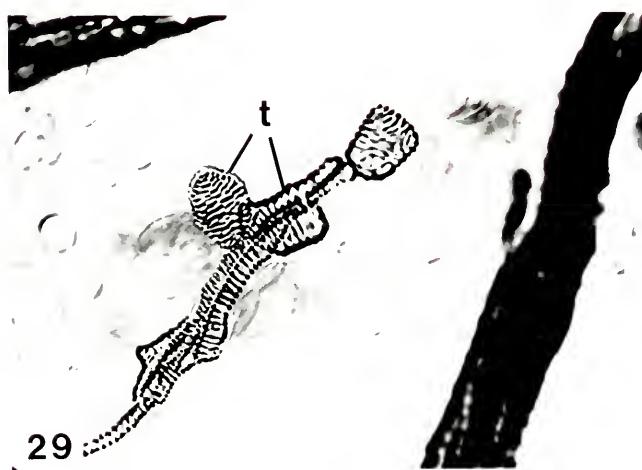
Figure 29. Vein ending of B. rubicoides. X437. Note helically thickened tracheids.

Details: t, tracheids.



27

28



29

Figure 30. Diagrammatic representation of a node and the nodal pattern of Bauera rubioides. X30. Leaves and stipules are not drawn to scale.

Details: BT, branch trace; L, leaf; LT, leaf trace; S, stipule; ST, stipular traces.

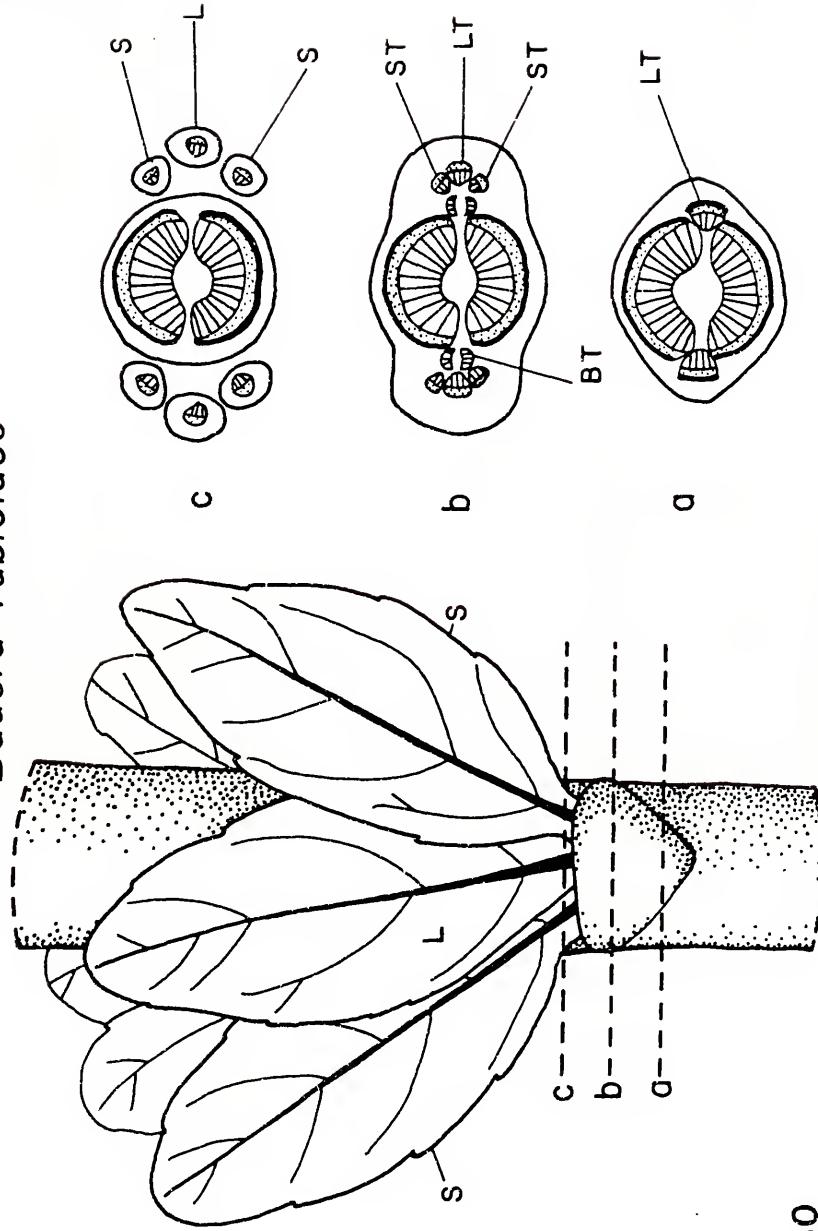
Bauera rubioides

Figure 31. Transverse section of a leaf of Bauera capitata. X175.

Figure 32. Transverse section of a leaf of B. capitata showing prismatic crystals near a vascular bundle. X700.

Figure 33. Transverse section of a leaf of B. sessiliflora. X110.

Figure 34. Transverse section of a leaf of B. sessiliflora. X110.

Figure 35. Paradermal section of the abaxial epidermis of a leaf of B. rubioides. X437. Note anomocytic stomatal apparatus.

Figure 36. Transverse section of the abaxial epidermis of a leaf of B. capitata. X700. Note the guard cells with prominent cuticular horns (arrows).

Figure 37. Marginal serration of a leaf of B. rubioides. X175. Note marginal trichome.

Figure 38. Transverse section of a leaf of B. capitata. X175. Note the protrusion (arrow) that represents a ridge of cells along the adaxial margin of a leaf.

Details: ab, abaxial epidermis; ad, adaxial epidermis; c, cuticle; cr, crystal; e, enlarged epidermal cells; f, fibers; g, gland; gc, guard cells; m, midvein;; pl, palisade layer; sl, spongy mesophyll layer; st, stoma; tr, trichome.

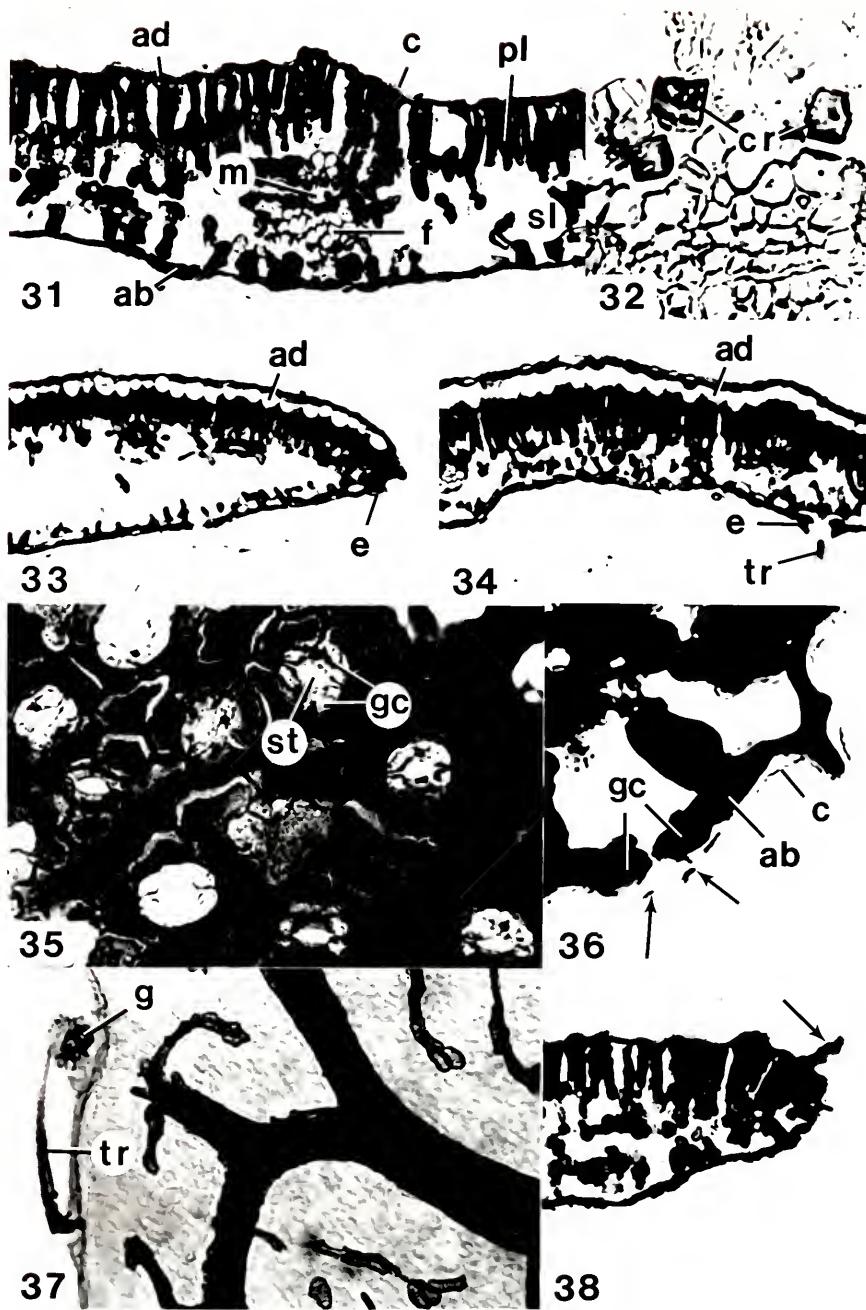


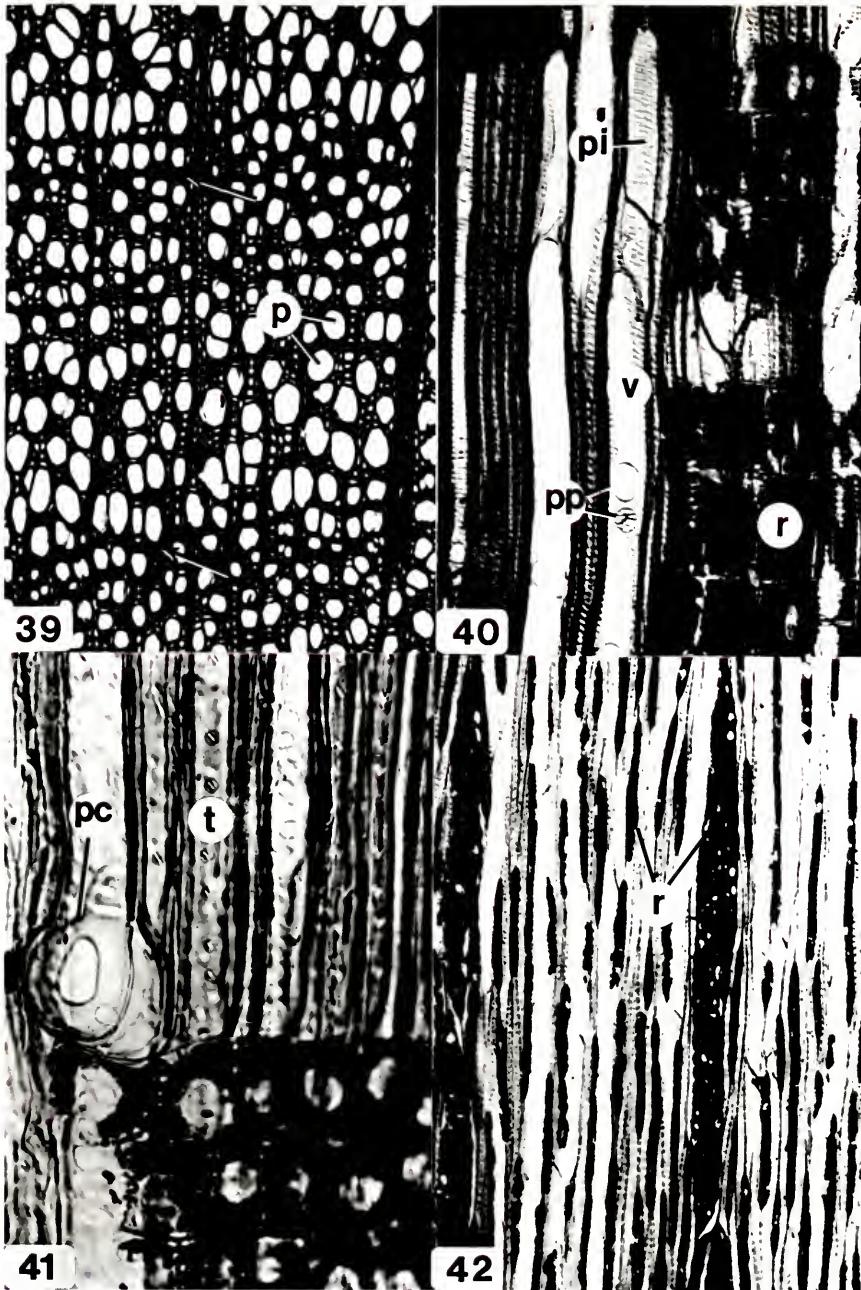
Figure 39. Transverse section of the secondary xylem of Bauera rubioides. X110. Note boundary of growth ring (arrow) and solitary, angular pores.

Figure 40. Radial section of the secondary xylem of B. rubioides. X175.

Figure 41. Radial section of the secondary xylem of B. sessiliflora. X437. Note tracheids with circular-bordered pits and perforated ray cell with a simple perforation plate.

Figure 42. Tangential section of the secondary xylem of B. sessiliflora. X110. Note uni-, bi- and multiseriate rays.

Details: p, pore; pc, perforated ray cell; pi, pits; pp, perforation plate; r, ray; t, tracheid; v, vessel element;



Anopterus Labill.Introduction

Anopterus was described from specimens of A. glandulosus by J.-J. Labillardiere in 1804. The generic name refers to the broad, membranaceous wing on the end of each seed produced by these plants (Bailey, 1900). The type species is endemic to Tasmania where it is widespread throughout the island, especially in subalpine forests (Bentham, 1864; Mosely, 1974b). The only other species in the genus, A. macleayanus, is endemic to eastern and south-eastern Queensland and northeastern New South Wales, Australia where it occurs up to elevations of 1500 m (Bailey, 1900; Bentham, 1864; Burbidge, 1963). Plants within the genus are shrubs or small trees with alternate, simple, exstipulate leaves (Bailey, 1900; Bentham, 1864). The six-to nine-merous flowers are borne in racemes, and each contains a bicarpellate, superior ovary that ripens into a capsule. Anopterus glandulosus commonly is used in ornamental horticulture for its handsome evergreen foliage (Bailey 1944; Bailey and Bailey, 1976; Syngle, 1974).

Most taxonomists have placed Anopterus in either the Saxifragaceae, subfamily Escallonioideae (Engler, 1890, 1928; Schulze-Menz 1964; Thorne, 1976, 1983) or the Escalloniaceae (Airy Shaw in Willis, 1973; Dahlgren, 1975, 1980, 1983; Takhtajan, 1980, 1983). Cronquist (1981), however,

included this genus in his Grossulariaceae. Although most of these systematists have included these taxa in the Rosales or some roughly equivalent order, some workers have placed them in either the Cunoniales (Hutchinson, 1967) or the Cornales (Dahlgren, 1975, 1980, 1983).

Wood, leaves, and nodes of A. glandulosus and A. macleayanus were examined in this study (Table 2). Unless noted otherwise, data apply to both species.

Observations

Anopterus macleayanus possesses very long, narrowly oblanceolate to oblanceolate leaves while A. glandulosus possesses smaller, oblanceolate leaves. The leaves of both species bear blunt crenations (Fig. 43). Venation is semi-crasspedodromous with a prominent midvein and conspicuous secondary veins whose branches extend near the leaf margin and arch distally to join with superadjacent secondary or tertiary veins (Fig. 43). Vein areoles are smaller and their development is imperfect in A. macleayanus, while they are larger and their development is incomplete in A. glandulosus. Veinlets vary from straight to once or twice branched. Vein endings are usually tapered and simple, but may be clavate or branched. These vein endings are composed of two to eight helically thickened tracheids that usually are elongate but, may have irregular shapes (Fig. 44). Some tracheids possess small protuberances on their side walls that are characterized by helical thickenings that differ in orientation from the thickenings in the remainder of the

cell. These protuberances are less common in A. macleayanus than in A. glandulosus. In the latter species they often correspond to the interface between two large, irregularly shaped bundle sheath cells. Bundle sheath cells are not visible in the vein endings of A. macleayanus.

Although the nodal pattern is trilacunar, three-trace in Anopterus (Fig. 45), the vasculature of the petiole is very different for the two species (Figs. 46 & 47). In A. glandulosus, three collateral bundles enter the base of a petiole, traverse its entire length and enter the lamina distally (Fig. 46). Three bundles also enter the base of a petiole in A. macleayanus (Fig. 47). However, only the middle bundle is collateral, while the two lateral bundles are amphicribral (Fig. 47). Near the base of a petiole in A. macleayanus, the middle, collateral bundle enlarges to form a horseshoe-shaped or concentric central bundle with the two lateral, amphicribral bundles on either side. In the proximal half of a petiole two large gaps form in the large central bundle opposite the lateral amphicribral bundles. The central bundle also may divide at positions other than opposite the lateral bundles. Near a median point on a petiole the two amphicribral bundles become collateral and arc-shaped with xylem internal, and each of these bundles fuses with the dissected central bundle (Fig. 47). All of the remaining bundles of the dissected central bundle fuse to form a large horseshoe-shaped bundle that enters the lamina distally (Fig. 47).

Leaves of Anopterus are dorsiventral with a narrow, typically uniseriate, rarely biseriate palisade layer and a lacunose spongy mesophyll layer (Fig. 48). The uppermost cells of the palisade layer are elongate and tightly appressed while the lowermost cells are shorter and more loosely arranged. These latter cells are typically intermingled with the spongy mesophyll cells. The elongate uppermost palisade cells of A. glandulosus are somewhat longer than those of A. macleayanus. The spongy mesophyll cells have various shapes and sizes and are separated by large intercellular spaces. Druses are common in the spongy mesophyll cells of A. macleayanus, but infrequently occur in A. glandulosus.

The vascular bundles of a leaf typically are collateral, however, certain bundles (secondary veins) in A. macleayanus are amphicribral. The midvein and larger bundles (secondary veins) of both species exhibit a moderate amount of secondary growth. The midvein of A. glandulosus is relatively small and flattened or arc-shaped (Fig. 49), whereas that of A. macleayanus is very large and horseshoe-shaped (Fig. 50). In A. glandulosus the midvein is surrounded by thick-walled, lignified parenchyma cells adaxially and thin-walled parenchyma cells abaxially. Bundle sheath extensions of large diameter, thick-walled, unlignified parenchyma cells occur abaxially and adaxially. The larger bundles in this species have thick-walled fibers adjacent to the primary phloem, and all vascular bundles, except the midvein, are surrounded by parenchymatous bundle

sheaths without bundle sheath extensions. In A. macleayanus thick-walled fibers occur adjacent to the primary phloem of the large midvein and the amphicribral bundles (secondary veins) (Fig. 50). The ground tissue adjacent to the primary xylem and abaxial to the midvein consists of large diameter parenchyma cells (Fig. 50). Smaller, thicker-walled, unlignified parenchyma cells occur adaxially to these large diameter parenchyma cells. The smaller bundles (minor veins) in A. macleayanus lack bundle sheaths and extensions.

Both epidermal layers are uniserial, and their cells have various shapes in transection (Fig. 48). The cell walls of the epidermal cells are slightly thicker than those of the mesophyll cells. In surface view epidermal cells are variously shaped and generally possess sinuous anticlinal walls, although the abaxial epidermal cells of A. glandulosus may have curved anticlinal walls. The cuticle is thin (<5 um) and trichomes are absent.

Numerous stomata are restricted to the abaxial epidermis, and the stomatal apparatus is anomocytic. In surface view guard cells are reniform and guard-cell pairs are virtually circular in outline. Guard-cell pairs have an average length of 36 um and a width of 34.5 um (length/width ratio 1.04) in A. glandulosus, while those of A. macleayanus have an average length of 31 um and a width of 33 um (length/width ratio .94). In transection guard cells are oval and thick-walled, and each cell bears a short, curved cuticular horn that represents the outer ledge overarching the stoma (Fig. 51).

The apex and marginal crenations of Anopterus leaves contain glands at their apices. In leaf clearings these glands are characterized by dark-staining, thick-walled parenchyma cells arranged in regular files (Fig. 52). In paradermal sections of uncleared leaves, the cytoplasm of these cells is very dense and stains very darkly (Fig. 53). Each marginal crenation is supplied by an arc of vascular tissue that is derived from the union of two or more secondary or tertiary veins (Fig. 52).

The wood of Anopterus exhibits distinct growth rings (Fig. 54). The wood of A. macleayanus is exclusively diffuse porous. While wood of A. glandulosus is mostly semi-ring porous, it also may be diffuse porous. Anopterus wood is fine-textured with very numerous angular pores (range 60-210/mm², $\bar{x} = 128$) that possess very small tangential diameters. Pores of A. glandulosus are narrower (range 25-47 um, $\bar{x} = 37$) than those of A. macleayanus (range 26-68 um, $\bar{x} = 48$). In both species pore distribution is mostly solitary (78%), although radial multiples of two to three cells (2%) and clusters of two to five cells (20%), mostly due to overlapping end walls of vessel elements, do occur (Fig. 54). The vessel elements of both species have very thin radial walls (range 1.1-3.7 um, $\bar{x} = 2.4$) and lack spiral thickenings. These cells are long in both species, although they are longer in A. macleayanus (range 667-2084 um, $\bar{x} = 1220$) than in A. glandulosus (range 483-1634 um, $\bar{x} = 1023$). Vessel elements possess oblique end walls with angles that range

from 3-21° ($\bar{x} = 10$). Perforation plates are exclusively scalariform with 7-44 bars per plate ($\bar{x} = 24$) (Fig. 55). Bars are thin and often forked or branched. Occasionally two scalariform perforation plates occur per oblique vessel element end wall. Perforations commonly lack a border, however, in the narrowest vessel elements they may be bordered at the ends or completely bordered. Only one specimen of A. glandulosus (F. M. Hueber 3/17/70) possesses a few thin-walled tyloses in some vessels and trabeculae in some vessels and tracheids. This specimen also is the only one with abundant fungal hyphae throughout the wood. Intervascular pitting is uncommon in Anopterus, but, when present, these pits are very irregular and confined to overlapping end walls (Fig. 55). Intervascular pitting may be scalariform, transitional, opposite, or alternate, although transitional and opposite are the most common patterns. These elongate or oval pits have minute to small diameters (range 3.2-7.4 um, $\bar{x} = 5.0$).

Tracheids bear circular-bordered pits with oval to slit-like inner apertures that may be included within or extend beyond the margins of the pit border. The diameter of these pits is similar to that of the intervacular pits. Tracheids are medium to moderately long, and these cells in A. macleayanus are slightly longer (range 984-2134 um, $\bar{x} = 1465$) than those in A. glandulosus (range 1000-1734 um, $\bar{x} = 1315$). These tracheary elements have relatively thick radial walls (range 3.2-7.4 um, $x = 5.2$) and fine spiral thickenings (Fig. 55).

Axial parenchyma is sparse and predominantly apotracheal diffuse, although a few cells may be paratracheal scanty, or apotracheal marginal at the beginning of a growth layer. Vessel to axial parenchyma pitting, although rarely seen, is transitional, opposite, or alternate. No ergastic substances are noted in these cells.

The xylem ray system is composed of homocellular, uniserial rays of upright cells and heterocellular, bi- and multiseriate rays (Fig. 56). One very young specimen of A. macleayanus has a few heterocellular, uniserial rays. Homocellular rays are 1-20 cells high (.10-2.83 mm) for both species of Anopterus. Heterocellular rays are taller in A. glandulosus (7-53 cells, .37-3.97 mm) than in A. macleayanus (height: 7-37 cells, .33-2.63 mm). Heterocellular rays are also a bit wider in A. glandulosus (2-10 cells, 31-187 um) than in A. macleayanus (2-3 cells, 44-62 um). These differences in width are relatively minor because most heterocellular rays are 2-4 cells wide in both species. Dark brown deposits and starch grains are present in some ray cells. Sheath cells are absent, while perforated ray cells with scalariform perforation plates are occasionally present in both species (Fig. 57). Vessel to ray parenchyma pitting is transitional to mostly opposite, or alternate. All types of rays may be fused end-to-end, and all types may be split by vessels and/or tracheids.

Figure 43. Leaf of Anopterus glandulosus. X1. Note marginal crenations and semicraspedodromous venation.

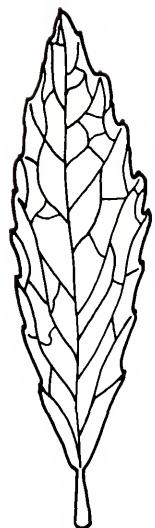
Figure 44. Vein ending of A. glandulosus. X175.

Figure 45. Transverse section of a node of A. glandulosus. X10.

Figure 46. Transverse sections of proximal (a), median (b) and distal (c) sections of a petiole of A. glandulosus. X10.

Figure 47. Transverse sections of proximal (a), median (b) and distal (c) sections of a petiole of A. macleayanus. X10.

Details: t, tracheids.

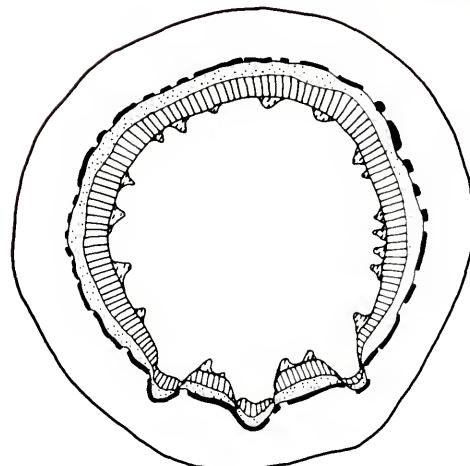


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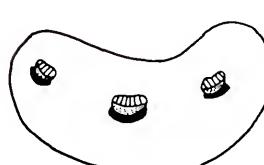


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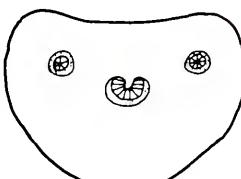
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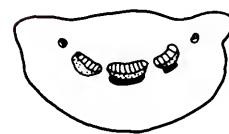
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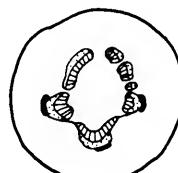
a



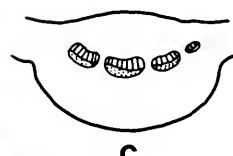
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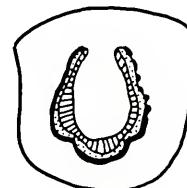
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b



c



c

47

Figure 48. Transverse section of a leaf of Anopterus glandulosus. X110.

Figure 49. Transverse section of the midvein of a leaf of A. glandulosus. X46.

Figure 50. Transverse section of the midvein of a leaf of A. macleayanus. X46. Note secondary vein.

Figure 51. Transverse section of the abaxial epidermis of a leaf of A. glandulosus. X700. Note guard cells with small cuticular horns (arrows).

Figure 52. Marginal crenation of a leaf of A. glandulosus. X110. Note the arc of vascular tissue which vascularizes the crenation.

Figure 53. Paradermal section of a marginal crenation of a leaf of A. glandulosus. X110.

Details: ab, abaxial epidermis; ad, adaxial epidermis; b, bundle sheath; be, abaxial bundle sheath extension; be', adaxial bundle sheath extension; c, cuticle; f, fiber; g, gland; gc, guard cells; gt, ground tissue; pl, palisade layer; sl, spongy mesophyll layer; sv, secondary vein; vb, vascular bundle; vt, vascular tissue.

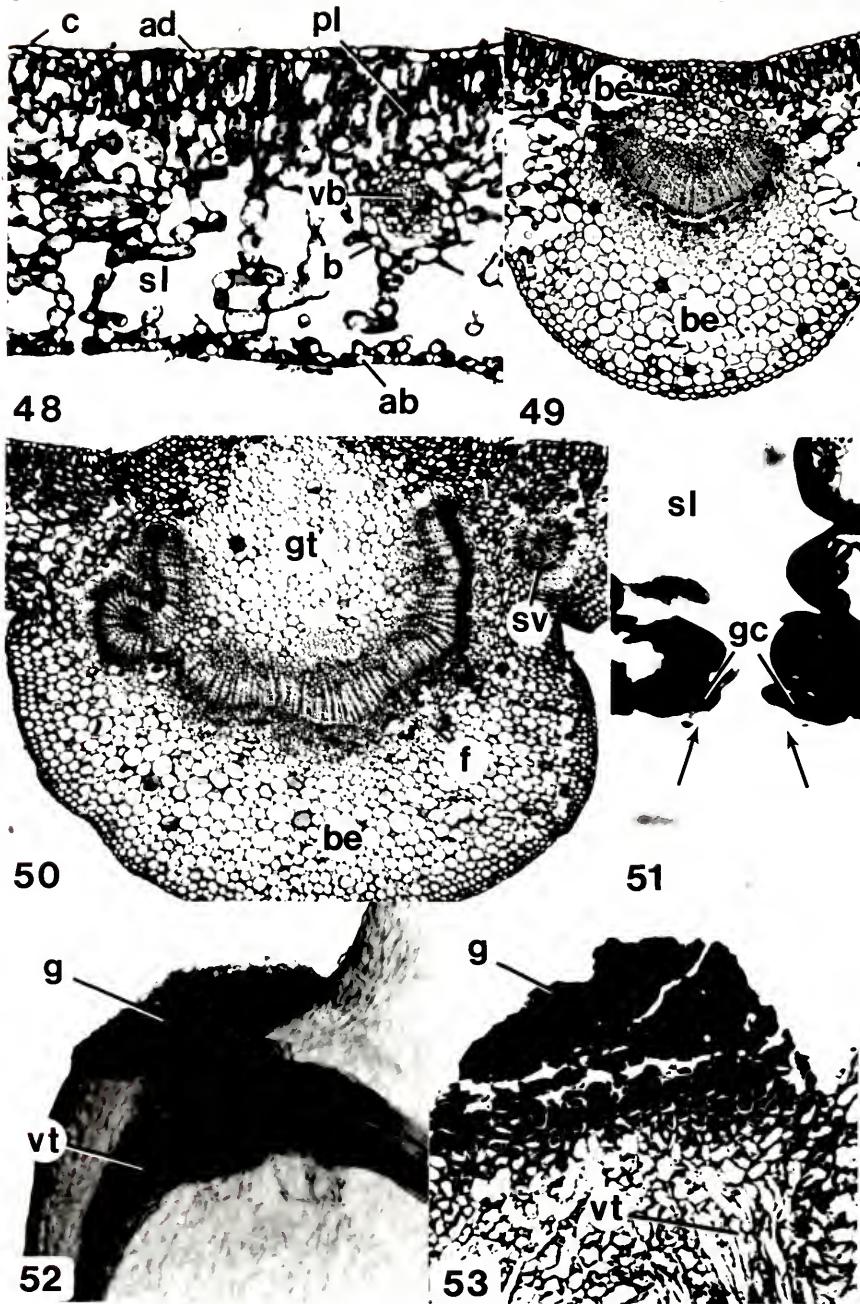


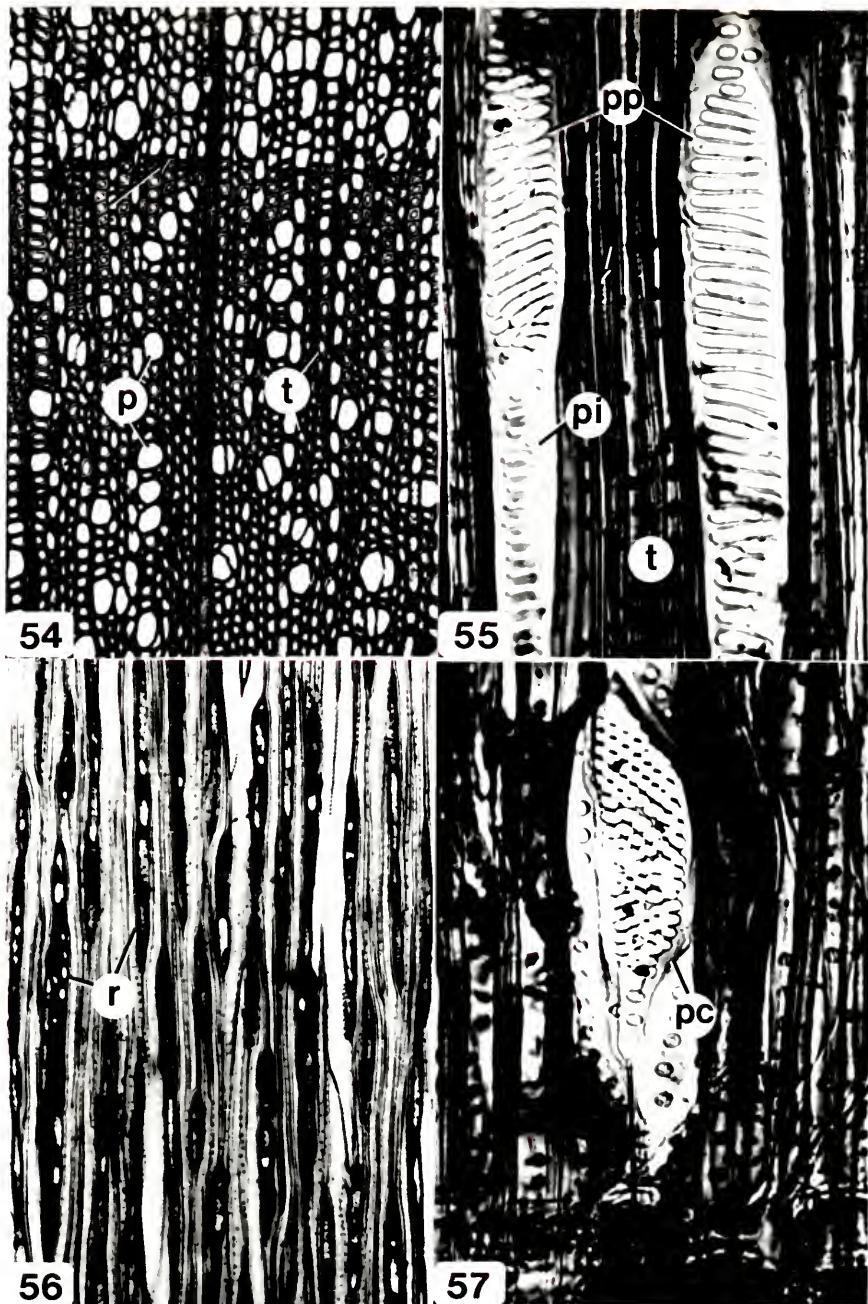
Figure 54. Transverse section of the secondary xylem of Anopterus glandulosus. X110. Note boundary of growth ring (arrow) and solitary, angular pores.

Figure 55. Radial section of the secondary xylem of A. glandulosus. X437. Note spiral thickenings (arrow) in tracheids.

Figure 56. Tangential section of the secondary xylem of A. glandulosus. X110. Note uni-, bi- and multiseriate rays.

Figure 57. Radial section of the secondary xylem of A. glandulosus. X437. Note perforated ray cell with scalariform perforation plate. X437.

Details: p, pore; pc, perforated ray cell; pi, pits; pp, perforation plate; r, ray; t, tracheid;



Cuttsia F. v. Muell.

Introduction

The monotypic genus Cuttsia was described by Ferdinand von Mueller in 1865 from specimens of C. viburnea. The generic name commemorates J. Cutts, the treasurer of the "Ladies Leichhardt Search Expedition," a group of women who raised money to support a search expedition to account for the disappearance of Ludwig Leichhardt (Mueller, 1865; Willis, 1949). This genus is endemic to southeastern Queensland and northeastern New South Wales, Australia and occurs along mountain streams (Bailey, 1900; Burbridge, 1963). Cuttsia viburnea is a shrub or small tree bearing exstipulate, simple, alternate leaves. The five-merous flowers are arranged in panicules, and each possesses a superior ovary that ripens into a capsule (Bailey, 1900; Engler, 1928).

Most systematists agree that Cuttsia belongs in either the subfamily Escallonioideae of the Saxifragaceae (Engler, 1890, 1928; Schulze-Menz, 1964; Thorne, 1976, 1983) or the Escalloniaceae (Airy Shaw in Willis, 1973; Dahlgren, 1975, 1980, 1983; Takhtajan, 1966, 1980). Cronquist (1968, 1981), however, placed this genus in his Grossulariaceae.

Observations

Cuttsia possesses simple, elliptic to ovate, serrate leaves. Venation is semicraspedodromous with a prominent

midvein and conspicuous secondary veins whose branches extend near the leaf margin and arch distally to join with superadjacent secondary or tertiary veins (Fig. 58). Areole development is incomplete. Veinlets may be straight, curved, or branched one to three times (Fig. 59). Vein endings are composed of two to five helically thickened tracheids that are surrounded by large-diameter parenchyma cells of the bundle sheath. These tracheids are usually elongate and possess very small protuberances whose position corresponds to the interface between two bundle sheath cells (Fig. 59).

The nodal pattern is trilacunar, three-trace, and three collateral bundles enter a petiole (Fig. 60). Near the base of a petiole a very small accessory vascular bundle branches from each of the lateral bundles near the adaxial surface of the petiole (Fig. 60). Distally from the point of divergence of these accessory bundles, the three main petiolar bundles fuse laterally to form a large horseshoe-shaped vascular bundle in the center of the petiole (Fig. 60). Two bundles may split from the adaxial side of this large central bundle (Fig. 60) or, in some petioles, the ends of the large central bundle may invaginate or become inrolled. In some petioles these inrolled ends may fuse to form a large, medullated concentric bundle with the xylem internal to the phloem. Distally each of the accessory bundles near the adaxial surface of a petiole splits to form two additional accessory bundles (Fig. 60).

Leaves of Cuttsia are dorsiventral with a well-differentiated biseriate palisade layer and a lacunose spongy mesophyll layer (Fig. 61). The palisade cells adjacent to the spongy mesophyll are widely spaced and exhibit various shapes and sizes compared to the columnar and closely appressed cells of the remainder of the palisade layer (Fig. 61). The spongy mesophyll is approximately the same thickness as the palisade layer and is composed of cells of various shapes and sizes and relatively large intercellular spaces. Crystal sand occurs sporadically in the larger cells of the spongy mesophyll (Fig. 62). In addition small clusters of yellowish cells are visible throughout the mesophyll of cleared leaves (Fig. 59).

The midvein of Cuttsia leaves may be arc-shaped, horseshoe-shaped with either collateral bundles or inrolled ends at the top of the horseshoe, or concentric and medullated (Fig. 63). Secondary growth is well-developed in the midvein and larger bundles (secondary veins). A large bundle sheath of thin-walled parenchyma cells surrounds each vascular bundle of a leaf (Fig. 61). Abaxial and adaxial bundle sheath extensions are associated with most bundles except for the very small veins. These bundle sheath extensions are composed of thick-walled parenchyma and collenchyma cells.

The adaxial epidermis is biseriate, whereas the abaxial epidermis is uniseriate (Fig. 61). In transection the cells of the abaxial epidermis and the outermost cells of the adaxial epidermis are rectangular to oval in outline. The

subjacent cells of the adaxial epidermis are square, round, oval, or rectangular (Fig. 61). In surface view the cells of the abaxial epidermis and the outermost cells of the adaxial epidermis are variously shaped and possess curved and sinuous anticlinal walls. The cuticle overlying both epidermides is very thin (<5 um). Unicellular, elongate, bulbous-based, thick-walled trichomes with tapered ends generally are sparse on abaxial leaf surfaces, but are common along the large veins.

Numerous stomata occur mostly in the abaxial epidermis, but also occur in the adaxial epidermis in association with hydathodes. The stomatal apparatus is anomocytic. In surface view individual guard cells are reniform, and guard-cell pairs are elliptic in outline (Fig. 64). Guard-cell pairs average 29 um in length and 21.3 um in width (length/width ratio 1.36). In transection the guard cells are galeate in outline, and each cell bears a small cuticular horn that represents the outer ledge overarching the stoma.

The apex and marginal teeth of a leaf of Cuttsia contain hydathodes. A prominent vein flares as it enters each marginal tooth (Fig. 65). In leaf clearings, a callosity composed of thick-walled cells is visible at the apex of the rounded marginal serrations. These thick-walled cells stain more darkly than other cells of a tooth (Fig. 65).

The wood of C. viburnea lacks growth rings (Fig. 66) and is fine-textured with numerous pores (range 10 -75/mm², $\bar{x} = 37$) that possess moderately small diameters (range 39-88 um, $\bar{x} = 64$) and relatively thin radial walls (range 1.6-6.3

um, $\bar{x} = 3.5$). Pores are predominantly solitary (87%), although radial multiples of two pores (1%) and clusters of two to four pores (12%) mostly due to overlapping end walls of contiguous vessel elements do occur. The pores primarily are angular in outline, however some may appear circular because their corners are often rounded (Fig. 66). The vessel elements are long (range 817 to 2367 um, $\bar{x} = 1368$) and possess steeply inclined oblique end walls. End-wall angles range from 6-30° ($\bar{x} = 15$). Perforation plates are exclusively scalariform and possess 32-104 bars per plate ($\bar{x} = 57$) (Fig. 67). Occasionally two scalariform perforation plates occur per oblique vessel element end wall. Scalariform perforation plate bars are thin and may be forked or branched. Perforations are bordered at the ends. Transitional, opposite to alternate intervacular pitting is confined to overlapping end walls, and the pits often intergrade with the scalariform perforation plates (Fig. 67). Pits are small in diameter and range from 3.2-5.8 um ($\bar{x} = 4.6$).

Tracheids have circular bordered pits with oval apertures that may be included within or extend beyond the margins of the pit border (Fig. 67). The diameter of these pits is similar to that of the intervacular pits. These cells are very long (range 1517-3267 um, $\bar{x} = 2396$ um). Tracheid wall thickness varies from 3.7 to 13.7 um ($\bar{x} = 7.5$ um). Fine spiral thickenings are present in most of these tracheary elements (Fig. 67).

Axial parenchyma is sparse and mostly apotracheal diffuse or diffuse-in-aggregates with short tangential bands

of two to four cells (Fig. 66). Rarely xylem parenchyma is paratracheal scanty. Vessel to axial parenchyma pitting is transitional, opposite or alternate. No ergastic substances are noted in these cells.

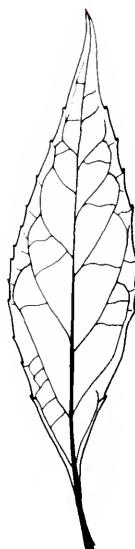
Although the xylem ray system is predominantly composed of homocellular, uniserial rays of upright cells and heterocellular, multiseriate rays (Fig. 68), a few homocellular, biseriate rays of upright cells are present in each specimen. Ray height ranges from 2-27 cells (1.33-3.23 mm) for uniserial rays, 4-30 cells (.65-3.92 mm) for biseriate rays, and 24-251 cells (1.40-11.37 mm) for multiseriate rays. Biseriate rays are 10-13 μm wide, and multiseriate rays mostly are 3-9 cells (34-163 μm) wide. One specimen (FPAw 18202) had rays up to 20 cells (650 μm) wide. No ergastic substances are noted in these cells. Sheath cells completely surround the multiseriate rays (Fig. 68), and perforated ray cells with scalariform or reticulate perforation plates are commonly found in the uniserial tails of multiseriate rays (Fig. 69). Vessel to ray parenchyma pitting is similar to pitting between vessels and axial parenchyma and is scalariform, transitional, opposite, or alternate. Multiseriate rays often are split by tracheids and/or vessels, and occasionally multiseriate rays are fused end-to-end.

Figure 58. Leaf of Cuttsia viburnea. X1/2. Note marginal serrations and semicraspedodromous venation.

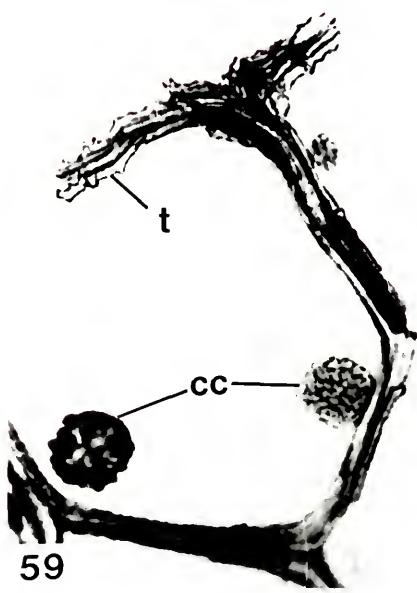
Figure 59. Vein ending of C. viburnea X175. Note small clusters of cells in the mesophyll.

Figure 60. Transverse sections of a node (a) and proximal (b), median (c) and distal (d) sections of a petiole of C. viburnea. X13.

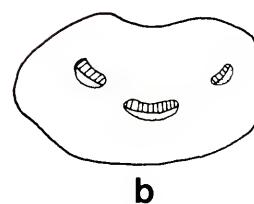
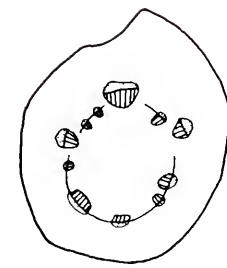
Details: cc, cluster of cells; t, tracheids.



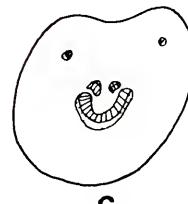
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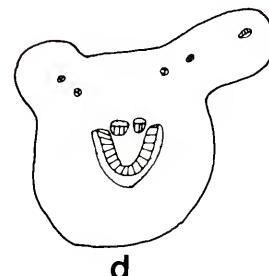
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b



c



d

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Figure 61. Transverse section of a leaf of Cuttsia viburnea. X175. Note biseriate adaxial epidermis.

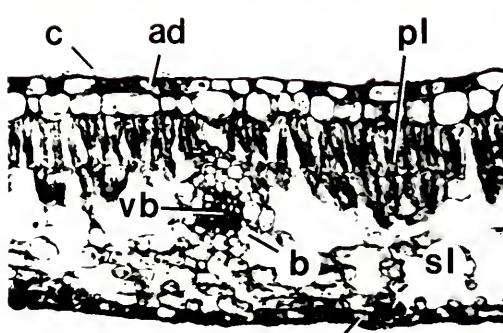
Figure 62. Crystal sand (arrows) in the spongy mesophyll layer of a leaf of C. viburnea. X700.

Figure 63. Transverse section of a midvein of a leaf of C. viburnea. X110. Note the constricted nature of the adaxial bundle sheath extension.

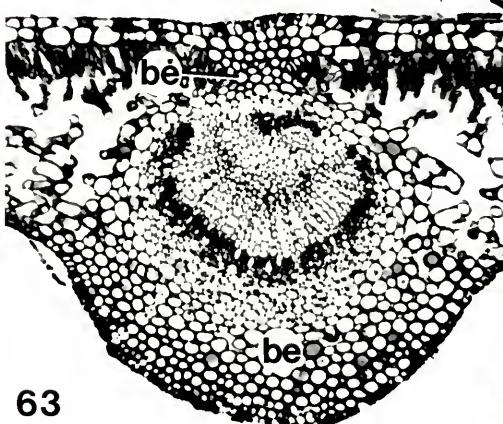
Figure 64. Paradermal section of the abaxial epidermis of a leaf of C. viburnea. X700. Note anomocytic stomatal apparatus.

Figure 65. Marginal serration of a leaf of C. viburnea. X110. Note the prominent flaring of vein and the apical callosity.

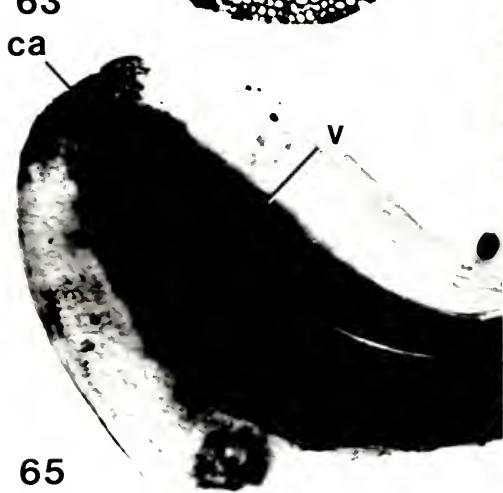
Details: ab, abaxial epidermis; ad, adaxial epidermis; b, bundle sheath; be, abaxial bundle sheath extension; be', adaxial bundle sheath extension; c, cuticle; ca, callosity; gc, guard cell; pl, palisade layer; sl, spongy mesophyll layer ; st, stoma; vb, vascular bundle; v, vein.



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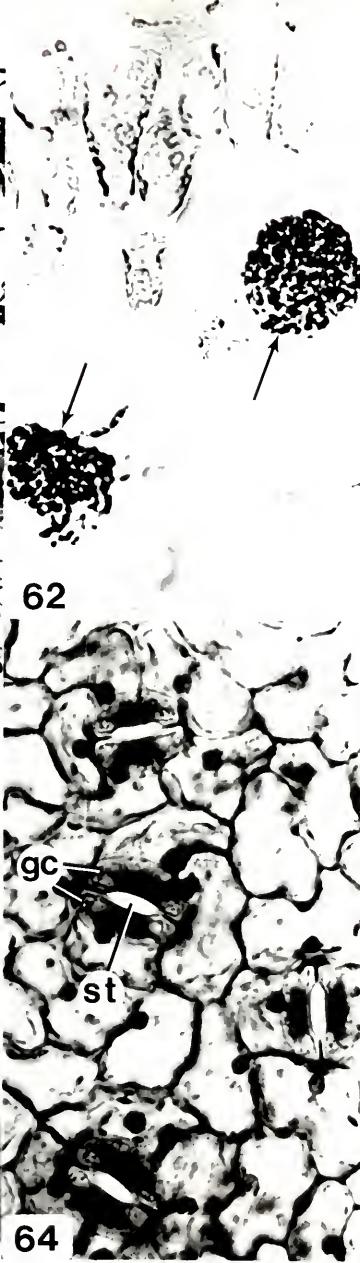


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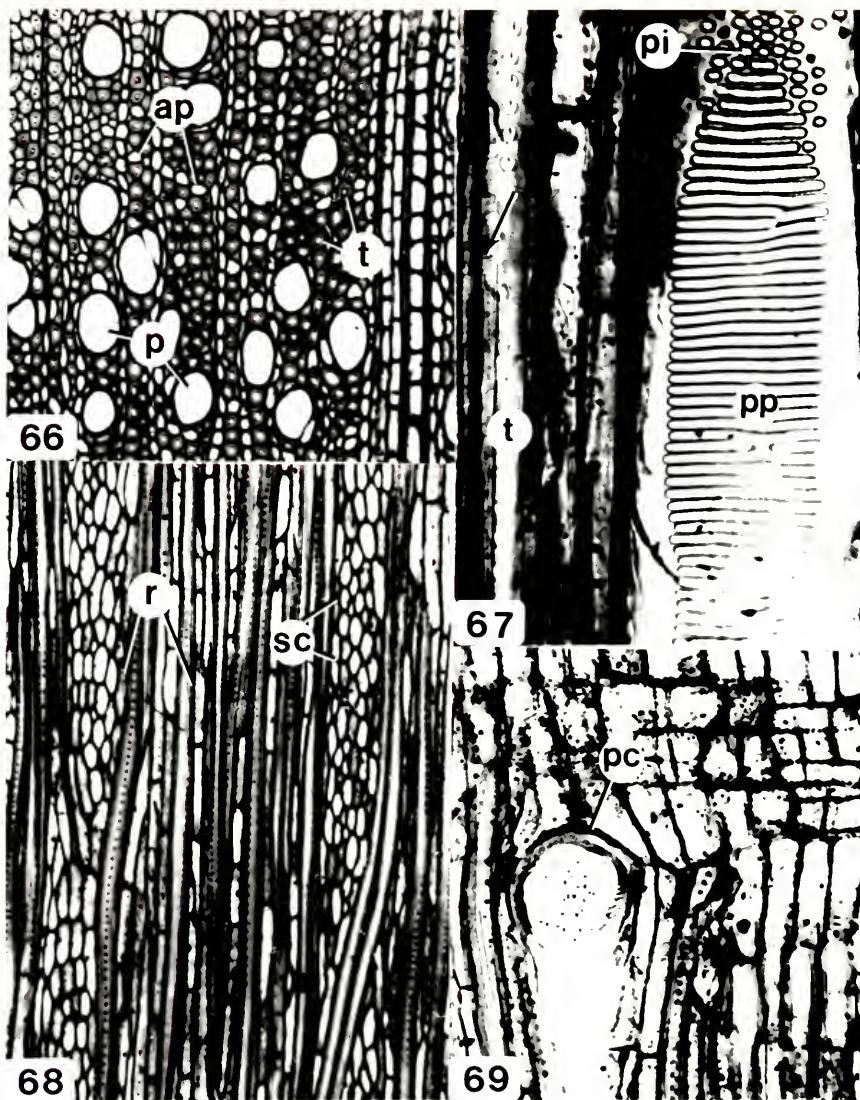
Figure 66. Transverse section of the secondary xylem of Cuttsia viburnea. X110. Note solitary, angular pores and diffuse and diffuse-in-aggregates axial parenchyma.

Figure 67. Radial section of the secondary xylem of C. viburnea. X437. Note fine spiral thickenings (arrow).

Figure 68. Tangential section of the secondary xylem of C. viburnea. X110. Note sheath cells.

Figure 69. Radial section of the secondary xylem of C. viburnea. X175. Note perforated ray cell with a scalariform perforation plate. X175.

Details: ap, axial parenchyma; p, pore; pc, perforated ray cell; pi, pits; pp, perforation plate; r, ray; sc, sheath cell; t, tracheid.



Abrophyllum Hook. f.Introduction

The type species for this genus was first described as Brachynema ornans by Ferdinand von Mueller in 1862. Mueller, however, was unaware that Brachynema had been used previously for some South American plants in the Ebenaceae (see discussion in Bentham, 1864). Thus J. D. Hooker changed the generic designation to Abrophyllum (Bentham, 1864). The name Abrophyllum refers to the delicate and beautiful leaves of plants within this genus (Bailey, 1883, 1900). Because of its foliage, Abrophyllum has limited use in ornamental horticulture (Bailey, 1944; Syng, 1974).

Abrophyllum contains two species, A. ornans and A. microcarpum, that are endemic and widespread in rainforests from eastern Queensland through eastern New South Wales (Beadle, Evans and Carolin, 1972; Burbidge, 1963). Plants of Abrophyllum are shrubs or small trees with large, serrate, alternate leaves. The five-merous flowers are arranged in panicles, and each possesses a superior ovary that ripens into a berry (Bailey, 1900, Bentham, 1864).

Most taxonomists have placed this genus either within the Escallonioideae of the Saxifragaceae (Engler, 1890, 1928; Hooker, 1865; Schulze-Menze, 1964; Thorne, 1976, 1983) or in the Escalloniaceae (Airy Shaw in Willis, 1973; Dahlgren, 1975, 1980, 1983; Hutchinson, 1967; Takhtajan,

1966, 1980). Cronquist (1981), however, has placed Abrophyllum in the Grossulariaceae.

The following observations are based upon specimens of A. ornans.

Observations

Abrophyllum ornans possesses large, ovate or elliptic, alternate leaves. These petiolate, exstipulate leaves bear small, rounded teeth along their margins, especially in the distal two-thirds of a leaf. Venation is semicraspedodromous with a prominent midrib and conspicuous secondary veins whose branches arch distally to join with a superadjacent secondary or tertiary vein or terminate in the marginal teeth (Fig. 70). Vein areole development is incomplete. Veinlets are curved or branched and terminal vein endings taper (Fig. 71). These vein endings are composed of two to five helically thickened and usually elongate tracheids. However, these cells may be short and often possess small protuberances which occur at the interface between two bundle sheath cells (Fig. 71).

The nodal pattern is trilacunar, three-trace (Fig. 72), and three collateral vascular bundles enter a petiole. Each bundle quickly splits twice to produce three groups of three bundles each at the base of a petiole (Fig. 72). One group of bundles occurs in the center of a petiole, while the other two groups occur near the adaxial surface of a petiole (Fig. 72). Distally a small accessory bundle separates adaxially from each of the two adaxial groups of bundles.

All the other bundles except the accessory bundles may split again, and these resultant bundles become reoriented to form a horseshoe-shaped, central group of vascular bundles (Fig. 72). Some of these central bundles also may fuse with one another (Fig. 72). Distally this central group of bundles may undergo further reorientation and fusion to form a concentric ring of vascular bundles in the center of the petiole (Fig. 72), or the horseshoe-shaped configuration may persist. Distally each accessory bundle also branches once to form four accessory bundles near the adaxial surface of the petiole (Fig. 72).

Leaves are dorsiventral with a well-differentiated biserrate palisade layer and a lacunose spongy mesophyll layer that is four cells thick (Fig. 73). The cells of the uppermost palisade layer are columnar and tightly appressed, while the cells of the innermost layer are spherical and more loosely arranged. The cells of the spongy mesophyll layer have various shapes and sizes and are loosely arranged with numerous small and large intercellular spaces. Crystal sand occasionally occurs in these spongy mesophyll cells. Enlarged, necrotic cells occur sporadically in the spongy mesophyll of both specimens examined. In addition, small clusters of yellowish cells are visible throughout the mesophyll in cleared leaves (Fig. 71).

The midvein of a leaf may be represented either by a concentric, medullated bundle with xylem internal and phloem external or by a concentric ring of collateral bundles that exhibit various degrees of fusion (Fig. 74). All other

vascular bundles are collateral. A small amount of secondary growth is visible in the midvein and all large bundles. A parenchymatous bundle sheath, and adaxial and abaxial bundle sheath extensions are associated with all vascular bundles. Bundle sheath extensions are composed of collenchyma cells around the larger bundles and parenchyma cells around the smaller bundles.

Both adaxial and abaxial epidermal layers are uniseriate. In transection epidermal cells are square, rectangular or oval with evenly thickened walls (Fig. 73). In surface view, these cells are irregularly shaped with sinuous and curved anticlinal walls. The adaxial epidermal cells are much larger than the abaxial epidermal cells. Cells of the abaxial epidermis have striations on their external surface. The cuticle overlying both epidermal layers is uniformly thin (<5 um).

Numerous stomata occur mostly in the abaxial epidermis, but do occur in the adaxial epidermis in association with hydathodes. The stomatal apparatus is anomocytic. In surface view guard cells are reniform and guard-cell pairs are elliptic in outline with an average length of 28.5 um and a width of 21 um (length/width ratio 1.36). In transection guard cells are oval to galeate and each cell bears a small, thin cuticular horn that represents the outer ledge over-arching a stoma (Fig. 75). Unicellular, elongate, bulbous-based, thick-walled trichomes with tapered ends are abundant over the abaxial epidermis and margins of a leaf, especially along the midvein and secondary veins.

The marginal teeth of a leaf contain hydathodes that are vascularized by a wide vein and possess water pores in the adaxial epidermis. These teeth are small and rounded, and the tooth apices often are composed of dark-staining, thick-walled cells which resemble glandular tissue.

Wood of A. ornans lacks growth rings (Fig. 76) and is fine-textured with very numerous angular pores (range 10-110/mm², $\bar{x} = 41$) that possess moderately small tangential diameters (range 38-125 μm , $\bar{x} = 75$) and thin radial walls (range 2.1-5.3 μm , $\bar{x} = 3.6$). Pore distribution is predominantly solitary (74%), although clusters of two to three cells (24%) mostly due to overlapping oblique end walls of vessel elements do occur. Vessel elements are long (range 834-2701 μm , $\bar{x} = 1705$) and lack spiral thickenings. End-wall angles of vessel elements range from 4-22° ($\bar{x} = 10^\circ$). Vessel element perforation plates are exclusively scalariform with numerous bars per plate (range 38-168, $\bar{x} = 93$) (Fig. 77). These thin bars may be branched, and the perforations are bordered only at their ends. Intervascular pitting only occurs on overlapping end walls and is mostly scalariform, transitional, or opposite, although alternate patterns may occur. These oval or elongate pits have small diameters (range 3.2-7.4 μm , $\bar{x} = 4.8$).

Tracheids bear circular bordered pits with slit-like apertures that extend beyond the pit border (Fig. 77). The diameter of these pits is similar to that of the intervascular pits. These tracheary elements are very long (range

1534-3351 um, $\bar{x} = 2464$) and possess thick radial walls ($\bar{x} = 8.4$ um). Coarse spiral thickenings are present in most tracheids (Fig. 77).

Axial parenchyma is sparse and mostly apotracheal diffuse or diffuse-in-aggregates with short tangential bands of two to four cells forming a link between uniseriate rays (Fig. 76). Rarely xylem parenchyma is scanty paratracheal. Vessel to axial parenchyma pitting is mostly transitional or opposite, rarely alternate.

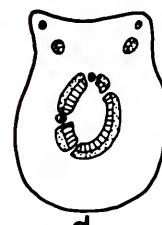
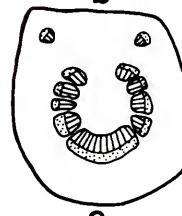
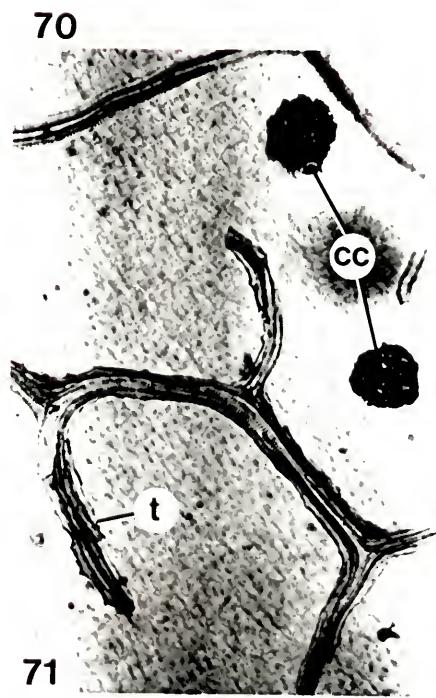
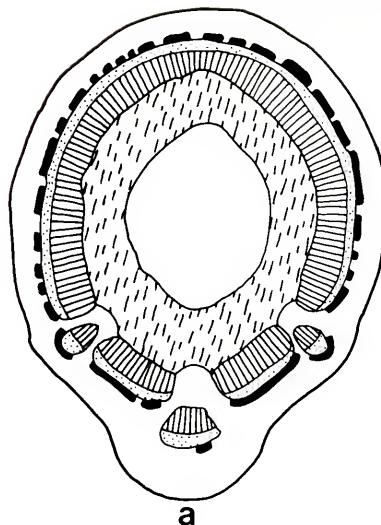
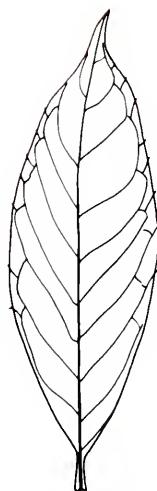
Ray tissue is abundant and mostly composed of homocellular, uniseriate rays of upright cells and heterocellular, multiseriate rays (Fig. 78). Rarely homocellular rays are biseriate. Uniseriate rays vary from 2-33 cells high (.47-4.92 mm) and multiseriate rays vary from 4-10 cells wide (91-429 um) and from 14-204 cells high (.53-15.40 mm). No ergastic substances are noted in these cells. Multiseriate rays are bordered by sheath cells, and perforated ray cells with scalariform or reticulate perforation plates occur occasionally in their uniseriate tails (Fig. 78). Vessel to ray parenchyma pitting is mostly transitional to opposite, although scalariform and alternate patterns may occur. Multiseriate rays often are split by vessels and/or tracheids, and aggregate rays are common.

Figure 70. Leaf of Abrophyllum ornans. X1/2. Note very small marginal serrations and semicraspedodromous venation.

Figure 71. Vein ending of A. ornans X175.

Figure 72. Transverse sections of a node (a) and proximal (b), median (c) and distal (d) sections of a petiole of A. ornans. X10.

Details: cc, cluster of cells; t, tracheid.



71

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Figure 73. Transverse section of a leaf of *Abrophyllum ornans*. X175.

Figure 74. Transverse section of a midvein of a leaf of *A. ornans*. X46. Note the constricted nature of the adaxial bundle sheath extension. X46.

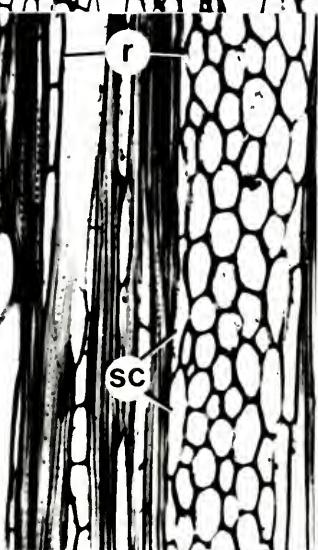
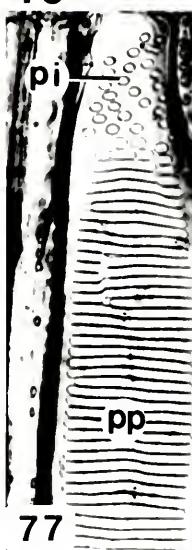
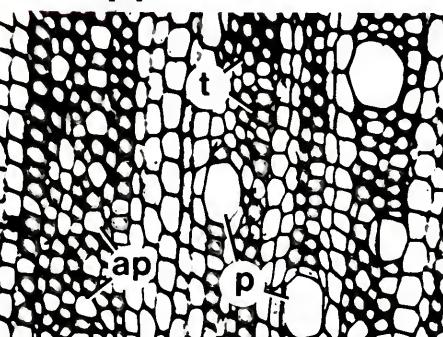
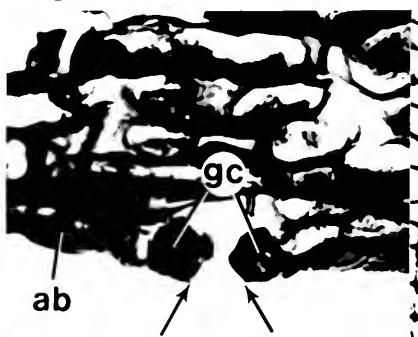
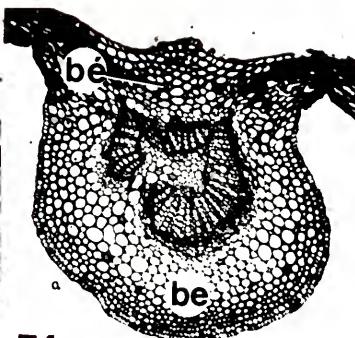
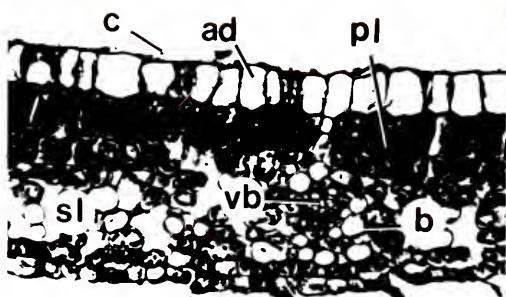
Figure 75. Transverse section of the abaxial epidermis of a leaf of *A. ornans*. X700. Note guard cells with small cuticular horns (arrows).

Figure 76. Transverse section of the secondary xylem of *A. ornans*. X110. Note solitary, angular pores and diffuse and diffuse-in-aggregates axial parenchyma.

Figure 77. Radial section of the secondary xylem of *A. ornans*. X437. Note spiral thickenings (arrow).

Figure 78. Tangential section of the secondary xylem of *A. ornans*. X110. Note sheath cells and perforated ray cells.

Details: ab, abaxial epidermis; ad, adaxial epidermis; ap, axial parenchyma; b, bundle sheath; be, abaxial bundle sheath extension; be', adaxial bundle sheath extension; c, cuticle; gc, guard cell; p, pore; pc, perforated ray cell; pi, pitting; pl, palisade layer; pp, perforation plate; r, ray; sc, sheath cell; sl, spongy mesophyll layer; t, tracheid; vb, vascular bundle.



Carpodetus J. R. & G. Forst.

Introduction

Although Carpodetus was described from specimens of C. serratus, which is endemic to New Zealand, (Forster and Forster, 1776), the center of diversity for the genus is New Guinea with nine species (Reeder, 1946; Schlechter, 1914). One other species, C. amplus Reeder, is endemic to the nearby Solomon Islands (Reeder, 1946). The generic name refers to the manner in which the fruit is girt by the cicatrix of the adnate calyx (Allan, 1961; Cheeseman, 1925; Forster and Forster, 1776; Laing and Blackwell, [1949]). Plants within this genus are shrubs or small trees that bear alternate, simple, exstipulate leaves (Cheeseman, 1925; Reeder, 1946; Allan, 1961). The four-, five-, or six-merous flowers are arranged in panicles or corymbs, and each contains an inferior or half-inferior ovary that ripens into an indehiscent capsule. Although the genus is not economically important, the strong and tough wood of C. serratus has been used for axe handles (Cheeseman, 1925). This species also has been used in ornamental horticulture (Bailey and Bailey, 1976).

Originally Carpodetus was believed to be monotypic (Cheeseman 1914, 1925; Cunningham, 1839). However, some specimens from southeastern New Guinea, described as Argyrocallymma K. Schumann & Lauterbach, were later reduced to Carpodetus (Engler, 1928; Schlechter, 1914), and two

sections (Argyrocallymma K. Schum. & Lauterb. and Eucarpodetus Engl.) were recognized. Reeder (1946) subsequently described three new species of Carpodetus and followed Engler (1928) and Schlechter (1914) in reducing three other species of Argyrocallymma to Carpodetus. Presently eleven species have been described for Carpodetus, and three were examined in this study (Table 2).

The type species, C. serratus, occurs on North, South, and Stewart Islands, New Zealand, in montane and coastal forests and along the banks of rivers and streams up to elevations of 1000 m (Allan, 1961; Cheeseman, 1914, 1925). Carpodetus major is endemic to New Guinea and is found in misty forests at elevations between 1300 and 1800 m (Reeder, 1946). Carpodetus arboreus, one of two species in the genus with four-merous flowers, is also endemic to New Guinea (Reeder, 1946).

Most taxonomists have placed Carpodetus in either in the Saxifragaceae, subfamily Escalloniodeae (Engler, 1890, 1928; Schulze-Menze, 1964; Thorne, 1976, 1983) or in the Escalloniaceae (Dahlgren, 1975, 1980, 1983; Hutchinson, 1967; Airy Shaw in Willis, 1973; Takhtajan, 1966, 1980). Cronquist (1981) has placed this genus in his Grossulariaceae. While most systematists have included these taxa in the Rosales, others have placed the Escalloniaceae in the Cunoniales (Hutchinson, 1967) or the Cornales (Dahlgren 1975, 1980, 1983).

Anatomical and morphological observations for this genus are based upon leaves, stems and wood of C. serratus

and wood of C. arboreus and C. major (Table 2). Unless noted otherwise, the data apply for all species examined.

Observations

Carpodetus serratus possesses elliptic to ovate, alternate, petiolate leaves. The small teeth of the serrate leaves are narrow and rounded. Venation is semicraspedodromous with a prominent midvein and conspicuous secondary veins that terminate at a leaf margin or arch distally to join a superadjacent secondary vein (Fig. 79). These leaves also possess a few to many domatia on the abaxial surface in the axils of the secondary veins (Figs. 79 & 80). The domatia are small pockets lined by thick-walled epidermal cells with short, thick-walled, unicellular trichomes (Fig. 80). Vein areole development is imperfect, and veinlets are variously branched (Fig. 81). Vein endings are composed of one to four elongate, helically thickened tracheids and large, thick-walled bundle sheath cells. In some cases, these tracheids possess short protuberances along their side walls at the interface of two bundle sheath cells.

The nodal pattern is trilacunar, three-trace, and three collateral bundles enter the base of a petiole (Fig. 82). These three bundles quickly fuse laterally near the base of a petiole to form a large, relatively flat, collateral bundle in the center of the petiole (Fig. 82). Two, small collateral bundles split adaxially from this large bundle (Fig. 82). These two accessory bundles and the large, central bundle of the petiole enter the lamina distally.

Leaves of C. serratus are dorsiventral with a well differentiated bi- to triseriate palisade layer and a compact spongy mesophyll layer (Figs. 83 & 84). In transection all palisade cells are tightly appressed, however, the cells adjacent to the spongy mesophyll are sometimes shorter and wider than the other elongate, columnar palisade cells. The spongy mesophyll is composed of variously shaped cells and very small intercellular spaces. Druses commonly occur in spongy mesophyll cells, but rarely occur in palisade cells.

The vascular bundles of a leaf are collateral and may be round or arc-shaped. A moderate amount of secondary growth is evident in the larger bundles (midvein and secondary veins) (Fig. 85). These larger bundles possess a bundle sheath of thick-walled, lignified parenchyma cells. Druses rarely occur in these cells. Bundle sheath extensions composed of thick-walled parenchyma and collenchyma cells occur both adaxially and abaxially. The smaller bundles (minor veins) also possess a bundle sheath and may possess a parenchymatous bundle sheath extension adaxially (Fig. 84).

Although the abaxial epidermis is uniseriate, the adaxial epidermis has both uniseriate and biseriate regions in transection. In most leaves the adaxial epidermis is uniseriate between the veins and biseriate above the veins (Fig. 83). However, in one specimen (B. F. Shore s.n. 4) with small, young leaves, the adaxial epidermis is almost entirely biseriate (Fig. 84). In transection all cells of both epidermal layers are square or rectangular and possess

evenly thickened walls. The cells of the innermost layer of the adaxial epidermis have numerous primary pit fields in their anticlinal walls. In surface view epidermal cells are variously shaped. The outermost cells of the adaxial epidermis possess straight or curved anticlinal walls, while the cells of the abaxial epidermis possess curved and sinuous anticlinal walls. The cuticle overlying both epidermal layers is very thin (<5 um).

Stomata occur mostly in the abaxial epidermis, but do occur in the adaxial epidermis in association with hydathodes. The stomatal apparatus is anomocytic. In surface view individual guard cells are reniform and guard-cell pairs are elliptic in outline. Average guard-cell-pair length is 30 um and width is 23 um (length/width ratio 1.29). In transection the guard cells are oval to circular and each cell possesses a very small cuticular horn that represents the outer ledge overarching the stoma. Elongate, unicellular, thick-walled, bulbous-based trichomes with tapered ends are generally distributed over both epidermal layers, but are especially abundant along the major veins (Fig. 80). The trichomes associated with domatia are shorter, wider and thicker-walled than the other foliar trichomes (Fig. 80).

The marginal teeth and apex of a leaf contain hydathodes. A prominent vein flares as it enters each tooth (Fig. 86). In leaf clearings dark-staining cells, which may be glandular tissue, are visible at the apex of the marginal serrations (Fig. 86).

Although Carpodetus wood is fairly uniform based upon cell types, morphology of vessel elements and composition of ray tissue, the three species studied exhibit some differences in the dimensions of cells, pore density and diameter and numbers of bars per scalariform perforation plate. These differences parallel the distributions of the three species. The two species from New Guinea, C. arboreus and C. major, are very similar, while the New Zealand species, C. serratus, is distinct from them.

The wood of C. serratus exhibits distinct growth layers, is semi-ring porous, and possesses numerous pores (range 45-185/mm², $\bar{x} = 99$) with narrow diameters (range 26-72 um, $\bar{x} = 46$) (Fig. 87). The wood of C. arboreus and C. major lacks growth rings and possesses fewer pores (range 10-45/mm², $\bar{x} = 22$; range 10-55/mm², $\bar{x} = 27$, respectively) with wider diameters (range 47-130 um, $\bar{x} = 94$; range 52-112 um, $\bar{x} = 77$, respectively) than the wood of C. serratus (Fig. 88). Pores are angular in outline and predominantly solitary for all species (range 66-90%, $\bar{x} = 78$). Radial multiples (range 0-4%, $\bar{x} = 0.5$) and clusters (range 10-34%, $\bar{x} = 21.5$) of pores are mostly due to overlapping end walls of vessel elements. Vessel walls are thicker in C. arboreus (range 2.1-5.3 um, $\bar{x} = 3.5$) and C. major (range 2.1-4.7 um, $\bar{x} = 3.4$) than in C. serratus (range 1.0-3.7 um, $\bar{x} = 2.4$). Vessel elements of C. serratus are shorter (range 550-1700 um, $\bar{x} = 1039$) than those of either C. arboreus (range 550-2217 um, $\bar{x} = 1593$) or C. major (range 650-2084 um, $\bar{x} = 1409$). End-wall angles range

from 2.5-31° ($\bar{x} = 10$) in C. serratus to 7-28° ($\bar{x} = 15$) in C. arboreus and C. major. In all species the perforation plates are exclusively scalariform, the perforations have complete borders, and the bars may be forked or branched (Fig. 89). Carpodetus serratus possesses more bars per scalariform perforation plate (range 19-116, $\bar{x} = 54$) than either C. arboreus or C. major (range 16-70, $\bar{x} = 40$). The perforation plates occasionally are compound with two scalariform plates in an oblique end wall. Some vessel elements of C. serratus also possess very fine spiral thickenings, which are lacking in the other two species. Intervascular pitting is confined to overlapping end walls of vessel elements and often intergrades with the scalariform perforation plates. This pitting varies from scalariform, transitional, or opposite in C. serratus to transitional, opposite, or alternate in C. arboreus and C. major. Pit diameter is largest in C. arboreus (range 5.3-8.4 um, $\bar{x} = 6.7$) and slightly smaller in both C. major (range 4.2-7.4 um, $\bar{x} = 5.6$) and C. serratus (range 4.2-6.3 um, $\bar{x} = 5.0$).

Tracheids bear circular bordered pits with oval apertures that are either included within or extend slightly beyond the pit border. The diameter of these pits is similar to that of the intervacular pits. Tracheids are much longer in both C. arboreus (range 1650-3051 um, $\bar{x} = 2355$) and C. major (range 1800-3601 um, $\bar{x} = 2591$) than in C. serratus (range 1050-3601 um, $\bar{x} = 1700$). Tracheid walls are approximately twice as thick in C. arboreus (range 6.3-17.9 um, $\bar{x} = 11.1$) and C. major (range 4.7-13.1 um, $\bar{x} = 9.1$) than in C.

serratus (range 3.2-8.9 um, $\bar{x} = 5.5$). Coarse spiral thickenings typically occur in the tracheids of all three species.

Axial parenchyma is sparse and predominantly apotracheal diffuse or diffuse-in-aggregates with short tangential bands of two to three cells forming a link between uniseriate rays (Fig. 88). Xylem parenchyma is occasionally paratracheal scanty. Vessel to axial parenchyma pitting is mostly opposite in all three species. Rarely alternate pitting occurs in C. arboreus and C. major and transitional, opposite to alternate pitting rarely is noted in C. serratus. Dark brown deposits are present in the axial parenchyma of one specimen of C. serratus that contains numerous fungal hyphae.

The ray system of Carpodetus is fairly uniform and composed mostly of homocellular, uniseriate rays of upright and square cells and heterocellular, multiseriate rays (Fig. 90). Homocellular, biseriate rays rarely occur. Uniseriate rays range in height from 1-18 cells (.60-1.78 mm), while multiseriate rays range in height from 11-402 cells (.67-10.59 mm) and range in width from 2-18 cells (26-697 um). Carpodetus serratus possesses the tallest and widest multiseriate rays among the three species. The multiseriate rays of Carpodetus are bordered by elongate sheath cells (Fig. 90), and perforated ray cells with scalariform or reticulate perforation plates commonly occur among the cells of the uniseriate tails (Fig. 87). All species possess prismatic crystals in the square and/or procumbent cells of the

multiseriate rays (Fig. 89). These crystals are probably nonoxalate because they did not dissolve in the ammoniacal iron alum used in the staining procedure. Although vessel to ray parenchyma pitting varies from scalariform and transitional to opposite or alternate, the most common pattern is opposite. Aggregate rays are common, and rays often are split by vessels and/or tracheids (Fig. 90).

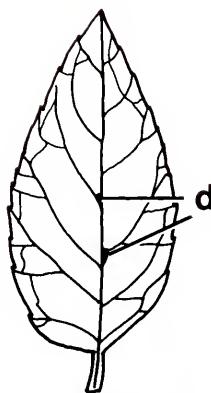
Figure 79. Leaf of Carpodetus serratus. X1. Note marginal serrations, semicraspedodromous venation and domatia in the axils of the secondary veins.

Figure 80. Domatium in the axil of a secondary vein of C. serratus. X110. Note trichomes.

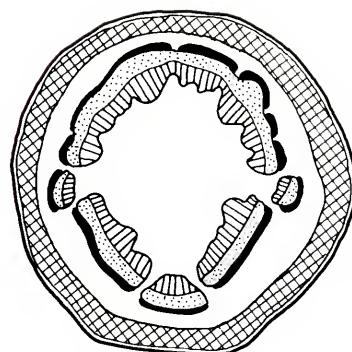
Figure 81. Vein endings of C. serratus. X175.

Figure 82. Transverse sections of a node (a) and proximal (b), median (c) and distal (d) sections of a petiole of C. serratus. X30.

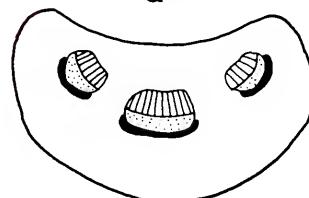
Details: d, domatia; t, tracheid; tr, trichome.



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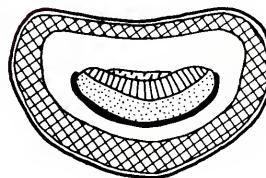
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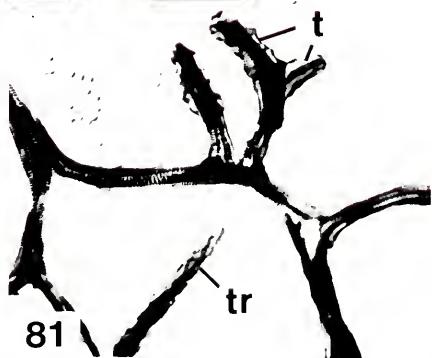
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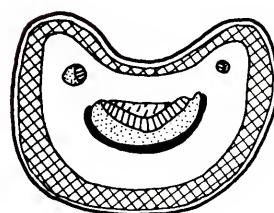
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c



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d

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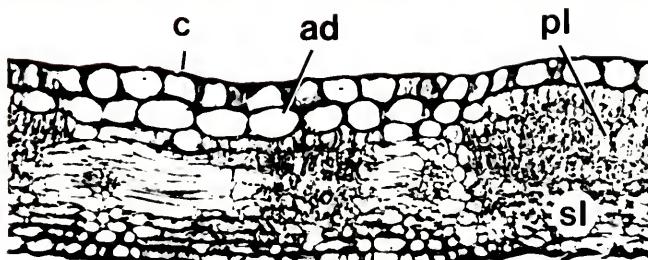
Figure 83. Transverse section of a leaf of Carpodetus serratus. X175. Note partially biseriate adaxial epidermis.

Figure 84. Transverse section of a leaf of C. serratus. X175. Note totally biseriate adaxial epidermis.

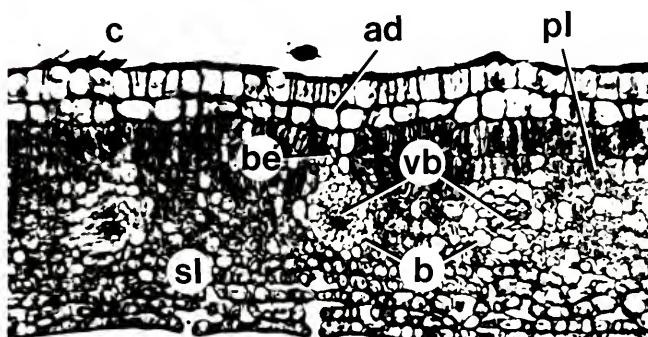
Figure 85. Transverse section of a midvein of a leaf of C. serratus. X110. Note the discontinuous and constricted nature of the adaxial bundle sheath extension, and the domatia on either side of the midvein.

Figure 86. Marginal serration of a leaf of C. serratus. X110. Note the apical callosity and the prominent vein which flares as it enters the serration.

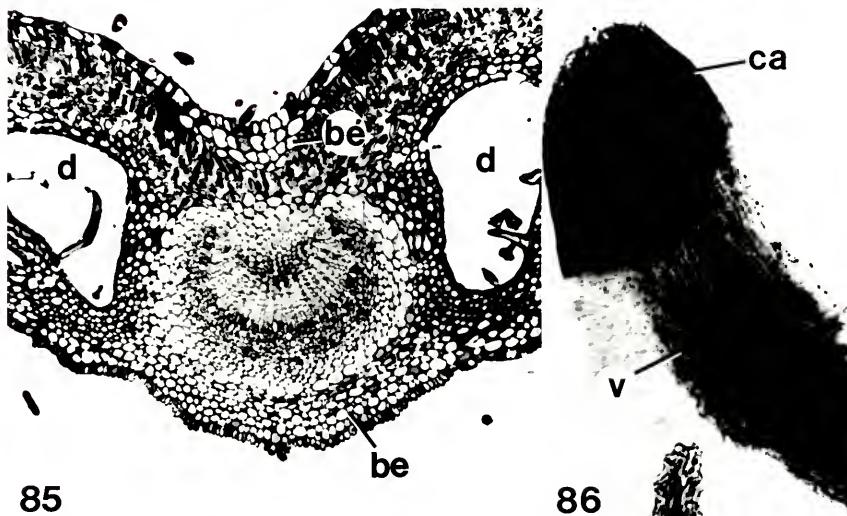
Details: ab, abaxial epidermis; ad, adaxial epidermis; b, bundle sheath; be, abaxial bundle sheath extension; be', adaxial bundle sheath extension; c, cuticle; ca, callosity; d, domatium; pl, palisade layer; sl, spongy mesophyll layer; st, stoma; vb, vascular bundle; v, vein.



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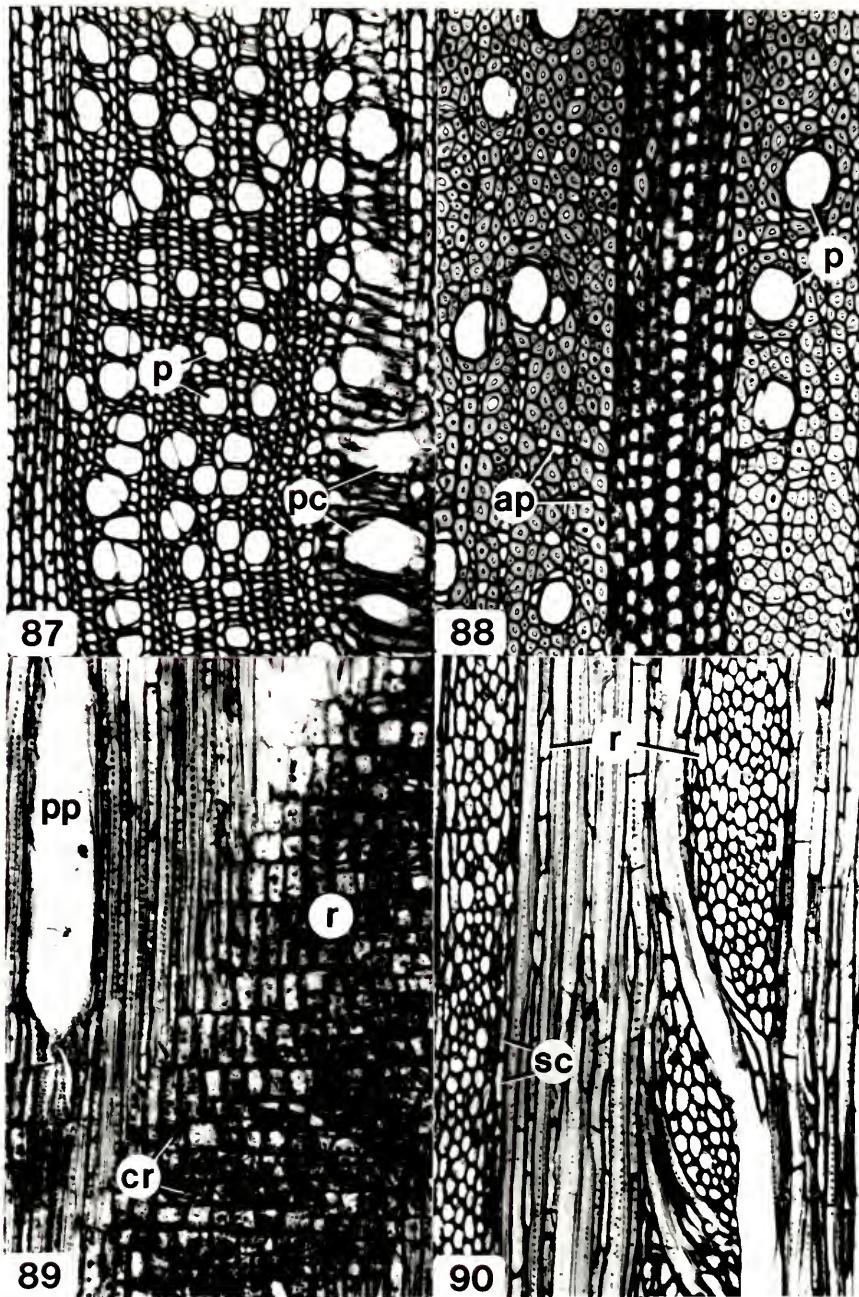
Figure 87. Transverse section of the secondary xylem of Carpodetus serratus. X110. Note solitary, angular pores and perforated ray cells.

Figure 88. Transverse section of the secondary xylem of C. major. X110. Note solitary, angular pores and diffuse and diffuse-in-aggregates axial parenchyma.

Figure 89. Radial section of the secondary xylem of C. arboreus. X110.

Figure 90. Tangential section of the secondary xylem of C. serratus. X110. Note uni- and multiseriate rays, and sheath cells.

Details: ap, axial parenchyma; cr, prismatic crystal; p, pore; pc, perforated ray cell; pp, perforation plate; r, ray; sc, sheath cell.



Corokia A. Cunn.Introduction

The genus Corokia was described by Allan Cunningham in 1839 from specimens of C. buddleoides collected in Wanga-roa, New Zealand. The generic name refers to the plant's common name, korokio-taranga, used by the Maori, a Polynesian people native to New Zealand (Cunningham, 1839).

Plants of Corokia are usually shrubs, rarely small trees, with alternate, simple, exstipulate leaves (Allan, 1961; Cheeseman, 1925; Smith, 1958). The five-merous flowers are borne in axillary or terminal cymes, panicles, or racemes, and each flower possesses an inferior ovary that ripens into a drupe.

Corokia has six to eight species distributed from eastern Australia and Lord Howe Island to New Zealand, Chatham Island and Rapa Island. The center of diversity for Corokia is New Zealand where three to four endemic species occur (Allan, 1961; Cheeseman, 1925). The most widely distributed species is C. cotoneaster which occurs throughout both North and South Islands in lowland shrub-lands, river flats, and rocky places up to elevations of 750 m. Corokia buddleoides is found only in the northern portion of Auckland District, North Island along the margins of coastal and lowland forests and in shrub-lands up to elevations of 900 m (Allan, 1961; Cheeseman, 1925). Corokia cotoneaster and

C. buddleiooides readily hybridize where they occur together, and hybrid specimens collected in the field were described as C. cheesemannii H. Carse in 1913 (Allan, 1961; Cheeseman 1925). Another name, Corokia virgata Turrill, was applied to specimens cultivated at the Royal Botanical Gardens, Kew from cuttings of uncertain origin (Allan, 1961). These cultivated specimens match fairly well with the hybrid specimens found in the field, and C. cheesemannii and C. virgata may be synonyms (Allan, 1961; Cheeseman, 1925). Corokia macrocarpa, originally considered a variety of C. buddleiooides, is restricted to forests and forest margins of Chatham Island. The westernmost representative of the genus, C. whiteana, occurs in New South Wales, Australia, in rainforests of high elevations in the Gibbergunyah Range (Smith, 1958). Corokia carpodetoides is endemic to Lord Howe Island and was originally the basis of the monotypic genus Colmeiroa (Engler, 1928; Smith, 1958). The easternmost representative of this genus, C. collenettei, is endemic to Rapa Island (Eyde, 1966). The New Zealand species and hybrid(s) of Corokia are commonly used in ornamental horticulture (Bailey and Bailey, 1976; Synge, 1974).

Cunningham (1839) noted that Corokia had affinities to the Rhamnaceae. However, subsequent authors (Allan, 1961; Cheeseman, 1925; Harms, 1897; Hooker, 1867; Hutchinson, 1967; Melchior, 1964) have placed this genus in the Cornaceae and include this family in the Cornales or some equivalent order. Other workers have placed Corokia in either the Escalloniaceae (Airy Shaw in Willis, 1973; Takhtajan,

1966, 1980, 1983), or the Escallonioideae of the Saxifragaceae (Engler, 1928; Thorne, 1976, 1983) and include these families among the Rosales or the Saxifragales. Dahlgren (1975) originally placed Corokia in the Escalloniaceae, but later made it the basis for the Corokiaceae in his Cornales (1980, 1983). Cronquist (1981) placed this genus in his large rosalean family Grossulariaceae. A taxonomic revision of Corokia is long overdue and desperately needed to help resolve the nomenclatural problems, the uncertain limits of the genus and the lack of agreement on its familial affinities.

Leaves and nodes of C. carpodetoides, C. macrocarpa, and C. virgata, and wood of C. buddleiodoides, C. collenettei, and C. whiteana were available for anatomical study (Table 2). Unless noted otherwise, data apply to all species examined.

Observations

Species of Corokia possess simple, entire, elliptic to obovate, alternate leaves. Venation is semicraspedodromous to brochidodromous with a prominent midvein and conspicuous secondary veins that form arches by joining with superadjacent secondary veins (Figs. 91 & 92). Vein areole development is imperfect, and veinlets may be straight, curved, or variously branched (Fig. 93). Vein endings are composed of one to six helically thickened tracheids. Each tracheid is usually elongate, but some may be branched, curved, or clavate. In addition, some tracheids possess small

protuberances in which the helical thickenings are oriented at right angles to the rest of the spiral thickenings.

The nodal pattern is trilacunar, three-trace in C. carpodetoides and C. macrocarpa (Fig. 94), and unilacunar, one-trace in C. virgata (Fig. 95). Three collateral vascular bundles enter the base of a petiole in C. carpodetoides and C. macrocarpa (Fig. 94). These three bundles fuse laterally approximately midway along the length of a petiole to form a single, wide, flattened, arc-shaped vascular bundle (Fig. 94). This wide central bundle enters the lamina distally. Only one collateral vascular bundle enters the petiole in C. virgata (Fig. 95). This single vascular bundle extends the length of the petiole and enters the lamina distally (Fig. 95).

Leaves of C. carpodetoides, C. macrocarpa and C. virgata are dorsiventral with a weakly differentiated, bi-seriate palisade layer and a lacunose spongy mesophyll layer (Figs. 96 & 97). The uppermost palisade cells are columnar, while the elongate palisade cells adjacent to the spongy mesophyll have various shapes and sizes and often intergrade with the spongy mesophyll cells. In all three species the cells in one or both layers of the palisade mesophyll typically contain dark brown deposits (Fig. 97). Most of the cells of the spongy mesophyll are isodiametric or variously shaped and separated by large intercellular spaces. In C. macrocarpa and C. virgata, however, the spongy mesophyll cells adjacent to the abaxial epidermis are

elongate periclinally and have much smaller intercellular spaces among them.

The arc-shaped or round vascular bundles of Corokia leaves are collateral. A small amount of secondary growth is present in the midvein of C. macrocarpa (Fig. 98). The midvein is surrounded by a parenchymatous bundle sheath in C. virgata and C. carpodetoides or by a partial bundle sheath composed of thin-walled parenchyma cells abaxially and thick-walled, lignified parenchyma cells adaxially in C. macrocarpa (Fig. 98). Abaxial and adaxial bundle sheath extensions of thin-walled parenchyma cells occur around the midvein in leaves of C. carpodetoides and C. macrocarpa. In addition, the portion of a bundle sheath extension adjacent to both epidermal layers in C. carpodetoides and C. macrocarpa is composed of thick-walled parenchyma cells and collenchyma cells. Only an abaxial bundle sheath extension of thick-walled parenchyma and collenchyma cells is associated with the midvein in leaves of C. virgata (Fig. 97). Bundle sheaths of thin-walled parenchyma cells surround the smaller vascular bundles (secondary veins and minor veins) in the leaves of all species (Fig. 96). These smaller bundles lack bundle sheath extensions.

Both epidermal layers are uniseriate. In transection epidermal cells are square or rectangular, however, the adaxial epidermal cells are much larger and have thicker walls than the abaxial epidermal cells (Figs. 96 & 97). The abaxial epidermal cells of all species have evenly thickened walls except for those abaxial epidermal cells beneath the

midvein of leaves of C. macrocarpa which possess unevenly thickened outer walls that resemble ridges in transection (Fig. 99). The adaxial epidermal cells of C. carpodetoides and C. macrocarpa have evenly thickened walls, whereas these cells in C. virgata have thin anticlinal and inner periclinal walls and very thick, cutinized outer periclinal walls (Fig. 97). In surface view the cells of both epidermides are mostly polygonal with straight to curved anticlinal walls. The cuticle is thin (<5 um) in C. macrocarpa and C. carpodetoides, but thick (>5 um) in C. virgata.

Abundant stomata occur mostly in the abaxial epidermis, but also occur in the adaxial epidermis in association with hydathodes in C. macrocarpa and C. virgata. The stomatal apparatus is anomocytic in the three species studied (Fig. 100). In surface view individual guard cells are reniform. Guard-cell pairs are circular in outline in C. macrocarpa and C. virgata while they are typically elliptic, rarely circular, in C. carpodetoides (Fig. 100). In the former two species guard-cell pairs have an average length of 24 um and a width of 23 um (length/width ratio 1.04), while in the latter species they have an average length of 36 um and a width of 27 um (length/width ratio 1.33). In transection guard cells are oval, and each cell bears a small cuticular horn that represents the outer ledge overarching a stoma. In addition, in C. macrocarpa and C. virgata, the guard cells are elevated above the abaxial epidermis by subsidiary cells which are curved or slightly enlarged (Fig. 101).

Multicellular, T-shaped trichomes with uniseriate stalks of two to six cells and an elongate, lignified terminal cell occur on the abaxial epidermis (Figs. 102 & 103). The terminal cell and uppermost stalk cell are separated by walls with elongate pits (Figs. 104 & 105). The abaxial leaf surfaces of C. macrocarpa and C. virgata are densely covered by T-shaped trichomes, whereas these unique trichomes are only conspicuous along the midvein and near the revolute margins of the leaves of C. carpodetoides.

Hydathodes only occur in the apex of the leaves of C. macrocarpa and C. virgata. A group of thick-walled cells is present near the leaf apex of C. macrocarpa.

Although Corokia wood is fairly uniform based upon cell types and dimensions, morphology of vessel elements, and composition of xylem ray tissue, the three species studied can be distinguished from one another based upon the morphology of the imperforate elements present in the wood.

Distinct growth layers are present in the diffuse porous wood of C. buddleiodoides and the semi-ring porous wood of C. whiteana (Fig. 106), but are absent from the wood of C. collenettei (Fig. 107). Axial parenchyma is absent from all three species. All species have very numerous pores per square mm, with ranges of $100-160/\text{mm}^2$ ($\bar{x}=140$) for C. collenettei, $150-315/\text{mm}^2$ ($\bar{x}=217$) for C. buddleiodoides, and $250-380/\text{mm}^2$ ($\bar{x}=305$) for C. whiteana. All species have thin-walled (range 1-4.2 μm , $\bar{x}=2.3 \mu\text{m}$), angular pores that are mostly solitary (74%). Occasionally true radial multiples of two to four cells occur (5%) (Fig. 107), while pore

clusters of two to four cells (21%) mostly result from overlapping vessel element end walls. Pore diameter is very small for all three species. Pores are narrowest in C. whiteana (range 18-33 μm ; $\bar{x} = 24$), wider in C. buddleoides (range 23-42 μm ; $\bar{x} = 33$), and widest in C. collenettei (range 29-51 μm ; $\bar{x} = 40$). All species possess medium to long vessel elements (range 368-1117 μm ; $\bar{x} = 784$) with steeply inclined oblique end walls. End-wall angles range from 2-24° ($\bar{x} = 11$). Perforation plates are exclusively scalariform with 13-17 thin bars per plate ($\bar{x} = 23$) (Fig. 108). The perforations are non-bordered. Perforation plates are rarely compound with two scalariform perforation plates per oblique end wall. Some vessel elements of C. buddleoides and C. collenettei possess very fine spiral thickenings at the ends of the cells. Intervascular pitting varies from transitional, opposite, to alternate for all species, although alternate is the most common pattern. Corokia collenettei infrequently exhibits a scalariform arrangement. The diameter of these oval or elongate pits is minute (range 3.2-4.2 μm , $\bar{x} = 3.4$).

All three species studied possess septate fiber-tracheids that bear circular bordered pits with medium to long inner apertures that extend well beyond the pit borders (Fig. 108). The pit border is larger in the septate fiber-tracheids of C. collenettei than in those of C. buddleoides or C. whiteana. The inner aperture of these pits is much longer in C. buddleoides than in C. whiteana. Corokia

buddleioides and C. whiteana also possess tracheids with circular bordered pits whose inner apertures extend slightly beyond the pit borders. Pit diameters for the tracheids are similar to those of the intervacular pits, whereas pit diameters for the septate fiber-tracheids in C. buddleioides and C. whiteana are extremely minute. Imperforate tracheary elements for all species are moderately short to medium long (range 717-1617 μm ; $\bar{x} = 1095$) with thin walls (range 3.2-7.4 μm , $\bar{x} = 4.5$). Both types of imperforate tracheary elements typically possess coarse spiral thickenings.

The xylem ray system of Corokia is composed mostly of homocellular uniseriate rays of upright cells and heterocellular bi- to multiseriate rays, although each species may have a few homocellular, biseriate and heterocellular, uniseriate rays (Fig. 109). Homocellular, uniseriate rays range in height from 1-13 cells (.07-.88 mm), while multiseriate rays range in height from 6-56 cells (.23-2.33 mm) and width from 3-20 cells (21-83 μm). Perforated ray cells are occasionally seen in all species (Fig. 108), while sheath cells are lacking. Dark brown deposits are abundant in most ray cells (Fig. 108), but crystals are absent. Although vessel to ray parenchyma pitting varies from transitional, opposite, or alternate, the most common pattern is alternate. Fusion of rays is uncommon, however, very few rays are joined end-to-end in C. collenettei.

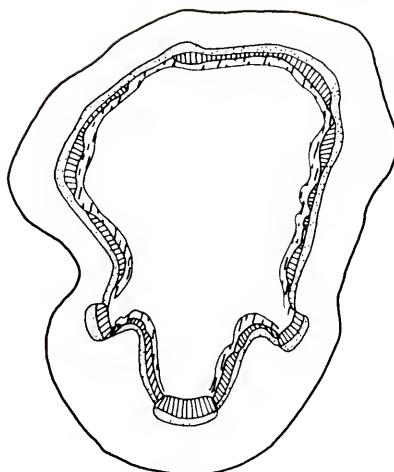
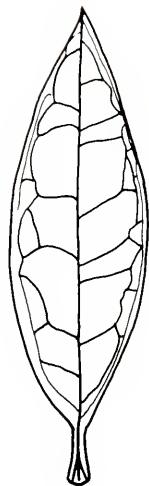
Figure 91. Leaf of Corokia macrocarpa. X1. Note semicraspedodromous to brochidodromous venation.

Figure 92. Leaf of C. carpodetoides. X1.

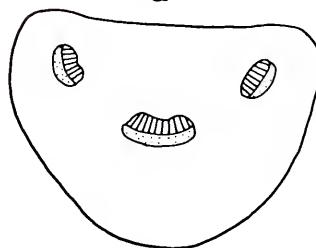
Figure 93. Vein ending of C. macrocarpa with helically thickened tracheids. X175.

Figure 94. Transverse sections of a node and proximal (b), median (c) and distal (d) sections of a petiole of C. macrocarpa. X20.

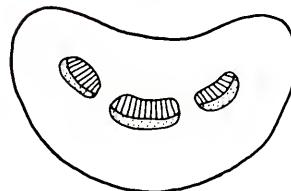
Details: t, tracheids.



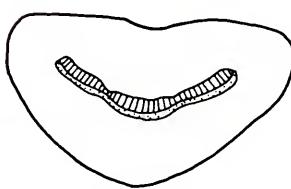
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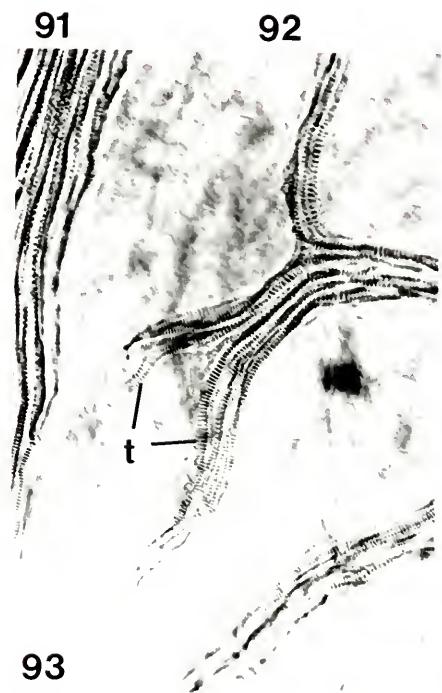
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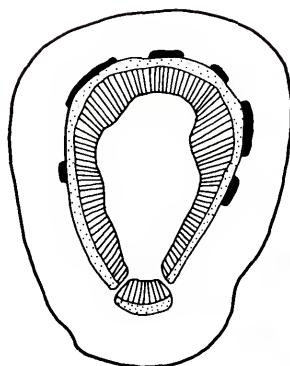
Figure 95. Transverse section of a node (a) and a distal section of a petiole (b) of Corokia virgata. X50.

Figure 96. Transverse section of a leaf of C. carpodetoides. X437.

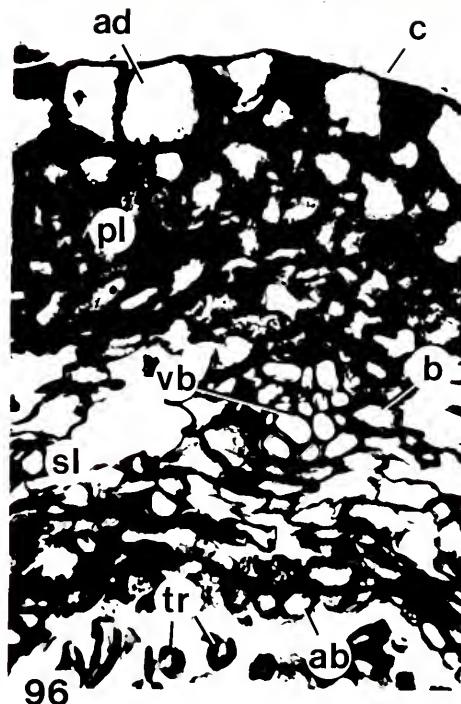
Figure 97. Transverse section of a midvein of a leaf of C. virgata. X175.

Figure 98. Transverse section of a midvein of a leaf of C. macrocarpa. X46.

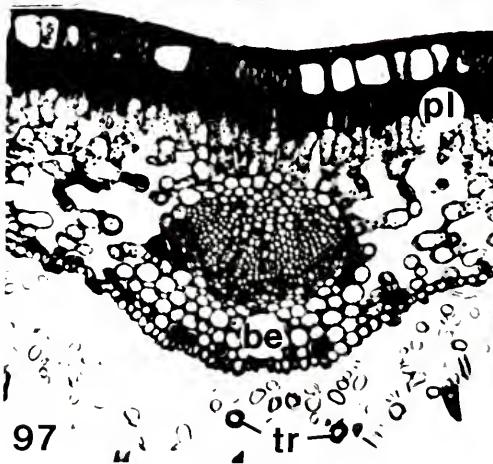
Details: ab, abaxial epidermis; ad, adaxial epidermis; b, bundle sheath; be, abaxial bundle sheath extension; be', adaxial bundle sheath extension; c, cuticle; pl, palisade layer; sl, spongy mesophyll layer; tr, trichome; vb, vascular bundle.



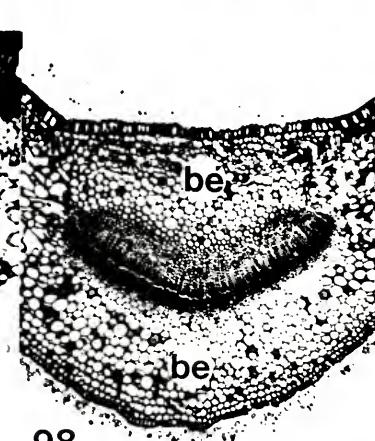
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Figure 99. Transverse section of a leaf of Corokia macrocarpa. X700. Note the ridges on the outer tangential walls of the abaxial epidermal cells located below the midvein.

Figure 100. Paradermal section of the abaxial epidermis of a leaf of C. macrocarpa. X437. Note anomocytic stomatal apparatus.

Figure 101. Transverse section of the abaxial epidermis of a leaf of C. virgata. X700. Note the elevated guard cells.

Figure 102. Multicellular, T-shaped trichome of C. macrocarpa. X175.

Figure 103. Multicellular, T-shaped trichome of C. virgata. X175.

Figure 104. Multicellular, T-shaped trichome of C. macrocarpa. X700. Note pitting (arrow) in the walls that separate the terminal cell from the uppermost stalk cell.

Figure 105. Surface view of the pits between the terminal cell and the uppermost stalk cell of a T-shaped trichome of C. macrocarpa. X1750.

Details: ab, abaxial epidermis; gc, guard cell; gt, ground tissue; pi, pits; r, ridges; sl, spongy mesophyll layer; st, stoma; tr, trichome.

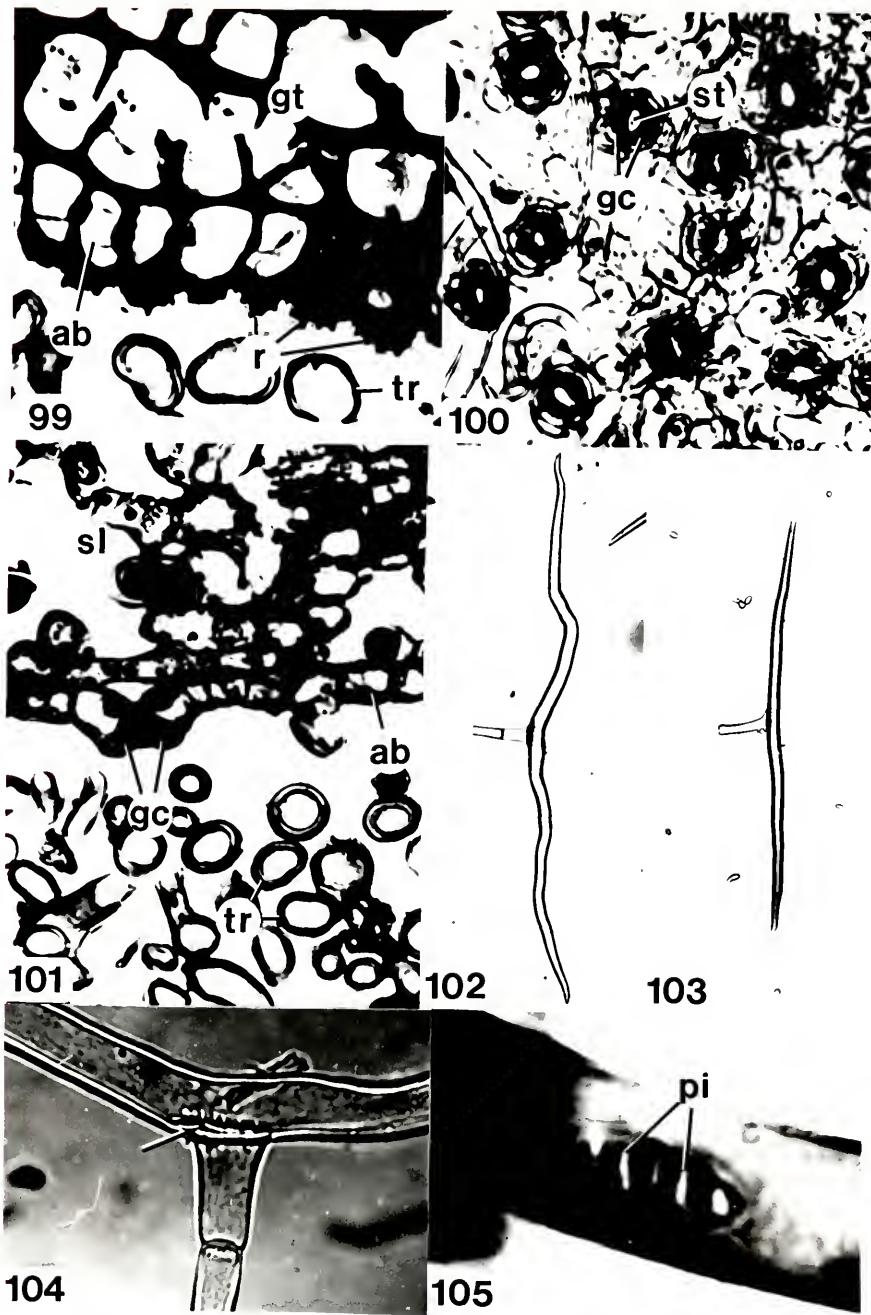


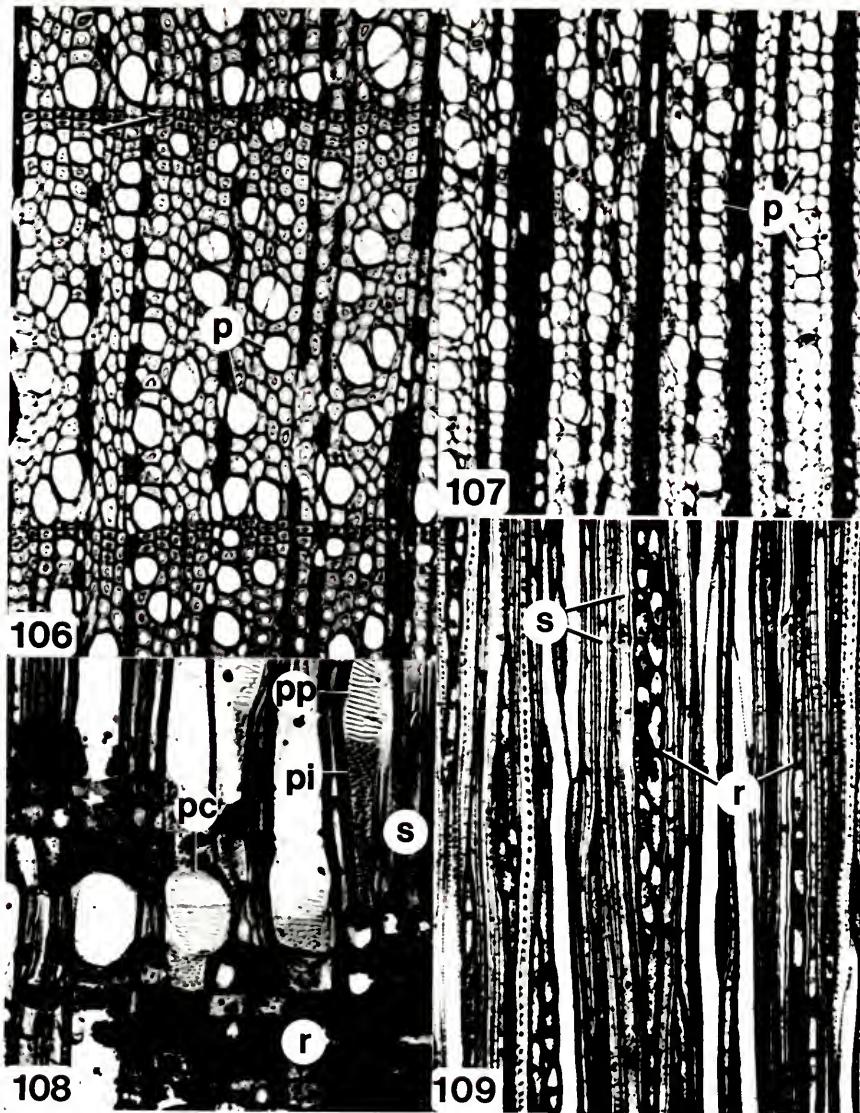
Figure 106. Transverse section of the secondary xylem of Corokia buddleoides. X175. Note the boundary of a growth ring (arrow) and solitary, angular pores. X175.

Figure 107. Transverse section of the secondary xylem of C. collenettei. X110. Note both solitary and radial multiples of pores.

Figure 108. Radial section of the secondary xylem of C. collenettei. X175. Note septum (arrow) of septate fiber-tracheids.

Figure 109. Tangential section of the secondary xylem of C. whiteana. X175. Note uni- and biseriate rays.

Details: p, pore; pc, perforated ray cell; pi, pits; pp, perforation plate; r, ray; s, septate fiber-tracheid.



Argophyllum J. R. & G. Forst.Introduction

The genus Argophyllum was described by J. R. and G. Forster in 1776 from specimens of A. nitidum, a species which occurs in both New Caledonia and eastern Australia (Forster and Forster, 1776; Zemann, 1907). The generic name refers to the silvery-white color of the lower surface of the leaves of these plants (Bailey, 1900; Forster and Forster, 1776). Argophyllum contains nine other species besides the type, with three species endemic to eastern Australia and six to New Caledonia (Zemann, 1907). Plants of Argophyllum are shrubs or small trees that bear alternate, exstipulate leaves. The flowers are mostly five-merous, rarely six-merous, and arranged in panicles or corymbbs. Each flower contains a two- to five-celled, half-inferior ovary which is adnate to the calyx tube and ripens into a capsule (Bailey, 1900; Bentham, 1864; Zemann, 1907).

Zemann (1907) divided Argophyllum into two sections. The section Brachycalyx contains species with a calyx that is much shorter than the corolla, while species in section Dolichocalyx have a calyx at least half as long as the corolla. Argophyllum ellipticum is endemic to humid, mountainous areas in the northern portion of New Caledonia (Zemann, 1907). Argophyllum cryptophlebum is restricted to

the mountains in northern Queensland, Australia, and A. nullumense is endemic to the mountains of northern New South Wales, Australia (Bailey, 1900; Zemann, 1907).

Most taxonomists agree that Argophyllum belongs in either the subfamily Escallonioideae of the Saxifragaceae (Engler, 1890, 1928; Schulze-Menz 1964; Thorne, 1976, 1983) or the Escalloniaceae (Airy Shaw [in Willis, 1973]; Dahlgren, 1975, 1980, 1983; Takhtajan, 1966, 1980). Cronquist (1968, 1981), however, placed this genus in his Grossulariaceae. Although most of these taxonomists agree that Argophyllum belongs in the Rosales or some roughly equivalent taxon, Dahlgren (1975, 1980, 1983) has placed this genus in his Cornales.

Wood of A. cryptophlebum, A. nullumense, and A. ellipticum, and leaves and nodes of the first two species were available for this study (Table 2). All three species are included in the section Brachycalyx. Unless noted otherwise, data apply to all species examined.

Observations

Leaves of A. cryptophlebum are simple and ovate with tiny serrations, while the leaves of A. nullumense are simple and elliptic with very widely-spaced, and relatively large serrations. Both species have alternate leaves. Venation is semicraspedodromous with a prominent midvein and conspicuous secondary veins whose branches extend near the leaf margin and arch distally to join with superadjacent secondary or tertiary veins (Fig. 110). Areole development

is imperfect, and veinlets may be straight, curved, or branched one to three times (Fig. 111). The tapered or blunt vein endings are composed of two to seven helically thickened tracheids that are usually elongate, but may be short and irregularly-shaped. Some of these cells also possess short protuberances on their lateral walls.

The nodal pattern is trilacunar, three-trace, and three collateral bundles enter a petiole (Fig. 112). These three bundles fuse laterally approximately midway along the length of a petiole to form a large, horseshoe-shaped bundle in the center of a petiole (Fig. 112). In A. nullumense the ends of this petiolar bundle inroll or invaginate, while the ends of the petiolar bundle in A. cryptophlebum do not (Fig. 112). The horseshoe-shaped bundle enters the lamina distally.

Leaves of A. cryptophlebum and A. nullumense are dorsiventral with a poorly differentiated palisade layer and a spongy mesophyll layer with relatively small intercellular spaces (Fig. 113). In transection cells of the palisade layer are square or oval, closely appressed, and usually stain very darkly. Often these cells contain tan or brown deposits (Fig. 113). The leaves of A. nullumense have a uni- or biseriate palisade cell layer while those of A. cryptophlebum have a biseriate palisade layer. The cells of the spongy mesophyll have various shapes and sizes, although many of them are elongate periclinally in transection (Figs. 113 & 115).

The midvein of A. nullumense is a concentric, medullated bundle with xylem internal to the phloem (Fig. 114). This bundle is surrounded by a parenchymatous bundle sheath with bundle sheath extensions of thick-walled, unlignified parenchyma cells both abaxially and adaxially. The midvein of A. cryptophlebum is an arc-shaped, collateral bundle. This bundle is also surrounded by a parenchymatous bundle sheath, however, the bundle sheath extensions are composed of thin-walled parenchyma cells adaxially and thin- and thick-walled, unlignified parenchyma cells and collenchyma cells abaxially. Although some of the smaller vascular bundles (secondary veins) of A. nullumense may be amphicribral (Fig. 114), these bundles commonly are collateral. All the smaller bundles of A. cryptophlebum are collateral. In both species these smaller bundles (secondary and minor veins) lack both bundle sheaths and bundle sheath extensions.

The epidermal layers are uniseriate and contain cells that are rectangular with rounded corners, or oval in transection (Fig. 113). In surface view the epidermal cells of Argophyllum leaves are variously-shaped and may possess curved or sinuous (A. cryptophlebum), or straight (A. nullumense) anticlinal walls. The cuticle is very thin (<5 um) in both species.

Abundant stomata are restricted to the abaxial epidermis, and the stomatal apparatus is anomocytic. In surface view individual guard cells are reniform and guard-cell pairs are almost circular in outline. Guard-cell pairs have

an average length of 19 μm and a width of 18 μm (length/width ratio 1.06). In transection guard cells are oval, and each cell bears a very small cuticular horn that represents the outer ledge overarching a stoma. In addition, the guard cells are raised above the level of the abaxial epidermis by curved or L-shaped subsidiary cells (Fig. 115). Multicellular, T-shaped trichomes with one to two stalk cells and an elongate, lignified terminal cell are abundant over the abaxial leaf surface (Figs. 113 & 115). The stalk cells are thin-walled and contain cytoplasm and a large nucleus. The terminal cell is thick-walled, lignified and devoid of protoplasm. The terminal cell and the uppermost stalk cell are separated by walls that possess elongate pits (Fig. 116).

Although the marginal teeth of A. cryptophlebum and A. nullumense have the tumid appearance of hydathodes, water pores are not visible in the adaxial epidermis of these serrations. A prominent vein flares as it terminates in each tooth (Fig. 117). In cleared leaves certain marginal teeth possess cells that stain more darkly than the other surrounding cells of the tooth. This darker staining may indicate that these cells are glandular.

The wood of the three species of Argophyllum studied is very similar with respect to cell types, vessel element morphology, most cell dimensions and composition of ray tissue. Nevertheless, some minor differences do occur among these species with regard to pore diameter, length of imperforate elements and size of the xylem rays. These

differences generally parallel the distribution of the three species. Based upon wood anatomy the two Australian species, A. cryptophlebum and A. nullumense, are similar, while the New Caledonian species, A. ellipticum, is different from them. Axial parenchyma is absent from all three species.

Weakly discernible growth rings are present in wood of A. nullumense, while distinct growth rings are present in A. cryptophlebum. Growth rings are absent in A. ellipticum. The former two species are diffuse porous, and all three species have fine-textured wood with very numerous, angular pores per square mm (range 55-205/mm², $\bar{x} = 129$). Although pores are predominantly solitary for all species (64%), true radial multiples of two to seven cells (22%) and clusters of two to nine cells (14%) are not uncommon (Fig. 118). Approximately one third of the pore clusters observed are due to overlapping end walls of vessel elements. Pore diameters are very small for all three species (range 27-61 um, $\bar{x} = 41$), however, the Australian species, A. cryptophlebum and A. nullumense, have narrower pores (range 27-48 um, $\bar{x} = 37$) than the New Caledonian species, A. ellipticum (range 36-61 um, $\bar{x} = 49$). Vessel walls are thinner in A. cryptophlebum and A. ellipticum (range 1-3.2 um, $\bar{x} = 2.4$) than in A. nullumense (range 3.2-5.3 um, $\bar{x} = 3.5$). Vessel elements are shortest in A. nullumense (range 517-1050 um, $\bar{x} = 755$), slightly longer in A. ellipticum (range 550-1217 um, $\bar{x} = 894$), and longest in A. cryptophlebum (range 500-1400 um, $\bar{x} = 1020$). Fine spiral thickenings may be present in vessel elements of all three species. Perforation plates are

exclusively scalariform on oblique end walls with 6-25 thin bars per plate ($\bar{x} = 15$) (Fig. 119). Rarely perforation plates are compound with two scalariform perforation plates per oblique end wall. The thin bars may be forked or branched. Perforations typically lack a border, however, complete borders occasionally are present around perforations in A. cryptophlebum. End-wall angles range from 0-21° ($\bar{x} = 10$). Oval to elongate intervacular pits are usually alternate, but transitional and opposite arrangements may occur (Fig. 119). These pits have minute diameters (range 2.1-3.2 μm , $\bar{x} = 2.8$).

Imperforate tracheary elements are septate fibers with non-bordered, slit-like pits in both A. cryptophlebum and A. nullumense. Argophyllum ellipticum possesses septate fiber-tracheids with pits characterized by a small, circular border and inner apertures that extend well beyond the margin of the pit border (Fig. 119). Most imperforate elements have medium length, although the septate fibers of A. cryptophlebum and A. nullumense are shorter (range 850-1817 μm , $\bar{x} = 1170$) than the septate fiber-tracheids of A. ellipticum (range 900-1667 μm , $\bar{x} = 1317$). All imperforate elements have thick walls (range 2.6-10.5 μm , $\bar{x} = 5.2 \mu\text{m}$).

The ray system of Argophyllum is predominantly composed of homocellular, uniseriate rays of upright cells and heterocellular, bi- to multiseriate rays (Fig. 120). Homocellular, biseriate and heterocellular, uniseriate rays rarely occur. Uniseriate rays range in height from 1-24 cells

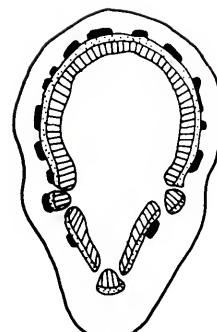
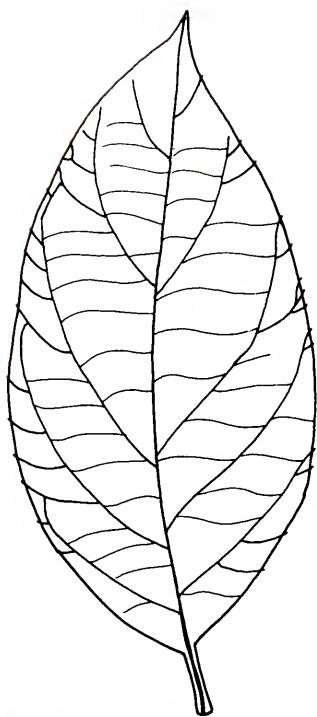
(.08-2.52 mm), while bi- and multiseriate rays range in height from 6-51 cells (.43-3.20 mm) and in width from 2-6 cells (23-78 um). The heterocellular rays of A. ellipticum are generally wider (3-6 cells) than those of A. cryptophlebum and A. nullumense (2-4 cells). Perforated ray cells with scalariform perforation plates are infrequent in the heterocellular rays of A. nullumense and A. ellipticum (Fig. 121), but are lacking in A. cryptophlebum. Sheath cells are absent from all three species. No ergastic substances are present in the ray tissue. Although vessel to ray parenchyma pitting may be transitional, it is mostly opposite or alternate. All types of rays may be joined end-to-end, and multiseriate rays are commonly split by vessels or imperforate tracheary elements.

Figure 110. Leaf of Argophyllum cryptophlebum showing marginal serrations and semicraspedodromous venation. X1.

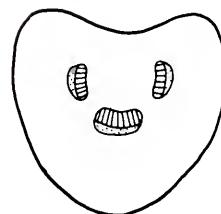
Figure 111. Vein ending of A. nullumense. X175.

Figure 112. Transverse sections of a node (a) and proximal (b), median (c) and distal (d) sections of a petiole of A. nullumense. X10.

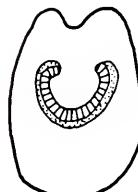
Details: t, tracheids.



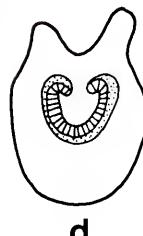
a



b

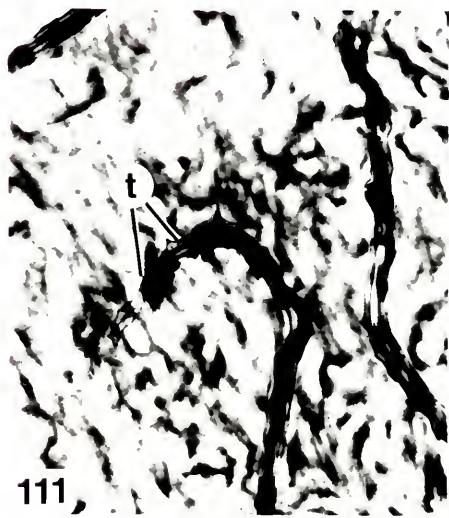


c



d

110



111,

112

Figure 113. Transverse section of a leaf of Argophyllum nullumense. X437. Note poorly differentiated biserrate palisade layer and T-shaped trichome.

Figure 114. Transverse section of the midvein of a leaf of A. nullumense. X46. Note secondary vein.

Figure 115. Transverse section of the abaxial epidermis of a leaf of A. nullumense. X700.

Figure 116. Surface view of the pitting between the terminal cell and uppermost stalk cell of a T-shaped trichome of A. cryptophlebum. X1750.

Figure 117. Marginal serration of a leaf of A. cryptophlebum. X110.

Details: ab, abaxial epidermis; ad, adaxial epidermis; be, abaxial bundle sheath extension; be', adaxial bundle sheath extension; c, cuticle; gc, guard cell; pi, pits; pl, palisade layer; sl, spongy mesophyll layer; tr, trichome; sv, secondary vein; vb, vascular bundle.

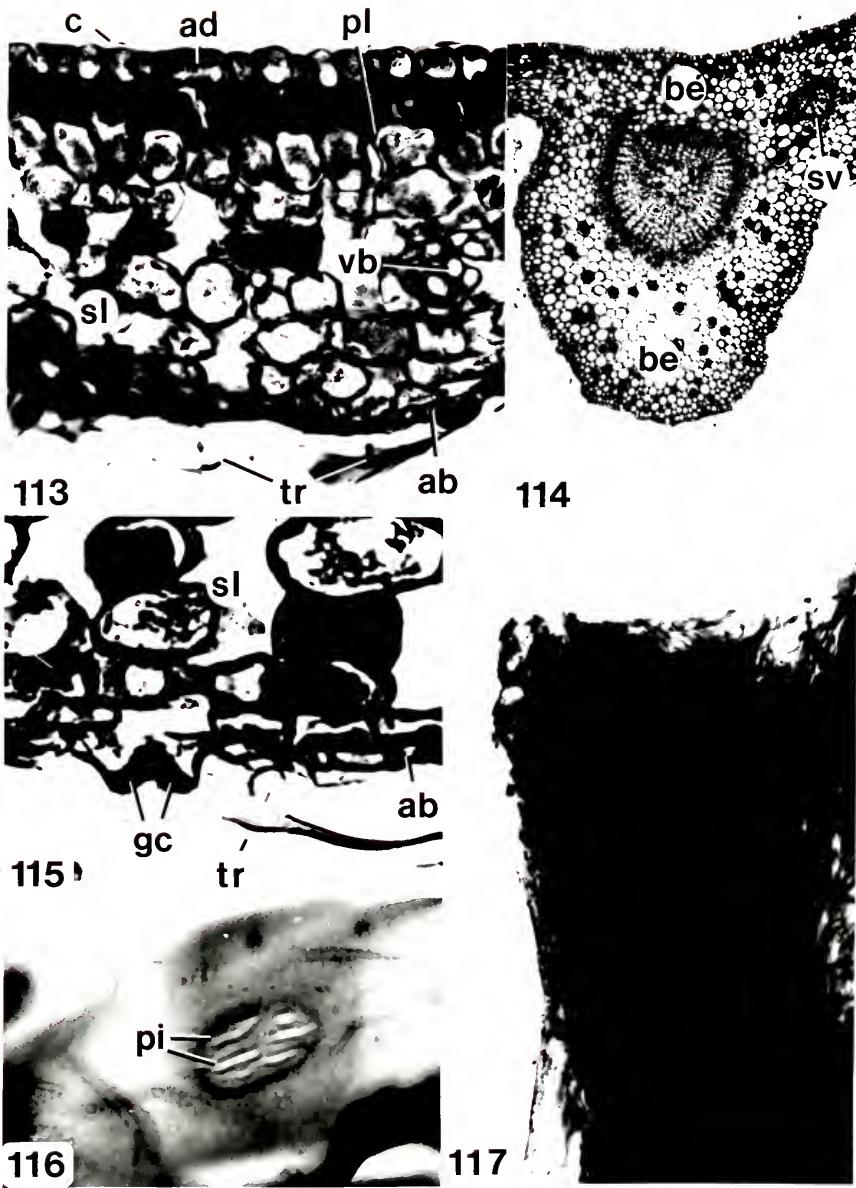


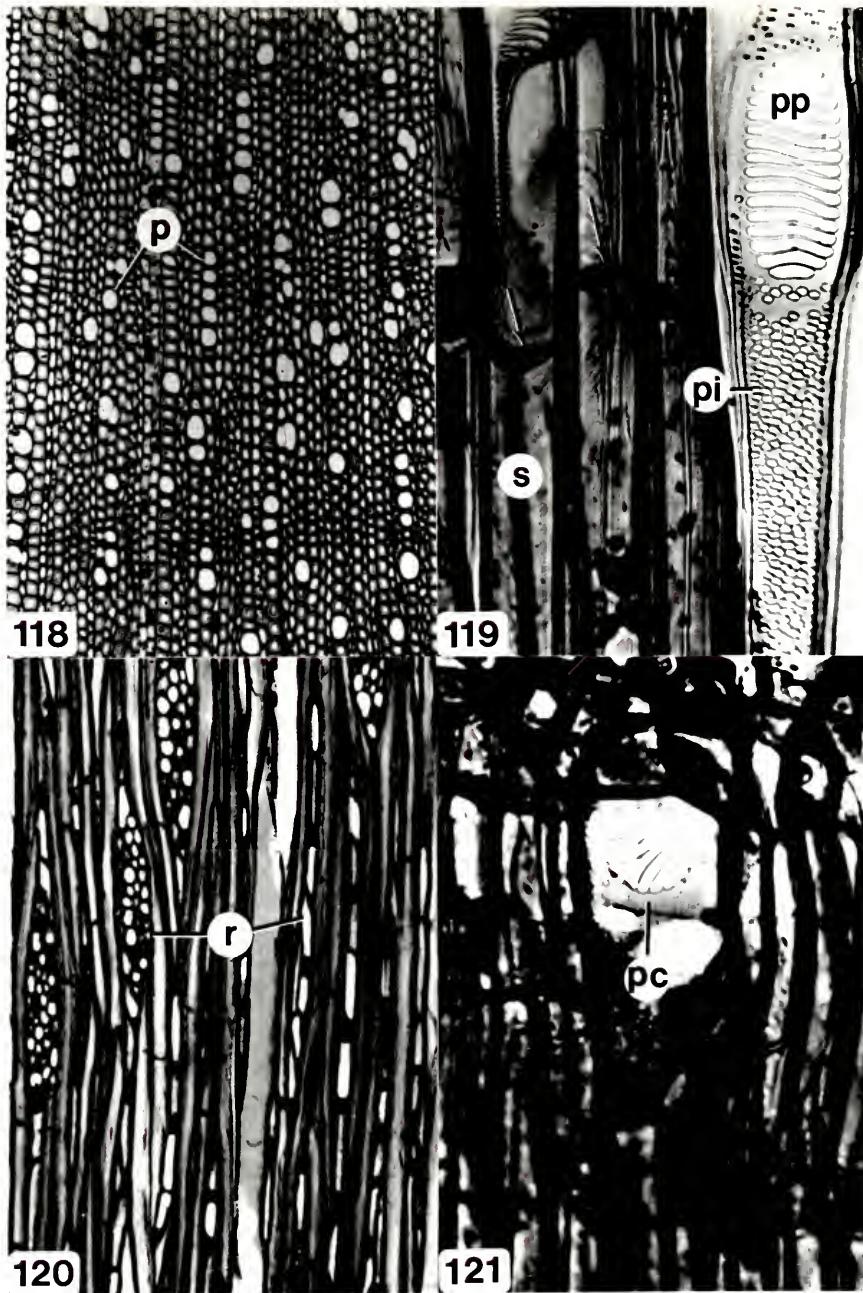
Figure 118. Transverse section of the secondary xylem of Argophyllum nullumense showing both solitary and radial multiples of pores. X110.

Figure 119. Radial section of the secondary xylem of A. ellipticum. X437. Note septa (arrows) of septate fibers.

Figure 120. Tangential section of the secondary xylem of A. ellipticum. X110. Note uni- and multiseriate rays.

Figure 121. Radial section of the secondary xylem of A. ellipticum. X315. Note perforated ray cell with scalariform perforation plate.

Details: p, pore; pc, perforated ray cell; pi, pits; pp, perforation plate; r, ray; s, septate fiber.



Donatia J. R. & G. Forst.Introduction

The genus Donatia was described in 1776 by J. R. and G. Forster based upon specimens of D. fascicularis collected in Tierra del Fuego. The generic name commemorates the Italian naturalist Vitalianus Donati (Forster and Forster, 1776). The only other species in this genus, D. novae-zelandiae, occurs in alpine areas of New Zealand and Tasmania (Allan, 1961; Bentham, 1864; Cheeseman, 1925; Curtis, 1963). The cushion or mat plants of Donatia are erect, perennial herbs which are densely covered with sessile, exstipulate, simple leaves (Allan, 1961; Bentham, 1864; Cheeseman, 1925; Curtis, 1963). The terminal or axillary, solitary flowers have five to seven sepals, five to ten petals, and two to three stamens which are inserted on a disc. The two- to three-celled, inferior ovary ripens into a capsule.

Hooker (1865) placed Donatia in the Saxifragaceae within the tribe Saxifrageae. Although Engler (1890) initially placed this genus in the rosalian Saxifragaceae within its own subfamily Donatioideae, he later was uncertain about its placement (Engler, 1928). Other workers have placed Donatia within the Stylidiaceae, in its own subfamily, the Donatioideae (Dahlgren, 1975, 1980, 1983; Mildbraed, 1908; Muel-ler, 1879; Thorne, 1976; Wagenitz, 1964). Some systematists have elevated this subfamily to form the monogeneric family Donatiaceae (Airy Shaw in Willis, 1973; Cronquist,

1981; Skottsberg, 1915; Takhtajan, 1980, 1983). Most of these workers have placed Donatia in the order Campanulales. Thorne (1976, 1983), however, included it in the Rosales and Dahlgren (1975, 1980, 1983) placed it in his Cornales.

The following observations are based upon a specimen of D. novae-zelandiae (Table 2).

Observations

Donatia novae-zelandiae possesses very small, entire, lanceolate leaves. These sessile, exstipulate leaves are spirally arranged and completely enclose the stem. Venation is perfectly developed, suprabasal acrodromous with a prominent midvein and two conspicuous secondary veins that diverge distally to the base of the lamina and extend to the leaf apex (Figs. 122 & 123). In the larger leaves two very small tertiary veins may diverge from one or both of the secondary veins. Vein areole development is lacking. Terminal vein endings taper and are composed of one or two helically thickened, elongate tracheids.

The nodal pattern is unilacunar, one-trace, and a single vascular bundle enters the base of a sessile lamina (Fig. 124).

The leaves are isobilateral with an undifferentiated mesophyll throughout most of a lamina (Fig. 125). A poorly differentiated, biserrate palisade layer composed of loosely arranged, elongate cells occurs only near the apex of a leaf (Fig. 126). Both the spongy mesophyll cells and undifferentiated mesophyll cells have various shapes and sizes and

are separated by numerous, large intercellular spaces.

Crystals are absent in Donatia leaves.

In transection a very small midvein occurs in the basal third of a leaf. In the distal two thirds of a leaf the midvein and two, three or more bundles (secondary and tertiary veins) occur, depending upon whether or not tertiary veins have diverged from the secondary veins (Fig. 125). Each bundle possesses three to seven tracheids, while phloem is not distinguishable in any bundle. All bundles are surrounded by a bundle sheath composed of parenchyma cells which are smaller and more compactly arranged than the surrounding mesophyll cells. No bundle sheath extensions occur. In the distal two thirds of most leaves a large, round or oval mass of lignified parenchyma tissue occurs abaxial to the midvein and smaller vascular bundles (secondary veins) (Fig. 125). This lignified parenchyma tissue is composed of thick-walled, elongate cells filled with a tan, densely staining, amorphous substance that is arranged concentrically in the cell lumen (Fig. 127).

Both epidermal layers are uniserial and composed of periclinally flattened cells of various shapes and sizes in transection (Fig. 125 & 126). In surface view the epidermal cells are rectangular or trapezoidal with the long axis of a cell oriented parallel to the long axis of a leaf (Fig. 128). The cuticle overlying both epidermal layers is very thick (>7 um).

Numerous stomata occur in both epidermal layers, and the stomatal apparatus is paracytic (Fig. 128). The two

elongate subsidiary cells often are very similar to the other epidermal cells and do not completely envelop the guard cells. In surface view guard cells are reniform and guard-cell pairs are elliptic in outline with an average length of 44 μm and a width of 30 μm (length/width ratio 1.47). In transection guard cells are oval to irregular in shape, and each cell bears a small, thin cuticular horn internally and a large, thick cuticular horn externally that represent the inner and outer ledges, respectively, overarchng a stoma (Fig. 129). Although foliar trichomes are absent, multicellular, uniseriate trichomes are abundant on the stem, especially in the axils of the leaves. The cells of these trichomes are separated by oblique septa that bear numerous small perforations or pit-like structures (Fig. 130). The basal cell of a trichome is filled with dense, darkly staining, granular cytoplasm, while the other cells are empty. The terminal cell of a trichome is tapered. Hydathodes are absent in D. novae-zelandiae. Dark brown fungal hyphae typically occur intermingled with the uniseriate trichomes and on the surface of the leaves.

Since D. novae-zelandiae is a herbaceous, perennial plant that produces a very small amount of secondary xylem, no measurements were made of this tissue. The wood of D. novae-zelandiae possesses angular pores with very small diameters (Fig. 131). These pores may be solitary, but more commonly are clustered. Vessel elements are connected by scalariform perforation plates and scalariform to

transitional intervacular pitting (Fig. 132). A few thick-walled fibers with simple pits also occur in the secondary xylem. Axial parenchyma is abundant, but arranged in no definite pattern. Spiral thickenings are absent from the vessel elements and fibers. No xylem ray system is visible.

Figure 122. Leaves of Donatia novae-zelandiae showing entire margins and perfectly developed, suprabasal acrodromous venation. X10. Note diagrammatic representation showing presence or absence of lignified parenchyma (lp) in association with the veins.

Figure 123. Portion of a lamina of D. novae-zelandiae. X46.

Figure 124. Unilacunar, one-trace nodal pattern of D. novae-zelandiae. X46.

Figure 125. Transverse section of a leaf of D. novae-zelandiae. X175. Note undifferentiated mesophyll and lignified parenchyma cells abaxial to vascular bundles.

Figure 126. Portion of lamina of D. novae-zelandiae proximal to the leaf apex. X175. Note poorly differentiated biseriate palisade layer.

Details: ab, abaxial epidermis; ad, adaxial epidermis; c, cuticle; lp, lignified parenchyma; lt, leaf trace; m, mesophyll; pl, palisade layer; sl, spongy mesophyll layer; v, vein with lignified parenchyma cells; vb, vascular bundle.

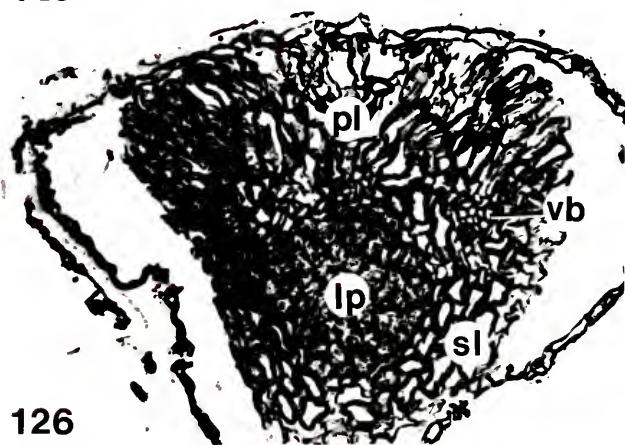
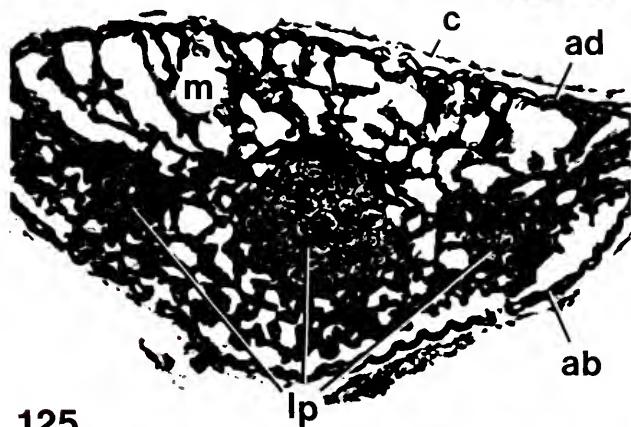
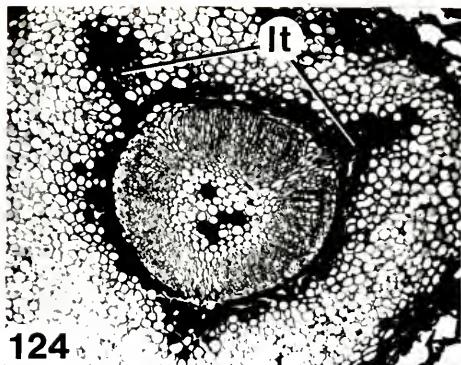


Figure 127. Transection of lignified parenchyma cells abaxial to vascular bundles in leaves of Donatia novae-zelandiae. X1750.

Figure 128. Paradermal section of a leaf of D. novae-zelandiae. X437. Note paracytic stomatal apparatus.

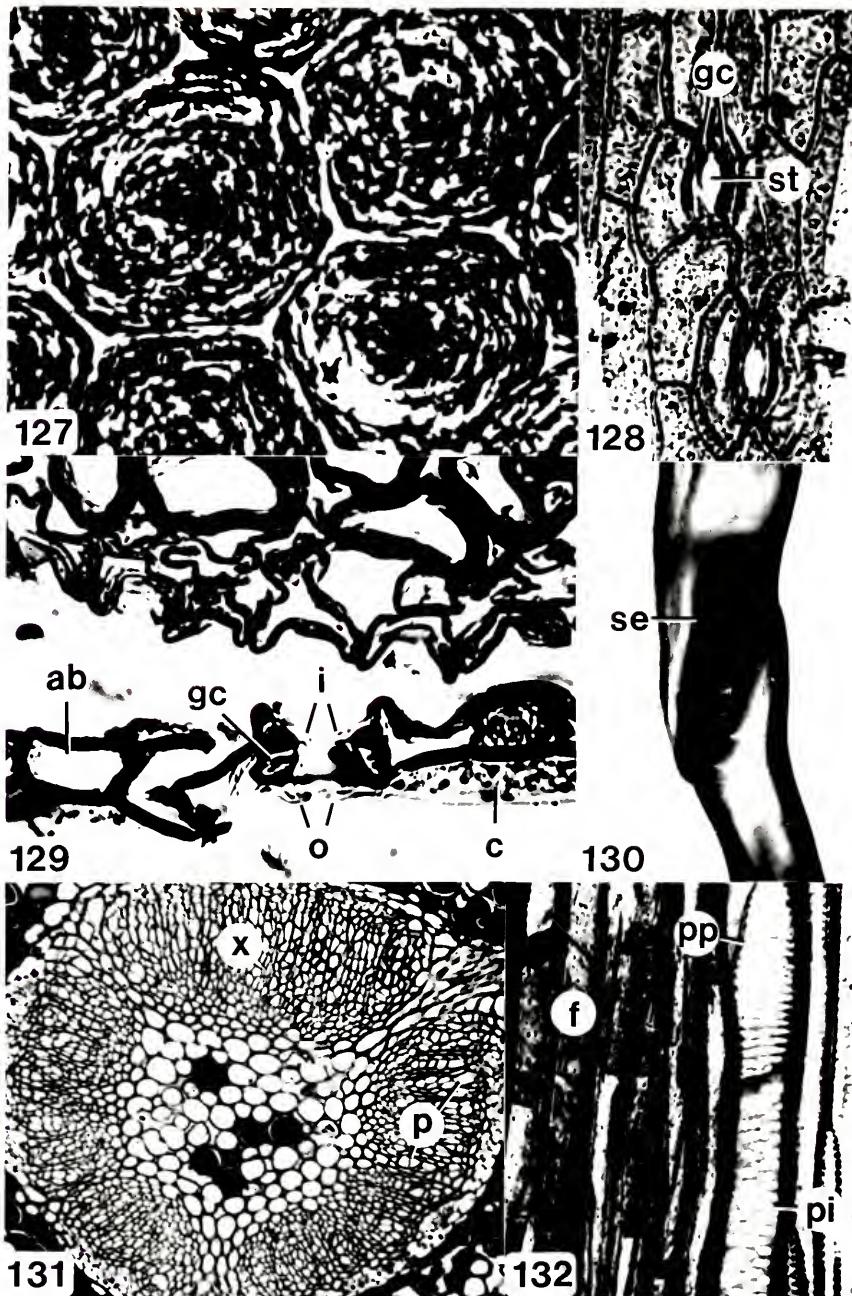
Figure 129. Transverse section of the abaxial epidermis of a leaf of D. novae-zelandiae. X700.

Figure 130. Oblique septum of a multicellular, uniseriate trichome of D. novae-zelandiae. X700.

Figure 131. Transverse section of a stem of D. novae-zelandiae. X110. Note small amount of secondary xylem.

Figure 132. Radial section of the secondary xylem of D. novae-zelandiae. X437.

Details: ab, abaxial epidermis; c, cuticle; f, fibers; gc, guard cells; i, inner ledges; o, outer ledges; p, pore; pi, pits; pp, perforation plate; se, septum; st, stoma; x, secondary xylem.



Anodopetalum A. Cunn.Introduction

The monotypic genus Anodopetalum was described by Allan Cunningham in 1839 (Bentham, 1864; Burbidge, 1963). Anodopetalum biglandulosum is endemic to wet lowland and subalpine areas of the southeast, southwest and west floristic zones of Tasmania (Beadle, 1981; Bentham, 1864; Mosley, 1974b). Plants of Anodopetalum are tall shrubs or trees with narrow-oblong, simple, opposite leaves and deciduous, interpetiolar stipules (Bentham, 1864). Flowers usually occur singly in the axils of the upper leaves, and each flower possesses a four- or five-merous perianth, twice as many stamens as petals and a superior ovary that ripens into a one-seeded berry (Bentham, 1864). Anodopetalum biglandulosum often forms monospecific stands owing to its peculiar growth habit whereby stems bend over to a horizontal position after growing a few meters (Beadle, 1981). Branches develop and grow upward from the nodes of these bent stems which remain more or less horizontal and continue to grow in diameter. Because of this unusual growth habit, A. biglandulosum forms impenetrable woodland thickets called "horizontal," in reference to the same common name of the species (Beadle, 1981).

Virtually all taxonomists include Anodopetalum in the Cunoniaceae within the Rosales or some other equivalent order (Airy Shaw in Willis, 1973; Cronquist, 1968, 1981;

Dahlgren, 1975, 1980, 1983; Engler, 1890, 1928; Hutchinson, 1967; Schulze-Menz, 1964; Takhtajan, 1966, 1980, 1983; Thorne, 1976, 1983).

Observations

Anodopetalum possesses opposite, narrow-elliptic leaves that bear rounded, widely spaced crenations. Venation is semicraspedodromous with a prominent midrib and conspicuous secondary veins that extend near the leaf margin and arch distally to join with the superadjacent secondary veins (Fig. 133). Vein areole development is imperfect. Veinlets may be straight, but are more commonly branched one to four times (Fig. 134). Vein endings are composed of helically thickened tracheids and parenchymatous bundle sheath cells with thick, primary cell walls (Fig. 134). These tracheids, which may be elongate, curved, forked, or clavate, often possess protuberances at the junction between two parenchymatous bundle sheath cells.

The nodal pattern is trilacunar, three-trace (Fig. 135). Each of the lateral traces divides to form several additional lateral traces. The median leaf trace and two lateral traces enter a petiole, while the other resultant lateral traces enter an interpetiolar stipule. Thus one median and two lateral bundles enter the base of a petiole (Fig. 135). Distally to the base of a petiole two very small bundles become visible in the ground tissue near the primary xylem of the two lateral bundles. The origin of these two small bundles is unclear. In one specimen, one of

these small bundles arose from one of the lateral petiolar bundles while the other arose from the median bundle. Distally in a petiole the three bundles which entered the petiole from the stem, fuse laterally to form a large, arc-shaped collateral bundle (xylem adaxial) in the center of the petiole (Fig. 135). The two small bundles also enlarge and fuse to form a small, inverted (xylem abaxial), dorsally flattened, collateral bundle adaxial to the large central bundle (Fig. 135). These two opposing bundles enter the lamina distally (Fig. 135).

Leaves of Anodopetalum are dorsiventral with a relatively narrow, biseriate palisade layer and a much wider, lacunose spongy mesophyll layer (Fig. 136). The palisade layer possesses larger, oval to rectangular cells in its uppermost layer and smaller, elongate or columnar cells in its lower layer (Fig. 136). These two types of cells may be interspersed with one another throughout the palisade mesophyll. The spongy mesophyll has cells of various shapes and sizes separated by numerous, large intercellular spaces (Fig. 136). Occasionally druses and rarely prismatic crystals occur in the spongy mesophyll cells.

The midvein of Anodopetalum leaves is composed of two opposing collateral bundles (Fig. 137). Both bundles are surrounded by a bundle sheath of lignified parenchyma cells and have sclerenchyma fibers adjacent to the primary phloem. Bundle sheath extensions composed of lignified parenchyma cells and collenchyma cells also occur both abaxially and

adaxially. The smaller, collateral bundles (secondary and minor veins) possess a bundle sheath of thick-walled, unlignified parenchyma cells without bundle sheath extensions (Fig. 136).

Both epidermal layers are uniserial and typically consist of square to rectangular cells in transection (Fig. 136). In surface view the epidermal cells are square to polyhedral with mostly straight, rarely curved, anticlinal walls. The cuticle is thick and undulate (>5 um). Anodopetalum leaves typically lack trichomes, however, a few elongate, thick-walled, bulbous-based trichomes with tapered ends may occur adaxially at the base of a petiole.

Numerous stomata are restricted to the abaxial epidermis, and the stomatal apparatus is anomocytic. In surface view the guard cells are oval to reniform. Guard-cell pairs are virtually circular in outline with an average length of 30 um and a width of 29 um (length/width ratio 1.03). In transection the guard cells are oval, and each cell has a cuticle over its outer wall. Some guard cells bear a very small cuticular protuberance that represents the outer ledge overarching the stoma.

The blunt, marginal crenations and the leaf apex contain glandular tissue characterized by thick-walled, unlignified parenchyma cells with very dense, darkly staining cytoplasm (Fig. 138). Each crenation is supplied by an arc of vascular tissue that is derived from the union of two secondary or tertiary veins.

The wood of Anodopetalum exhibits distinct growth rings and is diffuse porous. The wood is fine-textured with very numerous pores (range 190-370/mm², $\bar{x} = 277$) that are mostly angular, but may be circular, in outline. The pores have very small tangential diameters (range 18-44 um, $\bar{x} = 33$) and thin radial walls (range 1.6-4.2 um, $\bar{x} = 2.8$). The pores are usually solitary (54%) or in true clusters of two to seven cells (44%), although true radial multiples of two to four cells (2%) do occur (Fig. 139). Vessel elements have medium length (range 410-891 um, $\bar{x} = 638$) and possess oblique end walls with angles ranging from 17-38° ($\bar{x} = 26$). These cells lack spiral thickenings. Perforation plates are mostly simple, although a few are scalariform with 3-11 thin bars ($\bar{x} = 8$) per plate (Fig. 140). The simple perforations have complete borders, while the perforations in the scalariform perforation plates lack borders. Intervascular pitting is mostly scalariform, although transitional and opposite arrangements also occur (Fig. 140). These elongate to oval pits have small diameters (range 4.7-7.4 um, $\bar{x} = 5.5$).

Tracheids with circular-bordered pits and oval inner apertures that extend slightly beyond the pit border also occur (Fig. 141). The diameter of these pits is similar to that of the intervacular pits. Tracheids have moderately short to medium length (range 670-1170 um, $\bar{x} = 971$), relatively thin walls (range 2.6-5.3 um, $\bar{x} = 3.8$) and fine spiral thickenings. Some vessel elements and tracheids also contain brown, amorphous contents.

Axial parenchyma is common and is either apotracheal diffuse-in-aggregates with short tangential, uniseriate bands of four to five cells, or marginal at the end of a growth ring (Fig. 139). Very rarely paratracheal scanty parenchyma occurs. Axial parenchyma cells contain abundant dark brown deposits and starch grains (Fig. 139). Vessel to axial parenchyma pitting is scalariform.

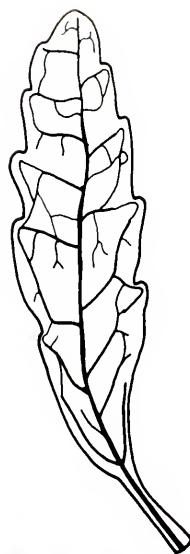
Although the xylem ray system predominantly is composed of homocellular, uni- and biseriate rays of upright cells, heterocellular, uni- and biseriate rays may also occur (Fig. 141). All rays are relatively short, with heights ranging from 1-24 cells (.08-.52 mm) for uniseriate rays and 8-24 cells (.17-.58 mm) for biseriate rays. Biseriate ray width ranges from 18-23 um. Dark brown deposits which are similar to those in the axial xylem parenchyma cells also are abundant in ray parenchyma cells. Perforated ray cells and sheath cells are absent. Vessel to axial parenchyma pitting is mostly scalariform, however, transitional patterns also occur. No fusion of rays is noted.

Figure 133. Leaf of Anodopetalum biglandulosum showing marginal crenations and semicraspedodromous venation. X2.

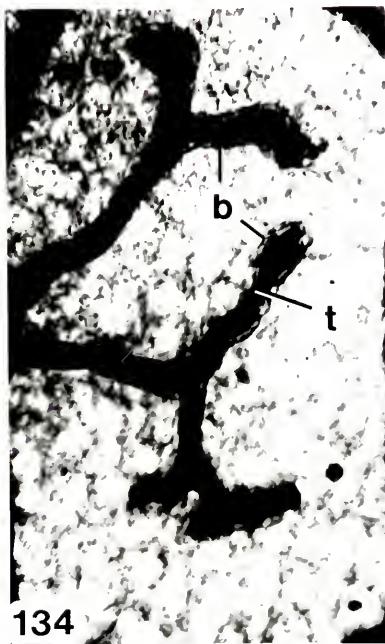
Figure 134. Vein ending of A. biglandulosum. X175.

Figure 135. Transverse sections of a node (a) and proximal (b), median (c) and distal (d) sections of a petiole of A. biglandulosum. X50.

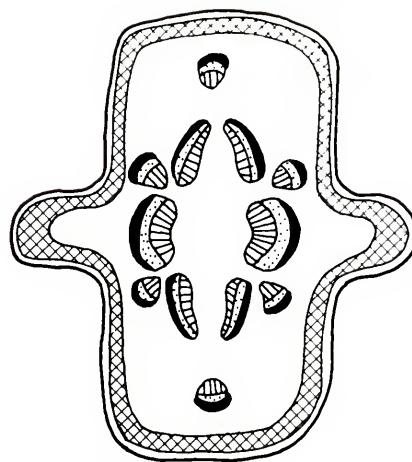
Details: b, bundle sheath; t, tracheid.



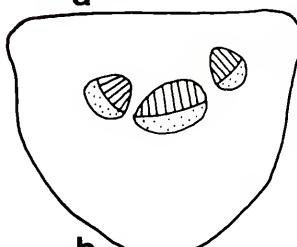
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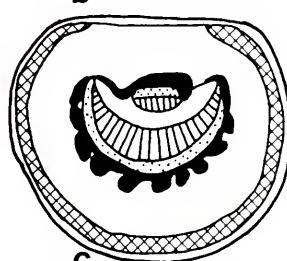
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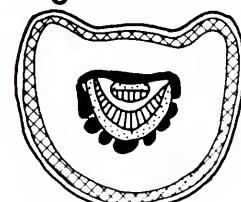
a



b



c



d

135

Figure 136. Transverse section of a leaf of Anodopetalum biglandulosum. X175.

Figure 137. Transverse section of a midvein of a leaf of A. biglandulosum. X175.

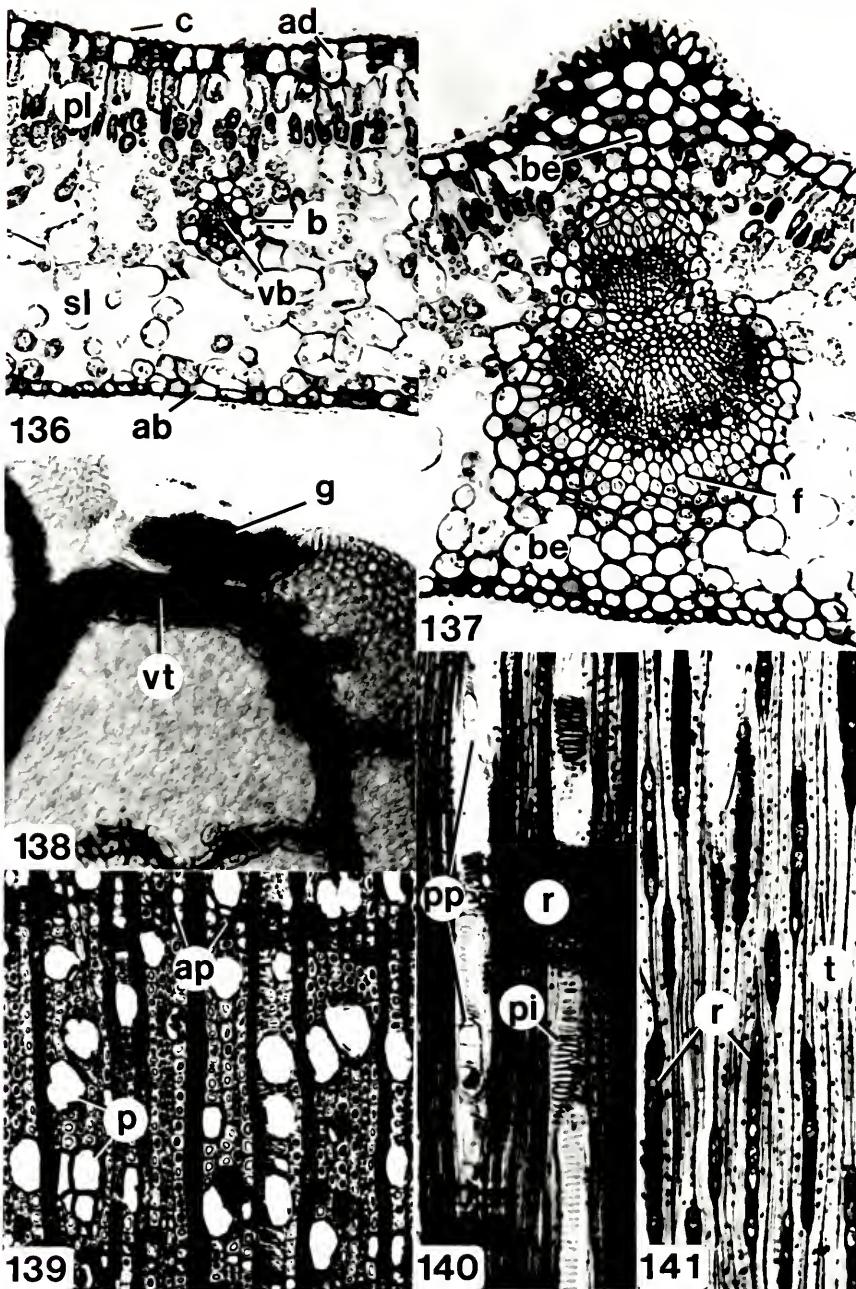
Figure 138. Marginal crenation of a leaf of A. biglandulosum. X110. Note the arc of vascular tissue which vascularizes the crenation.

Figure 139. Transverse section of the secondary xylem of A. biglandulosum. X175. Note clustered and solitary pores.

Figure 140. Radial section of the secondary xylem of A. biglandulosum. X175.

Figure 141. Tangential section of the secondary xylem of A. biglandulosum. X175.

Details: ab, abaxial epidermis; ad, adaxial epidermis; ap, axial parenchyma; b, bundle sheath; be, abaxial bundle sheath extension; be', adaxial bundle sheath extension; c, cuticle; f, fibers; g, gland; p, pore; pi, pits; pl, palisade layer; pp, perforation plate; r, ray; sl, spongy mesophyll layer; t, tracheid; vb, vascular bundle; vt, vascular tissue.



Aphanopetalum Endl.Introduction

The genus Aphanopetalum was described in 1839 by S. L. Endlicher based upon specimens of A. resinosum (Bailey, 1900; Bentham, 1864; Burbidge, 1963). The generic name refers to the obscure petals of the flowers (Bailey, 1900). Aphanopetalum contains two species that are endemic to Australia. Aphanopetalum resinosum is found in rainforests of eastern Australia from southeastern Queensland to southern New South Wales (Beadle, 1981; Burbidge, 1963). The other species, A. occidentale, is restricted to Western Australia (Bentham, 1864; Burbidge, 1963). Plants of A. resinosum are scrambling or viny shrubs with opposite, serrate to entire leaves that either possess minute stipules or are exstipulate (Bailey, 1900; Bentham, 1864). The flowers have four sepals and eight stamens, while the petals are minute or absent. Each flower has a four-celled, superior ovary that ripens into a hard, indehiscent, nut-like fruit (Bailey, 1900; Bentham, 1864; Engler, 1928).

Systematists typically have placed Aphanopetalum in the Cunoniaceae within the orders Rosales (Engler, 1928; Thorne, 1983), Saxifragales (Takhtajan, 1980, 1983), Grossulariales (Cronquist, 1981) or Cunoniales (Dahlgren, 1975, 1980, 1983; Hutchinson, 1967). However, recent studies by Dickison (1975c, 1980b) have cast doubt on the cunoniaceous affinity of this genus.

Only leafy stems of A. resinosum were available for this study (Table 2).

Observations

Aphanopetalum resinosum possesses elliptic, serrate, opposite leaves (Fig. 142). The marginal serrations are very small and rounded or acute. Leaves also have two minute, avascular, acicular stipules on each side of the petiole base (Fig. 143). The stipules are composed of cells filled with densely staining cytoplasm and appear glandular (Fig. 144). The stipules are morphologically and anatomically similar to the marginal serrations of the leaves. Venation is semicraspedodromous with a prominent midrib and conspicuous secondary veins whose branches arch distally to join with superadjacent secondaries and terminate in the marginal teeth (Fig. 142). Veinlets may be straight, curved or branched (Fig. 145). Terminal vein endings taper and are composed of three to four helically thickened, elongate tracheids.

The nodal pattern is unilacunar, one-trace. Two small traces, however, separate from this leaf trace shortly after it diverges from the stem vasculature (Fig. 146). Thus a large, central, flattened bundle and two small, lateral, round bundles enter the base of a petiole (Fig. 146). These three collateral bundles extend the length of a petiole and enter the lamina distally.

Leaves of A. resinosum are dorsiventral with a well-differentiated, biserrate palisade layer and a lacunose

spongy mesophyll layer (Fig. 147). The cells of the palisade layer are columnar and tightly appressed. The cells of the spongy mesophyll layer are variously shaped and separated by numerous small intercellular spaces. Frequently the cells of both layers contain darkly staining cytoplasm due to tan or brown deposits. No crystals occur in the palisade or spongy mesophyll cells.

The midvein of a leaf is a flattened collateral bundle surrounded by a bundle sheath composed of thick-walled fibers, thick-walled, lignified parenchyma cells and thin-walled parenchyma cells (Fig. 148). Bundle sheath extensions of thick-walled, unlignified parenchyma cells and collenchyma cells occur both adaxially and abaxially. Druses are present in a few of these parenchyma cells located abaxial to the midvein. The smaller bundles of a leaf (secondary and minor veins) are round collateral bundles surrounded by a bundle sheath composed of thin-walled parenchyma cells (Fig. 147). These smaller bundles lack bundle sheath extensions.

Both epidermal layers are uniseriate. In transection the adaxial epidermal cells are typically oval or round, while the abaxial epidermal cells are more flattened and elongate or elliptic. In surface view the epidermal cells are variously shaped with sinuous to curved anticlinal walls. The cuticle is thick (>5 um) and trichomes are absent. Stomata are restricted to the abaxial epidermis, and the stomatal apparatus is anomocytic. In surface view guard cells are reniform, and guard-cell pairs are circular

to elliptic in outline. Guard-cell pairs have an average length of 25 μm and a width of 19 μm (length/width ratio 1.32). In transection the guard cells are oval to rectangular and thick-walled, and each cell bears a short, thin cuticular horn that represents the outer ledge overarching a stoma.

The marginal leaf teeth of A. resinorum are composed of cells filled with densely staining cytoplasm. In cleared leaves the apical cells of a tooth stain lighter than surrounding cells which may indicate thinner cell walls. A large vein flares as it terminates in each tooth (Fig. 149).

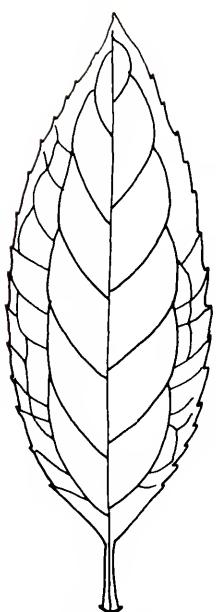
Figure 142. Leaf of Aphanopetalum resinosum showing small marginal serrations and semicraspedodromous venation. X1.

Figure 143. Transverse section of stem and petiole of A. resinosum. X46. Note the two stipules on either side of the petiole base. X46.

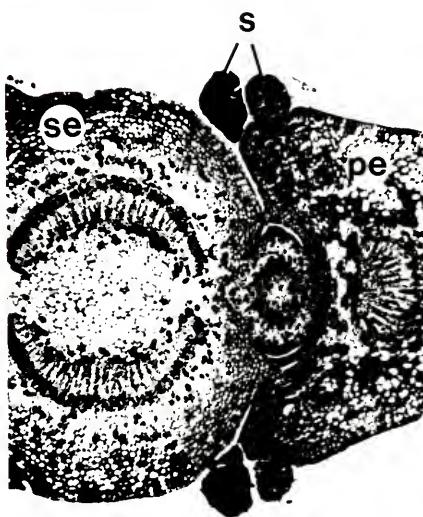
Figure 144. Transverse section of the avascular stipules of A. resinosum. X175.

Figure 145. Vein ending of A. resinosum. X175.

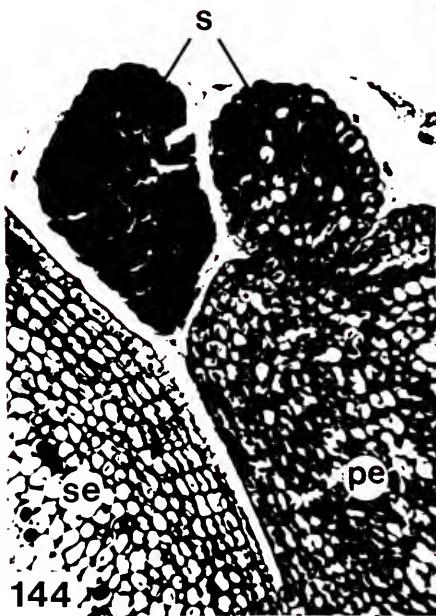
Details: pe, petiole; s, stipules; se, stem; t, tracheid.



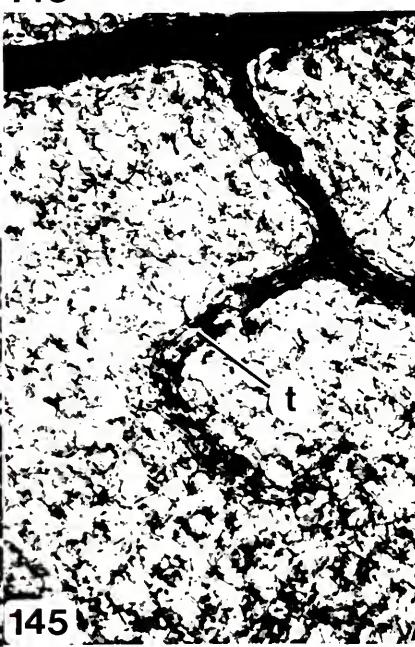
142



143



144



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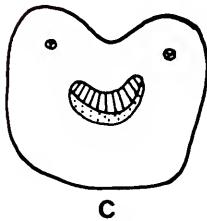
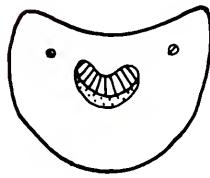
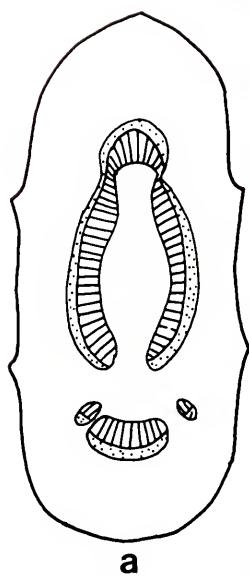
Figure 146. Transverse sections of a node (a) and proximal (b) and distal (c) sections of a petiole of Aphanopetalum resinosum. X30.

Figure 147. Transverse section of a leaf of A. resinosum. X175.

Figure 148. Transverse section of a midvein of a leaf of A. resinosum. X110.

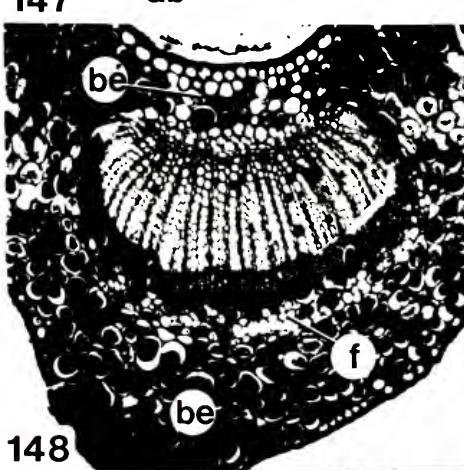
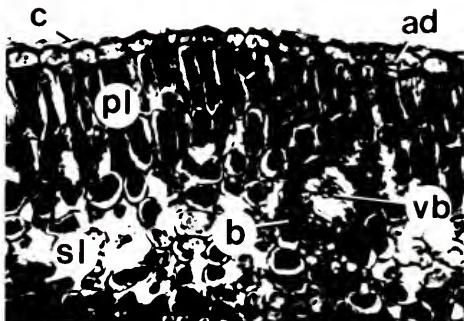
Figure 149. Marginal serration of a leaf of A. resinosum. X175.

Details: ab, abaxial epidermis; ad, adaxial epidermis; b, bundle sheath; be, abaxial bundle sheath extension; be', adaxial bundle sheath extension; c, cuticle; f, fibers; pl, palisade layer; sl, spongy mesophyll layer; vb, vascular bundle.



146

149



DISCUSSION

Anatomy of Twelve Australasian Genera

Despite the morphological and anatomical heterogeneity of the Saxifragaceae, sensu lato, recent work on the vegetative anatomy of the woody members of the group (Ramamontjariisoa, 1980; Stern, 1974a, 1978b; Styer and Stern, 1979a, 1979b) has revealed certain anatomical similarities in the wood and leaves of the genera studied. Specifically there appear to be at least eleven anatomical features in a hypothetical archetypical woody saxifrage (Stern, pers. comm.). A list of these eleven anatomical features and their presence or absence for the genera in this study is provided (Table 3). The presence of all or most of these anatomical features poses a strong probability of saxifrageous affinity for a given genus. Aphanopetalum is not included in Table 3 because wood was unavailable for study.

Although certain anatomical characteristics are peculiar to each of the twelve Australasian genera in this study, other features are fairly constant throughout these plants. While most genera have alternate, dorsiventral, exstipulate leaves, Bauera, Anodopetalum and Aphanopetalum have opposite, stipulate leaves. Only Donatia has isobilateral leaves. Most genera possess semicraspedodromous venation, although Bauera and Corokia also possess brochidodromous venation. Tetracarpaea and Donatia, however, are

Table 3. Anatomical features of eleven Australasian woody saxifrageous genera:
+, always present; (+), usually present; -, always absent; (-), usually absent.

ANATOMICAL FEATURE	GENERA ^a										
	Tet	Bau	Ixe	Anp	Cut	Abr	Car	Cor	Arg	Don	And
Predominantly solitary pores	+	+	+	+	+	+	+	+	-	-	-
Scalariform perforation plates	+	(-)	+	+	+	+	+	+	+	(-)	
Scalariform, transitional, opposite intervacular pitting	+	+	(-)	+	+	+	(+)	(+)	+	+	
Axial xylem parenchyma sparse or absent	(+)	+	+	+	+	+	+	+	-	+	
Tracheids or tracheids and fiber-tracheids	+	+	+	+	+	+	(+)	-	-	+	
Spiral thickenings in tracheary elements	+	+	+	+	+	+	+	+	-	+	
Homocellular, uniseriate/ heterocellular, multiseriate rays	+	+	+	+	+	+	+	+	-	-	
Perforated ray cells	+	+	+	+	+	+	(+)	(+)	-	-	
Unicellular, bulbous-based foliar trichomes	-	+	-	-	+	+	-	-	-	(-)	
Hydathodes/Glands	-	+	+	+	+	+	(-)	(-)	-	+	
Trilacunar, 3-trace nodes	-	-	+	+	+	+	(+)	(+)	-	+	

^aAbr, *Abrophyllum*; And, *Anodopetalum*; Anp, *Anopterus*; Arg, *Argophyllum*; Bau, *Bauera*; Car, *Carpodetus*; Cor, *Corokia*; Cut, *Cuttisia*; Don, *Donatia*; Ixe, *Ixerba*; Tet, *Tetracarpaea*.

distinctive because the former has simple craspedodromous venation while the latter has acrodromous venation. The vein endings of most genera consist of elongate, helically thickened tracheids, although the vein endings of Tetracarpaea and Ixerba also possess fiber-tracheids and fibers, respectively. The vein endings of Bauera also exhibit short, wide tracheids.

The nodal pattern in the genera studied is either unilacunar, one-trace (Tetracarpaea, Bauera, Donatia, Aphanopetalum and one species of Corokia) or trilacunar, three-trace (Ixerba, Anopterus, Cuttsia, Abrophyllum, Carpodetus, Argophyllum, Anodopetalum and two species of Corokia). A pentalacunar, five-trace nodal pattern previously had been reported for a species of Argophyllum (Swamy, 1954).

The epidermides of the leaves are typically uniseriate among these genera, although Bauera, Cuttsia and Carpodetus possess a biseriate adaxial epidermis. All twelve genera typically possess stomata in the abaxial epidermis, and the stomatal apparatus is anomocytic. Only Donatia has stomata in both epidermides and a paracytic stomatal apparatus. Donatia also is the only genus with both inner and outer cuticular ledges overarching a stoma. The other genera possess only an outer cuticular ledge overarching a stoma.

The palisade layer is typically well differentiated and may be uni-, bi- or triseriate in the genera studied, although Argophyllum and Corokia have a relatively poorly differentiated palisade layer. The spongy mesophyll is

usually lacunose, although it is compact in Carpodetus and Argophyllum.

Bundle sheaths composed of thin- or thick-walled parenchyma cells are common in all genera except Tetracarpaea and Bauera. Crystals occur in the leaves of all genera except Corokia, Argophyllum and Donatia. Although druses are the most common type of crystal in the leaves of these genera, Bauera possesses prismatic crystals, Cuttsia and Abrophyllum possess crystal sand and Ixerba possesses distinctive crystalloids.

In those genera with growth rings, the wood is typically diffuse porous with very numerous, predominantly solitary, angular pores with small diameters. The wood of Bauera, however, may be ring porous, and the wood of Anopterus, Carpodetus, and Corokia may be semi-ring porous. Growth rings are present in the wood of genera which occur in temperate climates, but are absent in the wood of those from tropical environments.

The vessel elements of most genera have medium to long length and oblique end walls with scalariform perforation plates. Vessel elements of Bauera and Anodopetalum, however, possess predominantly simple perforation plates. Intervascular pitting is variable in most genera and may be scalariform, transitional, opposite or alternate. The pits are typically oval or elongate and have a minute to small diameter.

Imperforate elements are typically tracheids, although Corokia and Argophyllum possess septate fiber-tracheids and

septate fibers. The imperforate cells typically have medium to long length, although Tetracarpaea and Bauera possess short tracheids. Spiral thickenings are typically present in the imperforate elements and/or the vessel elements of all genera except Donatia.

The axial parenchyma is sparse in most genera, although it may be abundant (Donatia and Anodopetalum) or absent (Corokia and Argophyllum). Axial parenchyma is typically apotracheal diffuse and diffuse-in-aggregates, although paratracheal scanty patterns rarely occur in Bauera, Ixerba, Anopterus, Abrophyllum and Carpodetus.

Xylem ray tissue is typically composed of homocellular uniserial rays of upright cells and heterocellular bi- to multiseriate rays. Cuttsia also has biseriate homocellular rays, while Bauera, Ixerba and Anopterus also have uniserial heterocellular rays. Perforated ray cells occur in all genera except Anodopetalum and Donatia. Carpodetus is the only genus studied that exhibits prismatic crystals in ray parenchyma cells.

Despite the similarities noted above, these genera are readily distinguishable from one another based upon various anatomical features. These distinctive anatomical characteristics confirm certain taxonomic groupings, but also allow for some taxonomic rearrangements. In the systematic discussion that follows the classification system of Engler (1928) will be used throughout for purposes of convenience and understanding. Thus the subfamilies listed in Table 1

will be mentioned repeatedly when taxonomic groupings and realignments among the genera in this study are discussed. Similar family names also will be used, however, because many workers have elevated Engler's subfamilies to family rank (Dahlgren, 1983; Takhtajan, 1983). Thus subfamily and family names sometimes will have to be used interchangeably when results and conclusions from these other studies are integrated with the present anatomical data. Unless noted otherwise, Engler's subfamilies (-oideae endings) are equivalent to the families (-aceae endings) mentioned.

Relationships of *Ixerba*

Ixerba has most of the anatomical characteristics of an archetypical woody saxifrage except for the lack of foliar trichomes and irregular pattern of intervacular pitting (Table 3). Although absent from the leaves, unicellular T-shaped trichomes occur on both the pedicels and flowers of *Ixerba*. These T-shaped trichomes were originally noted in *Ixerba* (Gardner, 1978), however, the exact location of this indument was not noted. These trichomes in *Ixerba* resemble the unicellular, T-shaped trichomes on pedicels and flowers of *Kirengeshoma* (Bensel and Palser, 1975b).

Ixerba has solitary angular pores, and vessel elements with scalariform perforation plates with numerous bars per plate. Patel (1973b) studied the wood anatomy of *Ixerba* and also noted the above wood anatomical features. *Ixerba* also possesses diffuse and diffuse-in-aggregates apotracheal parenchyma, and scanty paratracheal parenchyma. Besides

these types of axial parenchyma, Patel (1973b) noted vasicentric parenchyma as well. In the present study, very few intervacular pits were observed in Ixerba, and those present were usually arranged in irregular uniserial files (Fig. 24). Patel (1973b) found opposite to scalariform intervacular pitting in Ixerba. The infrequent and intermittent upright cells along the margins of the few multi-seriate wood rays of Ixerba are not sheath cells as previously reported (Patel, 1973b). These upright cells are too few and too widely spaced to form a sheath around the procumbent cells of the heterocellular, multiseriate rays. Although Patel (1973b) did not note spiral thickenings in the imperforate tracheary elements of Ixerba, some of the tracheids examined in this study exhibit fine to coarse spiral thickenings.

Many taxonomists have grouped Ixerba with Brexia and Roussea in either the Brexioidae (Engler, 1928; Schulze-Menz, 1964; Thorne, 1976) or the equivalent Brexiaceae (Airy Shaw in Willis, 1973; Dahlgren, 1975, 1980, 1983; Takhtajan, 1966). The taxonomic placement of Ixerba is very difficult, however, because the genus shares the wood and leaf anatomical characteristics of the Escallonioideae but has the pollen and ovular characteristics of Brexia. The vegetative anatomy of Ixerba, however, differs in many ways from that of Brexia, and argues for the taxonomic separation of the two genera. Work on floral morphology and anatomy also supports the separation of these two genera (Bensel and Palser, 1975a).

Ixerba has no stipules or foliar trichomes, and the vein endings are composed of helically thickened tracheids that are sometimes associated with fibers. Brexia, on the other hand, possesses stipules, foliar trichomes and vein endings that include peculiar sclereids with bulbous extensions (Ramamonjariisoa, 1980). Brexia also has a more complex petiolar vasculature (Ramamonjariisoa, 1980) than Ixerba. Ixerba has large glands composed of cells arranged in regular files in the marginal crenations of the leaves. Brexia, in contrast, lacks glands in the foliar serrations (Ramamonjariisoa, 1980). The vessel elements of Brexia (Ramamonjariisoa, 1980) are much shorter than those of Ixerba and typically have simple perforation plates, whereas, perforation plates in Ixerba are exclusively scalariform. Ixerba wood contains only tracheids but Brexia has both tracheids and fiber-tracheids. Some of the tracheids in Ixerba bear spiral thickenings, whereas, these are absent from all perforate and imperforate elements of Brexia (Ramamonjariisoa, 1980). Finally, Ixerba wood has sparse axial parenchyma that is predominantly apotracheal diffuse or paratracheal scanty. Brexia wood has abundant axial parenchyma that is apotracheal banded (Ramamonjariisoa, 1980).

Despite the differences noted above, both Ixerba and Brexia have bitegmic, crassinucellate ovules, while the Escalloniaceae possess unitegmic, tenuinucellate ovules (Davis, 1966; Philipson, 1974). In addition, Brexia and Ixerba are very similar palynologically and on this basis

could be grouped with Cuttsia, Abrophyllum and Argophyllum in the Escalloniaceae (Hideux and Ferguson, 1976).

In recent anatomical work on Brexia and Rousseia Ramamonjiarosoa (1980) argued that although Brexia and Rousseia are saxifragaceous, they are unrelated to the Escallonioid-eae and deserve independent status. Rousseia is also palynologically isolated from Brexia and Ixerba and more closely allied to Ribes than to any other saxifragaceous genus (Hideux and Ferguson, 1976).

Because of the numerous vegetative anatomical and morphological differences noted previously, Brexia and Ixerba probably are not closely related, and, therefore, Ixerba should be removed from the Brexioideae. The present study indicates that Ixerba is more closely related to Anopterus (Escallonioideae) than to any other saxifragaceous genus. Recent classification systems had advocated such a placement for Ixerba (Takhtajan, 1980, 1983; Thorne, 1983), and Patel (1973b) also included this genus in the Escalloniaceae based upon his study of the wood anatomy of New Zealand Escalloniaceae. Using floral morphology and anatomy, Bensel and Palser (1975a) also tentatively placed Ixerba in the Escallonioideae.

Relationships of Anopterus

Anopterus is another genus which has most of the anatomical features of an archetypical woody saxifrage (Table 3), and it shares many vegetative anatomical features with Ixerba. Both Anopterus and Ixerba have long vessel elements

with scalariform perforation plates that are not bordered, although Ixerba has more bars per scalariform perforation plate than Anopterus. Compared to the rare, irregular uni-seriate files of intervacular pits in Ixerba, the irregular intervacular pits of Anopterus are more numerous and are arranged in transitional, opposite or alternate patterns. Both genera possess medium length tracheids with coarse or fine spiral thickenings, although these thickenings are more obvious and numerous in Anopterus than in Ixerba. Anopterus glandulosus, which occurs in subalpine areas of Tasmania (Bentham, 1864), has shorter and narrower vessel elements and shorter tracheids than A. macleayanus which occurs in the subtropical regions of eastern and southeastern Queensland and northeastern New South Wales. The variation in length and diameter of the tracheary elements of the two species of Anopterus is probably attributable to adaptations to the different climatic conditions inherent in their latitudinal separation. This variation in length and diameter of the tracheary elements of Anopterus is consistent with trends noted in other studies of genera with species that grow in widely separated latitudes (Baas, 1973; Graaff and Baas, 1974; Oever, Baas, and Zandee, 1981). The tracheid walls of both Ixerba and Anopterus are approximately the same thickness.

The axial parenchyma in Ixerba and Anopterus is predominantly apotracheal diffuse, although paratracheal scanty parenchyma also occurs. Ray parenchyma is generally similar in Ixerba and Anopterus with regard to the types of rays

present (homocellular, uniserial and heterocellular, bi- to multiseriate rays) and the relatively short height and narrow width of these rays (Figs. 25 and 56).

Both Anopterus and Ixerba lack foliar trichomes but have prominent glands of similar structure in the marginal crenations of their leaves (Figs. 21, 22 and 52, 53). The leaves of both genera have a thick cuticle and round guard-cell pairs in surface view. In addition, the guard cells in transection are oval with small cuticular horns that represent the outer ledge overarching a stoma (Figs 20 and 51). The two genera differ somewhat in that Ixerba has a bi- to triseriate palisade layer, while Anopterus has a uni- to biseriate palisade layer. Also Ixerba has abundant crystalloids which are probably non-oxalate, whereas, Anopterus has druses which are probably oxalate in the spongy mesophyll.

Palynologically Anopterus belongs in the Escalloniaceae, and can be grouped with Escallonia, Forgesia and Valdivia (Hideux and Ferguson, 1976). But Anopterus pollen is intermediate between the above group of genera and the Ixerba, Brexia, Cuttsia, Abrophyllum and Argophyllum group (Hideux and Ferguson, 1976). Seed anatomy also supports inclusion of Anopterus in the Escalloniaceae but shows Ixerba to be an isolated genus (Krach, 1976). The similarities between Ixerba and Anopterus discussed above may indicate their close relationship and support their inclusion in the Escallonioideae (or the equivalent Escalloniaceae), as Takhtajan (1980, 1983) and Thorne (1983) have done.

Relationships of Cuttsia and Abrophyllum

Two other escallonioid genera, Cuttsia and Abrophyllum, possess all eleven characteristics of a hypothetical archetypical woody saxifrage (Table 3). The close relationship between Cuttsia and Abrophyllum advocated by Engler (1928) in his tribe Cuttsiae of the Escallonioideae is supported by the present study as well as by pollen morphology (Hideux and Ferguson, 1976) and seed anatomy (Krach, 1976, 1977).

Both Cuttsia and Abrophyllum possess homocellular, uniserial rays of upright cells. Both genera also exhibit tall and relatively wide heterocellular rays with perforated ray cells, sheath cells and long tails (Figs. 68, 69 and 78). In addition they both have diffuse or diffuse-in-aggregates axial xylem parenchyma with short tangential bands of parenchyma cells that link adjacent vascular rays (Figs. 66 and 76). The wood of both genera is fine-textured and lacks growth rings. Both Cuttsia and Abrophyllum have angular pores, although those of Cuttsia often have rounded corners. The vessel elements of both genera are long and have elongate scalariform perforation plates with perforations bordered only at the ends (Figs. 67 and 77). Vessel elements of Cuttsia are narrower and have fewer bars per scalariform perforation plate than those of Abrophyllum. The tracheids of both genera are very long and have thick walls. Although the tracheids of both genera possess spiral thickenings, these wall ornamentations are fine in Cuttsia and coarse in Abrophyllum.

Cuttsia and Abrophyllum leaves have similar marginal serrations with hydathodes in each tooth. A flared vein terminates in each serration, and often the tooth apex is composed of thick-walled, darkly staining cells. Ramamonjiarisoa (1980) compared the tooth types among the Escallonioidae and also noted the similarity of structure between the leaf teeth of Abrophyllum and Cuttsia. Both genera possess elongate, tapered, thick-walled, bulbous-based foliar trichomes. In Cuttsia and Abrophyllum the midvein and smaller vascular bundles of the leaves have a similar shape and size and are associated with a well-developed bundle sheath and bundle sheath extensions. Especially noteworthy is the constricted adaxial bundle sheath extension from the midvein in both genera (Figs. 63 and 74). Crystal sand occurs in the spongy mesophyll cells, and cleared leaves of certain specimens of both genera exhibit small clusters of yellowish cells in the mesophyll (Figs. 59 and 71).

Although Solereder (1908) and Metcalfe and Chalk (1950) stated that the leaves of Abrophyllum bore small glandular hairs, glandular trichomes do not occur on the leaves of Abrophyllum examined. Neither Holle (1893) nor Thouvenin (1890) noted glandular trichomes in this genus. Cuttsia and Abrophyllum display a trilacunar, three-trace nodal configuration which conflicts with a previous report of a unilacunar, one-trace nodal pattern for Abrophyllum ornans (Swamy, 1954). These two genera also show similar seed morphology (Krach, 1976, 1977) and pollen structure (Hideux and Ferguson, 1976).

Cuttsia and Abrophyllum belong in the Escallonioideae and appear to be closely related to one another based upon the numerous similarities in their vegetative anatomy.

Relationships of *Carpodetus*

Carpodetus, another genus in the Escallonioideae, shares many vegetative anatomical characteristics with both Cuttsia and Abrophyllum. Like the latter two genera, Carpodetus displays the anatomical characteristics of an archetypical woody saxifrage (Table 3). Engler (1928) placed Carpodetus in the tribe Argophylleae of the Escallonioideae with Argophyllum, Corokia, Colmeiroa and Berenice.

Of the three species of Carpodetus studied, C. arboreus was originally described as a separate genus, Argyrocallymma. The limited material examined in this study shows that C. arboreus is virtually identical to C. major, and both of these species, from New Guinea, are similar to C. serratus, from New Zealand, in almost all qualitative wood anatomical characteristics. The wood anatomy of the three species of Carpodetus examined supports the inclusion of the genus Argyrocallymma within the genus Carpodetus, as recommended by Schlechter (1914). The only differences among the three species are the abundance, length and diameter of the vessel elements and the length and wall thickness of the tracheids. Carpodetus arboreus and C. major have fewer pores, longer and wider vessel elements and longer and thicker-walled tracheids than C. serratus. These quantitative differences between C. arboreus and C. major, the two tropical species,

and C. serratus, the temperate species, probably reflect adaptations to widely differing climates rather than any taxonomic distinction between Argyrocalymma and Carpodetus. This pattern of variation of larger cell dimensions with decreasing latitude is consistent with other wood anatomical studies on genera with representatives in tropical and temperate latitudes as noted above for Anopterus (Graaff and Baas, 1974; Oever, Baas, and Zandee, 1981).

The wood of Carpodetus is similar to that of Cuttsia and Abrophyllum in possessing solitary, angular pores with moderately small diameters. The vessel elements are long with elongate scalariform perforation plates and numerous bars per plate (Fig. 89), as in Cuttsia and Abrophyllum. Carpodetus, however, is distinguished from the latter two genera in that all three species examined have perforations with complete borders, and one species has some vessel elements with fine spiral thickenings. The tracheids of Carpodetus have thick walls with spiral thickenings and are very long, as in Cuttsia and Abrophyllum. Axial xylem parenchyma in all three genera is predominantly diffuse or diffuse-in-aggregates with tangential bands of two to three cells that connect adjacent vascular rays (Fig. 88). The ray tissue is also similar to that of Cuttsia and Abrophyllum with homocellular, uniseriate rays of upright cells and relatively wide, heterocellular multiseriate rays (Fig. 90). Patel (1973b) also noted the similarities in the ray tissue among these three genera. The heterocellular rays of Carpodetus also have sheath cells and perforated ray cells

with scalariform perforation plates (Figs. 87 and 90), as in the other two genera. While Carpodetus ray cells often contain prismatic crystals (Fig. 89), these inclusions are lacking from the ray cells of Cuttsia and Abrophyllum.

A large vein flares as it enters each marginal serration in the leaves of C. serratus as previously noted for Cuttsia and Abrophyllum (Figs. 86 and 65). Each tooth apex in C. serratus is composed of a number of darkly staining, thick-walled cells as in Cuttsia and Abrophyllum. In addition, the midvein and smaller vascular bundles of the leaves of Carpodetus are very similar in shape, size and structure to those of Cuttsia and Abrophyllum (cf., Figs. 61, 63; 73, 74; 84, 85). The vascular bundles of all three genera are surrounded by a well developed bundle sheath, and the mid-vein in each also possesses a constricted adaxial bundle sheath extension (Figs. 63, 74 and 85). Although Abrophyllum has a uniseriate epidermis, Carpodetus and Cuttsia have an adaxial epidermis that is wholly or partially biseriate (Figs. 61, 83 and 84). The mesophyll differs in that Cuttsia and Abrophyllum have a lacunose spongy mesophyll with crystal sand in some cells, while Carpodetus has a compact spongy mesophyll with druses in some cells.

The stomatal apparatus is anomocytic in all three genera, although Philipson (1967) reported that Carpodetus has a paracytic stomatal apparatus. The guard-cell pairs are elliptic in surface view in all three genera. Carpodetus has round seeds that are somewhat similar to those of Cuttsia and Abrophyllum (Krach, 1976, 1977).

Carpodetus has certain features that differ from those in Cuttsia or Abrophyllum, such as the spiral thickenings in some of the vessel elements and the prismatic crystals in the ray parenchyma cells. Another distinguishing feature in Carpodetus is the presence of domatia on the abaxial surface of the leaves (Figs. 80 and 85), which had been noted previously (Sampson and McLean, 1965). Carpodetus also exhibits variation in the number of cell layers in the adaxial epidermis of its leaves (Figs. 83 and 84). Although Brook (1951) called the innermost layer of the biseriate epidermis of Carpodetus a hypodermis, he did not provide developmental evidence for this description. Thus the exact nature of this epidermal feature is uncertain due to the lack of developmental study. Nevertheless, Brook (1951) noted that the presence of a hypodermis is related to the type of leaf sectioned. Carpodetus has both juvenile and adult leaf forms, and a hypodermis typically is present in the adult leaves but is absent from the juvenile leaves. Thus, the stage of development of a leaf, may account for the variation in the extent of the biseriate adaxial epidermis observed in the present work. Because most of the specimens in this study were not designated as adult and juvenile leaf forms by the collectors, juvenile and adult leaves could not be distinguished. In one specimen of C. serratus (Tomlinson 2-I-69), which had adult and juvenile leaves clearly designated, the adaxial epidermis was partly biseriate in both types of leaves. This reported difference (Brook, 1951) in

the number of cell layers in the adaxial epidermis of the two types of leaves requires more intensive study with more material than was currently available. Another difference among Carpodetus, Cuttsia and Abrophyllum is that Carpodetus sheds its pollen in tetrads while the other two genera shed their pollen grains individually (Hideux and Ferguson, 1976).

Relationships of Corokia and Argophyllum

Besides Carpodetus, the other genera in the tribe Argophylleae of the subfamily Escallonioideae are Corokia, Argophyllum, Colmeiroa and Berenice (Engler, 1928). Berenice now has been placed in the Campanulaceae because of its distinctive pollen morphology and leaf and stem anatomy (Ernstman and Metcalfe, 1963).

Corokia carpodetoides was originally the basis of the monotypic genus Colmeiroa, but was combined with the genus Corokia based upon its floral and vegetative morphology (Smith, 1958). The trilacunar, three-trace nodal pattern and the petiolar vasculature of C. carpodetoides are essentially identical to those of C. macrocarpa (Fig. 94). The semicraspedodromous to brochidodromous leaf venation of these two species is also similar (Figs. 91 and 92). The leaves and twigs of C. carpodetoides were dried rather than fluid preserved, so detailed comparisons of the anatomy of the leaves with that in the other two species of Corokia is difficult. Nevertheless, the shape, size and structure of the midvein and smaller vascular bundles is similar to that

in the other species of Corokia examined. The adaxial epidermal cells are much larger than the abaxial epidermal cells in all three species (Figs. 96, 97 and 98). Although they are not as abundant as in the other two species examined, multicellular, T-shaped trichomes are common on the abaxial surface of the leaves of C. carpodetoides (Figs. 96, 97 and 98). One difference in the surface view of the leaves among these three species is the round guard-cell pairs of C. macrocarpa and C. virgata compared to the elliptic guard-cell pairs of C. carpodetoides. The present materials and observations indicate that C. carpodetoides should not be segregated as the monotypic genus Colmeiroa, but rather should be included in Corokia, in concert with the views of Smith (1958).

Corokia and Argophyllum show most of the characteristics of an archetypical woody saxifrage (Table 3), and are very closely related according to their vegetative anatomy. Although tracheids are present in two of the three species of Corokia examined, they are lacking in the species of Argophyllum studied. Nevertheless both genera possess abundant septate fibers and/or septate fiber-tracheids. The imperforate elements of both genera have medium length and walls of approximately the same thickness. Most of the tracheids and septate fiber-tracheids of Corokia have spiral thickenings while the septate fiber-tracheids and septate fibers of Argophyllum lack these thickenings. Although septate imperforate elements are absent from all other genera examined in this study, septate fiber-tracheids are

present in at least four other woody saxifragaceous genera: Choristylis, Hydrangea, Ribes and Deutzia (Ramamonjiarisoa, 1980; Stern, 1978a; Stern, Sweitzer and Phipps, 1970; Styer and Stern, 1979b).

Both Corokia and Argophyllum have predominantly solitary pores, although some radial multiples occur in both genera. Radial multiples of pores, however, are more typical of Argophyllum than of Corokia (Figs. 107 and 118). The vessel elements of both genera have extremely to very small diameter and medium to long length. These tracheary elements bear exclusively scalariform perforation plates with relatively few bars per plate (Figs. 108 and 119). Perforations are typically nonbordered. Fine spiral thickenings are present in the vessel elements of both genera. The oval to elongate, minute-diameter intervacular pits of Corokia and Argophyllum are typically alternate (Figs. 108 and 119).

Axial parenchyma was not observed in the woods of Corokia or Argophyllum, although Patel (1973a) noted very little scanty paratracheal and diffuse apotracheal parenchyma in three species of Corokia. All other escallonioid genera in this study contain axial parenchyma. The scarcity or lack of axial parenchyma in Corokia and Argophyllum may possibly be related to the abundance of septate fibers and/or fiber-tracheids in their woods. Harrar (1946) observed that septate fiber-tracheids probably function in place of axial parenchyma, especially where the fibers retain living protoplasts at maturity. Carlquist (1975)

also has noted that living or septate fibers substitute for axial parenchyma and commonly occur in woods which lack axial parenchyma. Choristylis, Hydrangea, Ribes, and Deutzia, four woody saxifragaceous genera, also possess septate fiber-tracheids, but generally lack axial parenchyma (Ramamonjarisoa, 1980; Stern, 1978a; Stern, Sweitzer and Phipps, 1970; Styer and Stern, 1979b).

Ray tissue of Corokia and Argophyllum comprises homocellular, uniseriate rays of upright cells and heterocellular, bi- to multiseriate rays (Figs. 109 and 120). The multiseriate rays of both genera are much shorter and narrower than the multiseriate rays of Cuttsia, Abrophyllum and Carpodetus but are similar in size to those of Ixerba and Anopterus. Corokia, Ixerba and Anopterus also possess dark-staining deposits in the ray parenchyma cells, although these deposits are much more common in Corokia than in the other two genera.

The nodal pattern in Corokia and Argophyllum, is typically trilacunar, three-trace, although variations occur in both genera. Corokia virgata is enigmatic with a unilacunar, one-trace nodal pattern (Fig. 95). The two species of Argophyllum examined are trilacunar, three-trace (Fig. 112), while a pentalacunar, five-trace nodal pattern has been reported for A. laxum (Swamy, 1954).

The leaves of Argophyllum typically possess small dentations along the margin whereas the leaves of Corokia are usually entire. Corokia collenettei, however, may have a few marginal dentations (Smith, 1958). The leaves of

Corokia and Argophyllum exhibit a weakly differentiated, typically biserrate palisade layer, although this layer is less distinct in Argophyllum than in Corokia (Figs. 96, 97 and 113). In both genera the cells in one or both layers of the palisade tissue typically contain dark-staining deposits (Figs. 97 and 113).

The two species of Argophyllum examined in this study belong to the section Brachycalyx. Plants within this section of the genus have either a hypodermis or a palisade mesophyll composed of square or rectangular cells rather than columnar cells in transection (Holle, 1893; Zemann, 1907). This type of palisade was not found in any other genus studied and is not typical of any other woody saxifragaceous genus.

Leaves of Corokia and Argophyllum bear unique T-shaped trichomes on the abaxial surface. The terminal cell of these trichomes is lignified and is separated from the uppermost stalk cell by a perforated or pitted septum (Figs. 102, 105, 115 and 116). Other workers also have noted the distinctive multicellular, T-shaped trichomes on leaves and flowers of Corokia (Eyde, 1966; Solereder, 1908; Sertorius, 1893; Weiss, 1890), and the similar trichomes in Argophyllum (Eyde, 1966; Holle, 1893; Zemann, 1907). In both genera the stomatal apparatus is anomocytic, and the stomata are raised above the level of the abaxial epidermis by enlarged or curved epidermal cells (Figs. 101 and 115). But the two genera differ because Corokia displays

ornamentations on the outer periclinal walls of abaxial epidermal cells below the midvein (Fig. 99), while Argophyllum lacks this feature.

The numerous anatomical similarities outlined above for Corokia and Argophyllum support their close taxonomic position. Corokia and Argophyllum also show resemblances in floral morphology and anatomy (Eyde, 1966) and in pollen morphology (Ferguson and Hideux, 1978). Palynologically these two genera are very closely related and may be linked with the tribe Cuttsiae of the Escallonioideae on the one hand and the Cornaceae on the other (Hideux and Ferguson, 1976). Despite these vegetative and floral anatomical, and palynological similarites, these two genera are very distinct from one another based upon seed anatomy (Krach, 1976).

The familial affinity of these two genera is still unclear. Most taxonomists have typically placed Argophyllum in the saxifrageous Escallonioideae (or the equivalent Escalloniaceae), while they have placed Corokia in either the Escallonioideae or the Cornaceae (Dahlgren, 1980, 1983; Takhtajan, 1980, 1983; Thorne, 1983).

Relationships Among the Escallonioideae

Vegetative anatomical data do not support the maintenance of the tribe Argophylleae of the Escallonioideae as envisioned by Engler (1928). Engler's Argophylleae contains the genera Argophyllum, Corokia and Carpodetus, discussed in detail above, as well as Berenice (to Campanulaceae, Erdtman

and Metcalfe, 1963) and Colmeiroa (=Corokia, Smith, 1958). Carpodetus, for example, shares more anatomical features with Cuttsia and Abrophyllum (tribe Cuttsieae) than with Argophyllum and Corokia. The latter two genera have shorter vessel elements with fewer bars per scalariform perforation plate and shorter imperforate elements than Cuttsia, Abrophyllum or Carpodetus. In addition, Corokia and Argophyllum have septate imperforate elements which are lacking in the other escallonioid genera. The radial multiples of pores in the wood of Argophyllum and Corokia are also unique features in the Escallonioideae. Likewise no other escallonioid genus has multicellular, T-shaped foliar trichomes or dark-staining deposits in the mesophyll cells such as occur in Corokia and Argophyllum. The entire leaf margin in Corokia is not the common condition among the Escallonioideae either. Hydathodes or glands are abundant in the other escallonioid genera studied, but are not common in either Corokia or Argophyllum.

Despite the vegetative anatomical differences between Argophyllum and Corokia, and the Escallonioideae (=Escalloniaceae), Hideux and Ferguson (1978) use palynological similarities to place Argophyllum in the Escalloniaceae in close proximity to Cuttsia, Abrophyllum, Ixerba and Brexia. In contrast, Hideux and Ferguson note that Corokia is intermediate between the Escalloniaceae and the Cornaceae. Krach (1976) also places Argophyllum in the Escalloniaceae because of its round seeds which are similar to those of Cuttsia and Abrophyllum.

Corokia and Argophyllum possibly should be removed from the Escallonioideae and placed among the Hydrangeoideae of the Saxifragaceae. Two hydrangeoid genera, Hydrangea and Deutzia, also possess complex, multiseriate, foliar trichomes and septate imperforate elements (Stern, 1978a; Styer and Stern, 1979b). As noted above, the ornamentations on the outer periclinal walls of the abaxial epidermal cells below the midvein of Corokia (Fig. 99) also occur in Philadelphus (Styer, 1978), another hydrangeoid genus. Much more work is needed, however, to confirm a relationship between Corokia and Argophyllum, and the Hydrangeoideae.

Some taxonomists place Corokia in the Cornaceae (Cronquist, 1981; Dahlgren, 1980, 1983). Previous workers have noted a similarity between the woods of Cornus and Corokia (Adams, 1949; Li and Chao, 1954), but these woods also have various differences. Although some species of Cornus may have septate fiber-tracheids (Li and Chao, 1954), Corokia wood has an abundance of these specialized imperforate elements. In addition, Cornus wood rays are heterocellular, uni-, bi- and multiseriate while wood rays of Corokia are homocellular, uniseriate with upright cells and heterocellular, bi- to multiseriate. Corokia wood also may have perforated ray cells, whereas these cells are lacking in Cornus (Adams, 1949; Li and Chao, 1954). Among the earlier wood anatomical studies of the Cornaceae (Adams, 1949; Li and Chao, 1954; Patel, 1973a), only Patel noted septate fibers in the wood of Corokia. Floral anatomy and morphology led

Eyde (1966) to reject any taxonomic affinity between Cornus and Corokia. Serological data also indicate that Corokia is distinct from the Cornaceae and is more closely allied to the Saxifragaceae (Fairbrothers, 1977 and pers. comm.; Fairbrothers et al., 1975).

According to Ferguson and Hideux (1978) Corokia pollen indicates a possible link between the Cornaceae and the Escalloniaceae, however, vegetative anatomy (Patel, 1973b), floral anatomy (Eyde, 1966) and phytochemistry (Fairbrothers, 1977; Fairbrothers, et al., 1975) contradict this connection. Corokia and Argophyllum are certainly closely related, but their position in the classification of the dicotyledons remains unclear. Cronquist (1981), interestingly, has recently designated Corokia as a nonmissing link between the Cornaceae and the Grossulariaceae (incl. Escalloniaceae). Detailed, systematic anatomical work on the Cornaceae is needed to determine the proper taxonomic placement of Corokia and Argophyllum and the relationship of the Saxifragaceae to the Cornaceae.

Possible Delimitation of the Escallonioideae

The six genera in the Escallonioideae examined in this study (i.e., Anopterus, Cuttsia, Abrophyllum, Carpodetus, Corokia and Argophyllum) possess most of the features of a hypothetical archetypical woody saxifrage (Table 3). Ixerba also can be added to these six genera because of its anatomical similarities to Anopterus. Besides the morphological and anatomical resemblances mentioned previously, these

seven genera also possess simple, predominantly alternate, petiolate, exstipulate leaves with serrate or crenate margins. Additionally they have a trilacunar, three-trace nodal pattern. This combination of nodal and leaf characteristics is not commonly found among the angiosperms (Sinnott and Bailey, 1914; Bailey, 1956). Sinnott and Bailey, and Bailey found that taxa with trilacunar nodes and dentate or serrate leaves generally possess stipules, while those with unilacunar nodes and entire leaves generally lack stipules. This distinctive set of nodal and leaf characteristics is present in all of these escallonioids except Corokia, which has mostly entire leaves and both unilacunar and trilacunar nodal configurations, and Argophyllum, which may have either a trilacunar, three-trace or a pentalacunar, five-trace nodal pattern (Swamy, 1954). Thus alternate, exstipulate, serrate or crenate leaves and a trilacunar, three-trace nodal pattern may delimit the Escallonioideae (Escalloniaceae) from other woody saxifrages.

Based upon recent anatomical work, Ramamonjarisoa (1980) has also placed Forgesia and Choristylis in the Escallonioideae. While Forgesia is similar anatomically to the escallonioid genera examined in this study, Choristylis is quite distinct. The only characteristic which links Choristylis with the Escallonioideae is the structure and morphology of the marginal teeth. Choristylis has rounded pores, septate fibers, relatively few bars per scalariform perforation plate, and relatively short vessel elements (Ramamonjarisoa, 1980). These characteristics in

Choristylis are inconsistent with a position in the Escallonioidae. The presence of minute stipules in Choristylis (Watari, 1939; Ramamonjarisoa, 1980), and the palynological similarity between this genus and Itea (Hideux and Ferguson, 1976) seems to exclude Choristylis from the Escallonioidae.

Relationships of Tetracarpaea

Another genus whose taxonomic affinities are uncertain is Tetracarpaea. Some taxonomists consider this genus to be a monotypic family, the Tetracarpaeaceae (Airy Shaw in Willis, 1973; Dahlgren, 1980, 1983). Other workers place Tetracarpaea in the Escalloniaceae (Hutchinson, 1967; Takhtajan, 1980, 1983), Grossulariaceae (Cronquist, 1981) or Cunoniaceae (Bentham, 1864).

Tetracarpaea possesses most of the characteristics of an archetypical woody saxifrage, but lacks the unicellular foliar trichomes, hydathodes or glands in the marginal serrations and a trilacunar, three-trace nodal pattern (Table 3). Qualitatively the wood of Tetracarpaea is very similar to that of the escallonioid genera Ixerba, Anopterus, Cuttsia, Abrophyllum and Carpodetus. Tetracarpaea wood, however, has cells with much smaller dimensions than those of the Escallonioidae. The vessel elements of Tetracarpaea have extremely small diameters, short to medium lengths and very few bars per scalariform perforation plate (Figs. 8 and 9). Tetracarpaea also has extremely short tracheids. The ray cells of Tetracarpaea also contain abundant dark-staining

deposits (Figs. 9, 11 and 12) which are typically absent from the ray cells of the Escallonioideae.

Although the wood is typically saxifragaceous, the nodes and leaves of Tetracarpaea are atypical for a woody saxifrage. Tetracarpaea possesses a unilacunar, one-trace nodal pattern, which confirms a previous report for the genus (Swamy, 1954). The leaves of Tetracarpaea possess simple craspedodromous venation and areole development is typically lacking or incomplete (Fig. 1). Other members of the Escallonioideae have semicraspedodromous venation, and areole development is incomplete to imperfect. Veinlets are straight and tapered in Tetracarpaea (Fig. 2), while they are straight, curved or branched and variously shaped in the escallonioid genera. The marginal serrations of Tetracarpaea have the appearance of hydathodes, but water pores are not visible in the adaxial epidermis. The genera of the Escallonioideae, however, typically possesses glands or hydathodes in their marginal serrations or crenations. In Tetracarpaea the outer ledge overarching a stoma is represented by two large cuticular horns (Fig. 5) while this ledge is represented by very small cuticular horns in Ixerba, Anopterus, Cuttsia, Abrophyllum and Carpodetus (Figs. 20, 51, 75). Abaxial fibers are typically associated with the foliar vascular bundles of Tetracarpaea, but they are not a common feature of the Escallonioideae. These cells, however, may be present in Ixerba and Anopterus. Bundle sheaths do not occur in Tetracarpaea but are

characteristic of all other woody saxifrages examined in this study and previous studies (e.g., Stern, 1974a, 1978a; Styer and Stern, 1979a, 1979b).

Despite the similarities in wood anatomy, the numerous differences in leaf anatomy between Tetracarpaea and the Escallonioideae (=Escalloniaceae) argue for the exclusion of this genus from the subfamily (family). The unilacunar nodal pattern, lack of bundle sheaths, craspedodromous venation, straight veinlets and lack of hydathodes or glands support the separation of Tetracarpaea from the Escallonioideae. The distinctive apocarpous gynoecium and tetramerous flowers (Dickison, pers. comm.) also support this conclusion.

Pollen morphology supports a position for Tetracarpaea in the Cunoniaceae (Hideux and Ferguson, 1976). Although recent studies of the wood anatomy of the Cunoniaceae (Dickison, 1980a) indicate that this may be a valid placement, the nodal structure, leaf anatomy and floral morphology and anatomy of Tetracarpaea are inconsistent with those of the Cunoniaceae (Dickison, 1975, 1980b and pers. comm.). Seed morphology and anatomy also support the view that Tetracarpaea is very isolated within the woody saxifrages and could easily be considered in its own family (Krach, 1976).

Because of the unilacunar, one-trace nodal pattern, the distinctiveness of its leaf structure, floral morphology, and seed morphology and anatomy, Tetracarpaea is isolated among the Saxifragaceae and may belong in its own family, the

Tetracarpaeaceae. The similarities in wood anatomy and palynology among the Tetracarpaeaceae, the Cunoniaceae and the Saxifragaceae lend support to a close relationship among these three families in the order Saxifragales.

Relationships of *Bauera*

Bauera, like *Tetracarpaea*, possesses most of the qualitative wood anatomical characteristics of an archetypical woody saxifrage, but nodal and leaf anatomy differ from that in most of the woody saxifrages for which anatomical data exist (Table 3). *Bauera* wood is similar to that of most woody saxifrages with scalariform, transitional to opposite intervacular pitting, sparse axial parenchyma, and the presence of tracheids (Table 3). Although the wood of *Bauera* possesses mostly solitary pores, radial multiples and clusters are common (Fig. 39). Most woody saxifrages, however, have very few, if any, radial multiples or clusters of pores. The vessel elements with predominantly simple perforation plates and transverse to oblique end walls (Fig. 40) also separate *Bauera* from other woody Saxifragaceae which display scalariform perforation plates and oblique vessel element end walls. The vessel elements and tracheids are much shorter in *Bauera* than in any of the Escallonioidae. Spiral thickenings, a characteristic feature of the woody saxifrages, are rarely present in the vessel elements of *Bauera*.

This genus is similar to the Escallonioidae with its homocellular, uniseriate rays of upright cells and

heterocellular, multiseriate rays. Bauera also has perforated ray cells, as in the Escallonioideae, although the perforations are simple rather than scalariform (Fig. 41). The rays of Bauera can be distinguished from those of other woody saxifrages because of the dark-staining deposits and the fenestriform pitting between the ray parenchyma and vessels.

Bauera is unique among the genera in this study because of the groups of three foliaceous appendages that occur at a given node. Most workers interpret these three structures as three leaflets of a sessile, trifoliolate leaf rather than a simple leaf accompanied by two lateral, foliaceous stipules (Bentham, 1864; Cronquist, 1981; Thouvenin, 1890; Watari, 1939; Willis, 1972). Baillon (1872), however, described Bauera with opposite simple leaves, with each leaf accompanied by two lateral foliaceous stipules. Thouvenin (1890) rejected this interpretation based upon his anatomical studies, and argued that the single leaf trace trifurcates in the extreme base of a leaf. He noted that in this part of a leaf the tissues of the leaf and stem intermingle and are not easily distinguishable from one another.

Thouvenin's interpretation is inappropriate for several reasons. First, each of the three foliaceous appendages has a small stalk and is vascularized by a single trace. If these appendages represent three leaflets of a trifoliolate leaf, then these stalks are petiolules. However, these "petiolules" are not attached to a petiole, but are attached

directly to the stem. The latter condition is rare among plants that bear compound leaves. Second, the single trace from a node trifurcates at approximately the same level in the stem as the separation of the two branch traces from the stem vasculature. This vascular pattern supports the contention that this trifurcation occurs in the stem of Bauera, and not in the extreme base of a sessile, compound leaf. Third, periderm is formed at the expanded portion of a stem where the three foliaceous appendages are attached. This location of periderm also supports the interpretation that this cushion is stem material and not the base of a leaf.

One drawback to the above interpretation of the three foliaceous appendages in Bauera is that unilacunar nodal configurations are not typically associated with stipules (Sinnott and Bailey, 1914; Bailey, 1956), although this combination of characteristics is found in some groups (e.g., Galium in the Rubiaceae). In fact, two lateral traces branch from a single trace in Galium to vascularize its interpetiolar or lateral stipules (Tyler, 1897). Foliaceous stipules also occur in a number of unrelated families (Lubbock, 1894). The same condition may exist in Bauera. More conclusive evidence about the proper morphological interpretation of these three foliaceous appendages will require developmental studies and the examination of much more material than was presently available.

The leaves of Bauera differ from those of the Escalloniaeae in several ways. Vein areole development is typically lacking, although it may be incomplete. In the

other woody saxifrages vein areole development is usually incomplete to imperfect. The vein endings of Bauera are unique because of the enlarged, short tracheids at the terminus of each vein ending (Fig. 29). The vein endings in the other genera are typically composed of helically thickened, elongate tracheids.

Although the upper epidermis of Bauera leaves may be biseriate, it differs from the biseriate adaxial epidermis in Cuttsia and Carpodetus. In Bauera the cells of the two layers of the biseriate epidermis differ widely in size and shape (Fig. 33), while in Cuttsia and Carpodetus the cells of the biseriate epidermis are relatively similar in size and shape (Figs. 61 and 83). In addition, the ledges over-arching a stoma are represented by large cuticular horns in Bauera (Fig. 36), while these ledges are represented by small cuticular horns in Ixerba, Anopterus, Cuttsia, Abrophyllum and Carpodetus. Bundle sheaths are typically present in woody saxifrages, however, bundle sheaths are absent from the leaves of Bauera. Unicellular, thick-walled trichomes occur in this genus as in other woody saxifrages (Table 3), although the base of these trichomes is surrounded by a ring of enlarged epidermal cells which do not occur in the other saxifragaceous genera (Fig. 33 and 34). Bauera is the only genus in this study which possesses prismatic crystals in its leaves (Fig. 32).

Bauera is morphologically and anatomically distinguishable from all other genera in this study as well as from

other woody saxifrages. Opposite leaves with foliaceous stipules do not occur in the Saxifragaceae. In addition, simple perforation plates in the vessel elements and unilacunar, one-trace nodes are not typical for members of the Saxifragaceae. Palynologically Bauera also is isolated from other Saxifragaceae and may be classified in its own subfamily or family (Wakabayashi, 1970) or placed among the advanced genera of the Cunoniaceae (Ernstman, 1952; Hideux and Ferguson, 1976). Work on embryology also supports the inclusion of Bauera in the Cunoniaceae (Prakash and McAlister, 1977). Current observations indicate that Bauera has some affinity to both the Saxifragaceae and the Cunoniaceae but in many ways is isolated from both families. Because of the numerous vegetative anatomical and morphological differences between Bauera and the other genera in this study it appears to be unrelated to them or to any other woody saxifrage. Bauera, like Tetracarpaea, possibly should be placed in its own family.

Relationships of Anodopetalum

Anodopetalum does not fit the anatomical pattern of an archetypical woody saxifrage and belongs in the Cunoniaceae, as suggested previously (Dickison, 1980a). Its opposite leaves with interpetiolar stipules and the trilacunar, three-trace nodal pattern with split lateral traces (Dickison, 1980b) have not been found among the woody Saxifragaceae. Its complex petiolar vasculature which results in a dorsally flattened concentric vascular bundle or ring of

bundles is also characteristic of the Cunoniaceae (Cronquist, 1981; Dickison, 1975) and atypical for the woody saxifrages. Although a concentric ring of vascular bundles does occur in the petioles of some woody saxifrages, such as Abrophyllum and Anopterus, these taxa have alternate leaves, lack stipules and possess trilacunar, three-trace nodes without split lateral traces. The epidermal leaf cells of Anodopetalum have straight anticlinal walls, as do most of the Cunoniaceae, while most of the woody saxifrages possess epidermal leaf cells with curved or sinuous anti-clinal walls.

Interestingly, Anodopetalum possesses glands in the marginal crenations of its leaves that are very similar to those found in the leaves of Ixerba and Anopterus. In all three genera the gland is relatively large and composed of radial files of cells that have dark-staining contents. In addition, the crenations in all three genera are vascularized by an arc of vascular tissue rather than a single vein (Figs. 21, 52 and 138). These genera also display guard-cell pairs with a circular rather than an elliptic outline in surface view. These few similarities in the leaves of these three genera are insufficient to support the inclusion of Anodopetalum in the Saxifragaceae, but may support a close connection between the Cunoniaceae and Saxifragaceae.

The wood of Anodopetalum has clustered pores and vessel elements with predominantly simple perforation plates, whereas the woody saxifrages typically possess solitary pores and vessel elements with scalariform perforation

plates. In addition heterocellular rays and perforated ray cells are largely absent from the wood of Anodopetalum, while these structures commonly occur in most woody saxifrages (Table 3). The length of the tracheids of Anodopetalum is moderately short to medium, while most woody saxifrages typically have medium to moderately long tracheids.

The axial parenchyma in Anodopetalum is relatively abundant compared to the sparse axial parenchyma in woody saxifrages. Axial parenchyma is diffuse-in-aggregates and marginal in Anodopetalum, but typically diffuse-in-aggregates in woody saxifrages. Axial parenchyma and ray parenchyma cells of Anodopetalum are filled with starch grains and dark-staining deposits, whereas these deposits are typically absent from woody saxifrages.

Based upon the numerous anatomical and morphological differences between Anodopetalum and the Saxifragaceae, this genus appears misplaced in the Saxifragaceae and should remain in the Cunoniaceae. Ingle and Dadswell (1956) and Dickison (1980a) also include Anodopetalum in the Cunoniaceae and place it among the more advanced members of the group. Seed anatomy (Dickison, 1984) and pollen morphology (Hideux and Ferguson, 1976) are consistent with this view.

Relationships of Aphanopetalum

Aphanopetalum is another genus often placed in the Cunoniaceae, although Dickison (1975c, 1980b) has questioned this taxonomic arrangement. Thorne (1983) also was unsure about the familial affinities of this genus and placed it

among his incertae sedis. The Cunoniaceae typically have trilacunar, three-trace nodes and vascularized stipules, whereas Aphanopetalum has unilacunar, one-trace nodes and avascular stipules.

Aphanopetalum is different from the Saxifragaceae in many ways. This genus is stipular with opposite leaves, while woody saxifrages are generally estipular with alternate leaves. Aphanopetalum has unilacunar, one-trace nodes, whereas trilacunar, three-trace nodes predominate in the woody saxifrages. The bundle sheaths of Aphanopetalum also are less well-developed and distinct than those in the woody saxifrages (Figs. 48, 61, 73, 84, 147). Although the biseriate palisade layer and lacunose spongy mesophyll of Aphanopetalum typically occur in the woody saxifrages, Aphanopetalum is distinctive because many of its mesophyll cells contain dark-staining deposits, a rare condition in the woody saxifrages (Figs. 97 and 113). Palynologically this genus also is isolated from the Saxifragaceae and the Cunoniaceae (Hideux and Ferguson, 1976).

Although Aphanopetalum has both differences and similarities with the woody Saxifragaceae, the differences outweigh the similarities and argue for the continued exclusion of this genus from the Saxifragaceae. The taxonomic placement of Aphanopetalum awaits further anatomical and morphological study, especially of the wood.

Relationships of *Donatia*

Another genus whose taxonomic position is uncertain is *Donatia*. Taxonomists have placed this genus in the Saxifragaceae (Engler, 1890; Hooker, 1865) the Styliadiaceae (Dahlgren, 1975, 1980, 1983; Mildbraed, 1908; Mueller, 1879; Thorne, 1976; Wagenitz, 1964) or the Donatiaceae (Airy Shaw in Willis, 1973; Cronquist, 1981; Skottsberg, 1915; Takhtajan, 1980, 1983). Engler (1928) later was uncertain of *Donatia*'s taxonomic placement (Table 1).

Donatia is unrelated to the genera examined in this study, nor does it share many anatomical characteristics with other woody saxifrages. The sessile leaves of *Donatia* contrast with the typically petiolate leaves of most of the Saxifragaceae. The suprabasal, acrodromous venation and lack of areole development in *Donatia* contrasts with the typically semicraspedodromous venation and imperfect to incomplete areole development of the other saxifrageous genera in this study. While *Philadelphus* also has suprabasal acrodromous venation, it possesses petiolate dorsiventral leaves with some areole development (Styer and Stern, 1979b). Although isobilateral leaves occur in both *Donatia* and some species of *Escallonia* (Stern, 1974a), only *Donatia* possesses an undifferentiated mesophyll. All other saxifrages studied have dorsiventral leaves with differentiated palisade and spongy mesophyll layers. *Donatia* also is distinctive because of the large masses of lignified, densely staining parenchyma cells abaxial to the small vascular bundles (Fig. 125). This lignified parenchyma previously

has been called sclerenchyma (Chandler, 1911; Rapson, 1953). Donatia leaves have stomata in both epidermal layers, an uncharacteristic condition in the Saxifragaceae. Multicellular, uniseriate trichomes are unknown from the woody saxifrages, although they do occur in Donatia and in the herbaceous saxifrages (Metcalfe and Chalk, 1950). These trichomes in herbaceous saxifrages, however, lack the oblique, pitted or perforated crosswalls characteristic of Donatia (Fig. 130).

The wood of Donatia is distinct from that of the Saxifragaceae because of its clustered pores, abundant axial parenchyma, fibers with simple pits and lack of spiral thickenings in tracheary elements. The poorly developed secondary xylem is similar to the wood of other Saxifragaceae, however, because of the vessel elements with scalariform perforation plates and scalariform intervascular pitting.

The small amount of wood produced by Donatia and the qualitative differences between Donatia wood and that of other Saxifragaceae argue for the exclusion of this genus from the family. The leaf anatomy of Donatia is distinct from that in most of the Saxifragaceae, as noted above. Previous workers have also excluded Donatia from the Saxifragaceae based upon anatomical data (Chandler, 1911; Rapson, 1953). Despite the numerous differences in vegetative anatomy, the woody Saxifragaceae and Donatia both have unicellular tenuinucellate ovules (Philipson, 1974; Philipson

and Philipson, 1973). This similarity is insignificant, however, because the saxifrages have no haustorial development during endosperm formation (Davis, 1966), as is characteristic of Donatia (Philipson and Philipson, 1973).

Palynologically, Donatia is more similar to the Campanulaceae than to the Saxifragaceae (Erdtman, 1952).

Donatia has been included among the Styliadiaceae primarily because of its resemblance to Phyllachne, another cushion plant, and the presence of inulin as its food storage product (Mildbraed, 1907; Mueller, 1879). Mildbraed (1907) placed Donatia within its own subfamily in the Styliadiaceae. Donatia also has a similar embryology to the stylidiaceous genus Forstera with its unitegmic tenuinucellate ovules and endospermal haustoria, but is distinct from other Styliadiaceae in the development of its ovules (Philipson and Philipson, 1973). The Philipsons have suggested that Donatia should be placed in its own family, and that the Donatiaceae is allied to the Styliadiaceae. Carolin (1960), however, has supported the inclusion of Donatia in the Styliadiaceae, and has argued that the flowers of Donatia formed the basis from which the more specialized sympetalous flowers of other Styliadiaceae were derived. Floral anatomy is uniform in the Styliadiaceae regarding the number of vascular bundles supplied to the floral organs, but Donatia forms no column or gynostemium, a characteristic of the other stylidiaceous genera (Carolin, 1960). Donatia, however, is anatomically different from the Styliadiaceae because of its scalariform perforation plates, lignified

ground tissue in the stem, "sclerenchyma" adjacent to the main veins and paracytic stomatal pattern (Chandler, 1911; Rapson, 1953).

This and other studies have shown that Donatia is apparently an independent lineage and should be placed in its own family, but the closest relatives of the Donatiaceae remain obscure. More work is needed to determine the taxonomic placement of this enigmatic genus.

Australasian Genera and Geological History

The anatomical similarities and possible taxonomic affinities among selected groups of genera discussed in detail above may lend support to Raven and Axelrod's (1972) ideas about the influence of past continental movements on biogeography in Australasia. Specifically, similarities among certain pairs or groups of genera may support the idea of an ancient connection between Australia, New Zealand, New Caledonia, New Guinea and other South Pacific Islands. Those genera with comparable anatomy and which occur in Australia and New Zealand include: Anopterus and Ixerba; Cuttsia, Abrophyllum and Carpodetus; and Argophyllum and Corokia. The latter two genera also are found in New Caledonia and other South Pacific Islands, respectively, and Carpodetus also occurs in New Guinea. Thus the affinities among these genera provide evidence for the possibility of an ancient connection among these Australasian land masses. This possibility, however, must be tempered by the likelihood of long distance dispersal and subsequent adaptive

radiation of some of these taxa. Long distance dispersal is especially pertinent to the biogeography of Corokia, which has one species on Rapa, a volcanic island. Further conclusions about geological history, long distance dispersal and biogeography of these plants from the antipodes would require more precise analysis of their pollination biology, seed dispersal, distributions and habitats than possible here. These studies remain to be done.

CONCLUSIONS

Although certain anatomical features are distinctive for each of the twelve Australasian genera in this study, other characteristics are fairly constant throughout these plants. The leaves of the genera studied are typically dorsiventral and possess uniseriate epidermides, although isobilateral leaves and biseriate epidermides also occur in certain genera. Most genera also have an anomocytic stomatal apparatus. The vein architecture is typically semicraspedodromous, although some genera possess craspedodromous, brochidodromous or acrodromous venation. The nodal pattern is usually trilacunar, three-trace, although unilacunar, one-trace patterns also occur.

The wood of these plants is typically diffuse porous with narrow diameter, thin-walled, angular, solitary pores and long vessel elements with oblique end walls and scalariform perforation plates. Scalariform, transitional and opposite intervacular pitting patterns also are common. The imperforate elements are usually tracheids. Both tracheids and vessel elements typically possess spiral thickenings. The axial xylem parenchyma in these genera is mostly sparse or absent. The ray parenchyma is composed of homocellular uniseriate rays of upright cells and heterocellular, bi- to multiseriate rays. Perforated ray cells occur in most of these genera.

Of the twelve genera examined in this study, Cuttsia, Abrophyllum and Carpodetus possess all eleven anatomical features of an archetypical woody saxifrage. Ixerba and Anopterus are similar to these three genera in this respect, except they lack foliar trichomes (Table 3). Corokia and Argophyllum possess most of the eleven anatomical features, except for multicellular trichomes and general lack of hydathodes and/or glands in their leaves (Table 3). The wood of Tetracarpaea and Bauera exhibits most of the characteristics of an archetypical woody saxifrage, although Bauera has predominantly simple perforation plates. The leaf anatomy of these two genera, however, differs from the other woody saxifrages. Both Donatia and Anodopetalum share few characteristics of an archetypical woody saxifrage (Table 3). The leaves and nodal anatomy of Aphanopetalum also are distinct from the other saxifrages.

Ixerba and Anopterus exhibit prominent glands of similar structure in the marginal crenations of their leaves, and share many other anatomical features. Both genera have long vessel elements with scalariform perforation plates that are not bordered. They also possess medium length tracheids with coarse or fine spiral thickenings. The ray parenchyma also is generally similar between the two genera. Their rays are shorter and narrower than those of the other escallonioid genera. These two genera differ in that Ixerba possesses large crystalloids while Anopterus has druses.

Although Ixerba previously has been allied with Brexia and Roussea in the Brexioidae, Ixerba and Brexia are not

closely related because of their differences in vegetative anatomy as well as floral morphology and anatomy. Ixerba should be removed from the Brexioidae, as it appears more closely allied to the Escallonioideae, especially Anopterus, than to any other members of the Saxifragaceae.

Three other escallonioid genera, Cuttsia, Abrophyllum and Carpodetus, possess all the characteristics of an archetypical woody saxifrage and undoubtedly belong in the Escallonioideae (Table 3). Cuttsia and Abrophyllum are very similar, and, despite a few anatomical differences, Carpodetus is clearly allied to these genera. Leaf serrations in all three genera exhibit an apical callosity composed of thick-walled, dark-staining cells. Also, a large vein flares as it enters the marginal leaf serrations. Carpodetus, however, is the only genus studied which has domatia on the abaxial leaf surface. The midvein and smaller vascular bundles of the leaves of all three genera are similar in size, shape and cellular composition. In addition, the midvein of each genus displays a constricted adaxial bundle sheath extension. Abrophyllum has a uniseriate adaxial epidermis, while Cuttsia and Carpodetus possess a biseriate adaxial epidermis.

The wood of Cuttsia, Abrophyllum and Carpodetus is similar in having solitary, angular pores with moderately small diameters. All three genera possess long vessel elements with elongate scalariform perforation plates and numerous bars per plate. The tracheids are very long and have thick walls with spiral thickenings. Axial parenchyma

is diffuse or diffuse-in-aggregates with tangential bands of two to three cells that connect adjacent vascular rays. Their ray tissue is similar with homocellular, uniseriate rays of upright cells and relatively wide, heterocellular, multiseriate rays. The heterocellular rays exhibit sheath cells and perforated ray cells with scalariform perforation plates. Carpodetus, though, is distinct from Cuttsia and Abrophyllum because some of its ray cells contain prismatic crystals and its vessel elements have spiral thickenings.

The other members of the Escallonioideae examined in this study, Corokia and Argophyllum, are very similar anatomically and possess most of the characteristics of an archetypical woody saxifrage (Table 3). Both genera, however, differ in many ways with these other genera and may not belong in the Escallonioideae. The leaves of Corokia are typically entire while those of Argophyllum possess small marginal dentations. Escallonioid leaves are usually serrate. The palisade layer of both genera is weakly differentiated and these cells may contain dark-staining deposits that are atypical of the other Escallonioideae. Both Corokia and Argophyllum also bear unique, multicellular, T-shaped, foliar trichomes. Although the stomatal apparatus is anomocytic in all Escallonioideae, the guard cells in Corokia and Argophyllum are unique in that they are raised above the rest of the abaxial surface by enlarged epidermal cells. Guard cells are even with the abaxial epidermis in other escallonioids.

Although Corokia and Argophyllum have predominantly solitary pores in their wood, radial multiples also occur. Among the genera studied only Corokia and Argophyllum possess septate imperforate elements. The ray tissue of both Corokia and Argophyllum is composed of homocellular uniseriate and heterocellular bi- to multiseriate rays as in other escallonioids. The multiseriate rays of both genera, however, are much shorter and narrower than the multiseriate rays of Cuttsia, Abrophyllum and Carpodetus but are similar in size to those of Ixerba and Anopterus. Corokia, Ixerba and Anopterus also possess dark-staining deposits in their ray parenchyma cells. These deposits are typically lacking in the other genera.

Corokia and Argophyllum are certainly closely related, but their taxonomic position is uncertain. They share certain characteristics with both the woody Saxifragaceae and the Cornaceae. Based upon vegetative anatomy, as well as floral morphology and anatomy, Corokia and Argophyllum are readily distinguishable from the Escallonioideae and should possibly be placed elsewhere among the woody Saxifragaceae. Their taxonomic placement awaits further study, especially of the vegetative anatomy of the Cornaceae.

The six genera in the Escallonioideae examined in this study (cf., Table 1) possess most of the features of an archetypical woody saxifrage (Table 3). Ixerba also can be included among this group because of its anatomical similarities with Anopterus. Except for some exceptions in Corokia and Argophyllum, these seven genera typically possess

simple, predominantly alternate, petiolate, exstipulate leaves with serrate or crenate margins that arise from a trilacunar, three-trace node. This atypical combination of nodal and leaf characteristics may delimit the Escallonioidae from all other woody Saxifragaceae.

Tetracarpaea possesses most of the characteristics of an archetypical woody saxifrage, but lacks the unicellular foliar trichomes, hydathodes or glands in the marginal serrations and a trilacunar, three-trace nodal pattern (Table 3). Tetracarpaea wood is qualitatively similar to the wood of the other escallonioids. The wood of Tetracarpaea differs, however, because of the small diameter and short to medium length vessel elements, and the short tracheids compared to the larger diameter and longer length vessel elements, and the long tracheids of the other Escallonioideae. Tetracarpaea also is distinguishable from the Escallonioidae because of the dark-staining deposits in its ray parenchyma cells. The leaves and nodes of Tetracarpaea are atypical for a woody saxifrage. The leaves have simple craspedodromous venation, and areole development is lacking or incomplete, while the other Escallonioideae studied possess semicraspedodromous venation, and areole development is incomplete to imperfect. The unilacunar, one-trace nodes of Tetracarpaea also contrast with the typically trilacunar, three-trace nodes of the Escallonioideae. Bundle sheaths also do not occur in Tetracarpaea, but are found in all other woody saxifrages.

Despite the similarities in wood anatomy, these differences in leaf and nodal anatomy argue for the separation of Tetracarpaea from the Escallonioideae. Indeed, Tetracarpaea is isolated among the Saxifragaceae and may belong in its own family.

Bauera, like Tetracarpaea, possesses most of the qualitative wood anatomical characteristics of an archetypical woody saxifrage, but its nodal and leaf anatomy differ from that of most woody saxifrages (Table 3). Bauera wood has tracheids, sparse axial xylem parenchyma and homocellular, uniseriate and heterocellular, multiseriate rays as in other woody saxifrages. The presence of radial multiples and clusters of pores and simple perforation plates in the vessel elements, however, separates Bauera from the other woody saxifrages. Bauera also has dark-staining deposits in its ray parenchyma cells, a feature atypical of woody Saxifragaceae.

Bauera is unique among all the genera in this study because of its opposite leaves and lateral, foliaceous stipules. Bauera leaves also are distinctive because of the enlarged, isodiametric tracheids in the vein endings. These and other anatomical differences support the separation of Bauera from the Saxifragaceae, and its placement in either the Cunoniaceae or its own family.

Anodopetalum does not fit the anatomical pattern of an archetypical woody saxifrage (Table 3). The opposite leaves with interpetiolar stipules and the trilacunar, three-trace nodal pattern with split lateral traces are not found in the

woody Saxifragaceae. The complex petiolar vasculature also is atypical for the woody saxifrages. The wood of Anodopetalum has clustered pores and vessel elements with simple perforation plates, whereas, the woody saxifrages typically possess solitary pores and vessel elements with scalariform perforation plates. Anodopetalum is not saxifragaceous and should remain in the Cunoniaceae.

Aphanopetalum is another genus placed in the Cunoniaceae. The differences outweigh the similarities between Aphanopetalum and the woody Saxifragaceae and argue for the continued exclusion of this genus from the family. Aphanopetalum has opposite, stipulate leaves and unilacunar, one-trace nodes, while alternate, exstipulate leaves and trilacunar, three-trace nodes are typical for the woody saxifrages. Although the palisade and spongy mesophyll of the leaves of Aphanopetalum are similar to that in many woody saxifrages, these cells contain dark-staining deposits that are atypical for the woody Saxifragaceae. The taxonomic placement of this genus remains uncertain, especially until the wood can be studied.

Donatia is unrelated to the woody Saxifragaceae examined in this study as it does not share many anatomical similarities with other woody saxifrages. The sessile leaves with acrodromous venation and lack of areole development in Donatia contrast with the petiolate leaves with typically semicraspedodromous venation and incomplete to imperfect areole development in most woody saxifrages.

Donatia also has isobilateral leaves and a large mass of lignified parenchyma cells abaxial to its very small foliar vascular bundles. The leaves of the woody Saxifragaceae are typically dorsiventral and lack a large mass of lignified tissue associated with their vascular bundles.

This study shows Donatia to be an isolated genus that probably should be placed in its own family, although the closest relatives of this family remain obscure.

SUMMARY

In summary, the present anatomical data:

1. contradict a close relationship among Ixerba, Brexia and Rousseia, which are often placed together in the Brexioidae;
2. reveal many similarities between Ixerba and Anopterus in the Escallonioideae;
3. confirm the taxonomic affinity between Cuttsia and Abrophyllum in tribe Cuttsieae of the Escallonioideae;
4. do not support the maintenance of tribe Argophylleae of the Escallonioideae;
5. show Carpodetus to be more similar to Cuttsia and Abrophyllum than to Corokia and Argophyllum;
6. support a close relationship between Corokia and Argophyllum, however, their taxonomic position remains obscure;
7. validate the combination of the genus Argyrocallymma with Carpodetus and the combination of the genus Colmeiroa with Corokia;
8. show Tetracarpaea, Bauera and Donatia to be distinctive genera, and each genus may warrant a monogeneric family;
9. indicate that while Donatia is isolated, Tetracarpaea is close to Saxifragaceae and Bauera is allied to Cunoniaceae;
10. readily segregate Anodopetalum from the Saxifragaceae and place it in the Cunoniaceae;
11. separate Aphanopetalum from the Saxifragaceae, although its taxonomic position remains obscure.

APPENDIX

Table 4. Specimens of Australasian woody Saxifragaceae examined anatomically.

SPECIES	COLLECTOR	LOCALITY	XYLIARIUMA OR GARDEN	TYPE OF MATERIAL ^b
<u><i>Abrophyllum</i></u> <u><i>ornans</i></u>	Hoogland 11693	Australia		L, N, W, F
	F. M. Hueber #1	Australia		L, N, W, F
	W. T. Jones 2393	CANBw 7335		W, D
	H. C. Hayes s.n.			W, D
	White 10696	Aw H-27147		W, S
<u><i>Anodopetalum</i></u> <u><i>biglandulosum</i></u>	Hoogland 11743	Tasmania		L, N, W, F
<u><i>Anopterus</i></u> <u><i>glandulosus</i></u>	Hoogland 11727	Tasmania		L, N, W, F
	F. M. Hueber 3/17/70	Australia	RBG-Mel. c	L, N, W, F
	Carlquist 1134	Australia	USw 36041	W, D
		Tasmania	FPAw 18257	W, D
		Tasmania	FPAw 31583	W, D
		Tasmania	MAD-SJRW 19382	W, D, S
		Tasmania	FPAw 14002	W, S

Table 4--continued.

SPECIES	COLLECTOR	LOCALITY	XYLARIUM ^a OR GARDEN	TYPE OF MATERIAL ^b
<i>Anopterus macleayanus</i>	Hoogland 11651 W.T. Jones s.n. H.C. Hayes	Australia CANB 7324	L, N, W, F W, D W, D	
		Australia MAD-SJRW 15918	W, D, S	
		Australia FPAW 17327	W, D	
<i>Aphanopetalum resinosum</i>	Hoogland 11649	Australia	L, N, F	
<i>Argophyllum cryptophlebium</i>	F.M. Hueber 3/2/70	Australia	L, N, W, F	
		Aw 27645	W, S	
<i>Argophyllum ellipticum</i>		Australia	W, D	
<i>Argophyllum nullumense</i>	Hoogland 11801 H.C. Hayes s.n.	Australia	L, N, W, F W, D	

Table 4--continued.

SPECIES	COLLECTOR	LOCALITY	XYLARIUM ^a OR GARDEN	TYPE OF MATERIAL ^b
<i>Bauera</i> <u>capitata</u>	Hoogland	11784		L, N, F
<i>Bauera</i> <u>rubrioides</u>	Hoogland	11753	Tasmania	L, N, F
	Hoogland	12226		L, N, F
			Australia	W, D
<i>Bauera</i> <u>sessiliflora</u>	Hoogland	11704	Victoria	L, N, W, F
	Hoogland	11890		L, N, F
			Victoria	W, D
<i>Carpodetus</i> sp.	B.F. Shore s.n.	1	New Zealand	L, N, W, F
<i>Carpodetus</i> <u>arboresus</u>			NGF 10127 ^d	W, D
			New Guinea	W, S
			New Guinea	W, S
<i>Carpodetus</i> <u>major</u>	Hoogland & Pullen	5582	New Zealand	W, D
	Saunders	799	New Zealand	W, D

Table 4--continued.

SPECIES	COLLECTOR	LOCALITY	XYLARIUM ^a or GARDEN	TYPE OF MATERIAL ^b
<u><i>Carpodetus</i></u> <u><i>major</i></u>		New Guinea	FPAw H5582	W, D
		New Guinea	FPAw S799	W, S
<u><i>Carpodetus</i></u> <u><i>serratus</i></u>	W. Phillipson #3	New Zealand	L, N, W, F	
	Tomlinson 2-1-69	New Zealand	L, N, W, F	
	B.F. Shore s.n. 4	New Zealand	L, N, F	
	R. Wilson 70/3	New Zealand	W, F	
		New Zealand	PRFw 1274	W, D
		New Zealand	FPAw 12036	W, D
		New Zealand	FPAw 12071	W, D
		New Zealand	MAD-SJRW 47201	W, D
		New Zealand	MAD-SJRW 25445	W, D
<u><i>Corokia</i></u> <u><i>buddleoides</i></u>	L.H. MacDaniels	New Zealand	MAD-SJRW 25438	W, D
<u><i>Corokia</i></u> <u><i>carpodetoides</i></u>	J.D. McCornish 147	Lord Howe Island		L, N, D

Table 4--continued.

SPECIES	COLLECTOR	LOCALITY	XYLARIUM ^a or GARDEN	TYPE OF MATERIAL, ^b
<i>Corokia collenettei</i>	J. & T. Clarke R25	Rapa Island	USw 34143	W, D
<i>Corokia macrocarpa</i>		Chatham Islands	Kew 118-54-11801 ^e	L, N, F
<i>Corokia virgata</i>		New Zealand	Kew 118-54-11801 ^e	L, N, F
<i>Corokia whiteana</i>	R.D. Hoogland & H.C. Hayes s.n.	Australia	MAD-SJRW 55149	W, D
<i>Cuttisia viburnea</i>		Hoogland 11664	Australia	L, N, W, F
	F.M. Hueber #1			L, N, F
	F.M. Hueber #2			L, N, W, F
	W.T. Jones s.n.	Australia	CANB 7325	W, D
	H.C. Hayes			W, D
	Phillipson 20404	Australia		W, D
			FPAW 20404	W, D
		Australia	FPAW 18202	W, D

Table 4--continued.

SPECIES	COLLECTOR	LOCALITY	XYLARIUM ^a OR GARDEN	TYPE OF MATERIAL ^b
<i>Donatia</i> <i>novaeseelandiae</i>	Hoogland	11755	Tasmania	L, N, F
<i>Ixerba</i> <i>brixoides</i>	Tomlinson	9-IV-69A	New Zealand	L, N, W, F
	W. Phillipson	#2	New Zealand	L, N, F
	B.F. Shore s.n.	2	New Zealand	L, N, W, F
	W. Phillipson	249	New Zealand	W, D
	H.J. Deutzman		New Zealand	W, D
			MAD-SJRW 47058	
			New Zealand	W, D
			FPAW 14170	
			New Zealand	W, D
			WZw 47	
Cockayne	4978		Aw 27700	L, N, S
Kirk	531		Aw 27699	L, N, S
			New Zealand	W, S
			New Zealand	W, S
			FHOw 18961	

Table 4--continued.

SPECIES	COLLECTOR	LOCALITY	XYLARIUM ^a or GARDEN	TYPE OF MATERIAL ^b
<u>Tetracarpaea</u> <u>tasmaniaca</u>	Hoogland	11745	Tasmania	L, N, W, F
	Hoogland	11738	Tasmania	L, N, F
	Comber	2251	Aw 27721	W, S

^aAbbreviations follow those recommended by Stern (1978c).^bL, leaf; N, node; W, wood; F, fluid preservation; D, dried specimen; S, slideC_{RBC-Mel.}, Royal Botanic Garden, Melbourned_{NGF}, Department of Forests, Division of Botany, Lae, New Guinea

eKew, Royal Botanic Gardens, Kew, Richmond, Surrey, England

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