

Comparative Wood Anatomy of Epacrids (Styphelioideae, Ericaceae *s.l.*)

FREDERIC LENS^{1,*}, PETER GASSON², ERIK SMETS¹ and STEVEN JANSEN^{1,2}

¹Laboratory of Plant Systematics, K.U.Leuven, Institute of Botany and Microbiology, Kasteelpark Arenberg 31, B-3001 Leuven, Belgium and ²Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, UK

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The wood anatomy of 16 of the 37 genera within the epacrids (Styphelioideae, Ericaceae *s.l.*) is investigated by light and scanning electron microscopy. Several features in the secondary xylem occur consistently at the tribal level: arrangement of vessel-ray pits, distribution of axial parenchyma, ray width, and the presence and location of crystals. The primitive nature of Prionoteae and Archerieae is supported by the presence of scalariform perforation plates with many bars and scalariform to opposite vessel pitting. The wood structure of Oligarrheneae is similar to that of Styphelieae, but the very narrow vessel elements, exclusively uniseriate rays and the lack of prismatic crystals in Oligarrheneae distinguish these two tribes. The secondary xylem of *Monotoca tamariscina* indicates that it does not fit in Styphelieae; a position within Oligarrheneae is possible. Like most Cosmelieae, all Richeeae are characterized by exclusively scalariform perforation plates with many bars, a very high vessel density and paratracheal parenchyma, although they clearly differ in ray width (exclusively uniseriate rays in Cosmelieae vs. uniseriate and wide multiseriate rays in Richeeae). Several wood anatomical features confirm the inclusion of epacrids in Ericaceae *s.l.* Furthermore, there are significant ecological implications. The small vessel diameter and high vessel frequency in many epacrids are indicative of a high conductive safety to avoid embolism caused by freeze–thaw cycles, while the replacement of scalariform by simple vessel perforation plates and an increase in vessel diameter would suggest an increased conductive efficiency, which is especially found in mesic temperate or tropical Styphelieae.

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Key words: Ecological wood anatomy, epacrids, Ericaceae *s.l.*, Styphelioideae, systematic wood anatomy.

INTRODUCTION

The formerly recognized family Epacridaceae includes small to large shrubs and small trees of about 37 genera and more than 450 species. Most representatives occur in Australia, especially in the south-west, west and south-east, and in Tasmania. Non-Australian species range from Indo-Malaysia to South America, New Zealand, New Caledonia and Hawaii. The epacrids grow in a wide variety of habitats ranging from Mediterranean and temperate to (sub)tropical climates, covering coastal dunes, lowland forests, sandy heaths, upland areas and even montane to (sub)alpine regions (Burrows *et al.*, 1979; George *et al.*, 1979; Specht 1979*a, b*; Specht and Womersley, 1979).

Until recently, this plant group was recognized at family level and most taxonomists considered it to be the Australian counterpart of Ericaceae. Epacridaceae were separated from Ericaceae on the basis of their distribution pattern, parallel leaf venation, presence of unicellular hairs, number of stamens and anther dehiscence by slits (Stevens, 1971). However, owing to a high degree of variation in both families, these so-called distinguishing characters have never maintained the two families as distinct entities. Indeed, some botanists had already merged epacrids in Ericaceae over 150 years ago (e.g. Don, 1834). Recently, DNA-sequence data have again supported this view showing that epacrids, although strongly supported as a monophyletic group, are sister to the subfamily

Vaccinioideae within Ericaceae *s.l.* (Kron, 1996; Kron *et al.*, 1999, 2002). In the most recent classification of Ericaceae, epacrids are given subfamilial rank. Due to nomenclatural rules, the group should now be called Styphelioideae (Kron *et al.*, 2002).

The taxonomic position of the epacrid genera according to several classification systems is shown in Table 1. On the basis of ovary and fruit characters, Bentham and Hooker (1876) and Drude (1889) provided the first major classifications within the epacrids. Based on leaf fibre patterns, stomata, nodal anatomy and pith structure, Watson (1967) erected the subfamily Richeoideae and the tribe Cosmelieae, which are now considered as two tribes. A cladistic analysis of morphological characters presented further support for three monophyletic subgroups (Cosmelieae, Richeeae and Styphelieae including *Needhamiella* and *Oligarrhena*), but the other representatives were clustered in an unnatural assemblage (Powell *et al.*, 1996). The classification system within epacrids was further refined using *rbcL*-data, resulting in seven tribes (Crayn *et al.*, 1998). Although tribal relationships and affinities within Styphelieae remain uncertain, additional *atpβ-rbcL* intergeneric spacer data concurred with this classification (Crayn and Quinn, 2000). However, *marK* data contradict the proposed tribal relationships based on *rbcL* data, although these relationships are not strongly supported either (Kron *et al.*, 2002).

There is still an under-representation of shrubs and subshrubs in wood anatomical descriptions (e.g. Dickson, 1999), as illustrated by, for example, our fragmentary

* For correspondence. Fax +32 16 32 19 68, e-mail frederic.lens@bio.kuleuven.ac.be

TABLE 1. A comparison of the tribal classifications of epacrids

Drude (1889)	Watson (1967)	Powell <i>et al.</i> (1996)	Crayn <i>et al.</i> (1998)
Prionoteae	Epacroidaeae	Epacrideae	Prionoteae
LEBETANTHUS	EPACRIDEAE	<i>Archeria</i>	<i>Lebetanthus</i>
Prionotes	<i>Archeria</i>	Epacris	Prionotes
Epacrideae	Epacris	<i>Lebetanthus</i>	ARCHERIEAE
(1) <i>Dracophyllum</i>	<i>Lebetanthus</i>	<i>Lysinema</i>	<i>Archeria</i>
Richea	<i>Lysinema</i>	Prionotes	OLIGARRHENEAE
<i>Sphenotoma</i>	Prionotes	<i>Rupicola</i>	Needhamiella
Andersonia	<i>Rupicola</i>	<i>Woollisia</i>	Oligarrhena
Cosmelia	<i>Woollisia</i>	COSMELIEAE	COSMELIEAE
Sprengelia	NEEDHAMIELLEAE	Andersonia	Andersonia
(2) <i>Archeria</i>	Needhamiella	Cosmelia	Cosmelia
Epacris	OLIGARRHENEAE	Sprengelia	Sprengelia
<i>Lysinema</i>	Oligarrhena	RICHEEAE	RICHEEAE
<i>Rupicola</i>	COSMELIEAE	Dracophyllum	Dracophyllum
<i>Woollisia</i>	Andersonia	Richea	Richea
STYPHELIEAE	Cosmelia	<i>Sphenotoma</i>	<i>Sphenotoma</i>
<i>Acrotriche</i>	Sprengelia	STYPHELIEAE	EPACRIDEAE
<i>Astroloma</i>	STYPHELIEAE	<i>Acrotriche</i>	<i>Budawangia</i>
<i>Brachyloma</i>	<i>Acrotriche</i>	<i>Astroloma</i>	Epacris
<i>Choristemon</i>	<i>Astroloma</i>	<i>Brachyloma</i>	<i>Lysinema</i>
<i>Coleanthera</i>	<i>Brachyloma</i>	<i>Choristemon</i>	<i>Rupicola</i>
<i>Conostephium</i>	<i>Choristemon</i>	<i>Coleanthera</i>	<i>Woollisia</i>
Cyathodes	<i>Coleanthera</i>	<i>Conostephium</i>	STYPHELIEAE
<i>Cyathopsis</i>	<i>Conostephium</i>	Cyathodes	<i>Acrotriche</i>
<i>Decatoca</i>	Cyathodes	<i>Cyathopsis</i>	<i>Astroloma</i>
Leptecophylla*	<i>Cyathopsis</i>	<i>Decatoca</i>	<i>Androstoma*</i>
Leucopogon	<i>Decatoca</i>	Leptecophylla*	<i>Brachyloma</i>
<i>Lissanthe</i>	Leptecophylla*	Leucopogon	<i>Choristemon</i>
<i>Melichrus</i>	Leucopogon	<i>Lissanthe</i>	<i>Coleanthera</i>
Monotoca	<i>Lissanthe</i>	<i>Melichrus</i>	<i>Conostephium</i>
Needhamiella	<i>Melichrus</i>	Monotoca	Cyathodes
Oligarrhena	Monotoca	Needhamiella	<i>Cyathopsis</i>
<i>Pentachondra</i>	<i>Pentachondra</i>	Oligarrhena	<i>Decatoca</i>
Styphelia	Styphelia	<i>Pentachondra</i>	Leptecophylla*
Trochocarpa	Trochocarpa	Styphelia	Leucopogon
	RICHEOIDEAE	Trochocarpa	<i>Lissanthe</i>
	Dracophyllum		<i>Melichrus</i>
	Richea		Monotoca
	<i>Sphenotoma</i>		<i>Pentachondra</i>
			<i>Planocarpa*</i>
			Styphelia
			Trochocarpa

Genera are listed alphabetically by tribe. Genera in bold are included in this study.

* *Androstoma*, *Leptecophylla* and *Planocarpa* are genera recently erected by Weiller (1996a, b, 1999). The classification according to Crayn *et al.* (1998) is followed in this paper.

knowledge of the wood structure of epacrids and Ericaceae in general. Etienne (1919) was one of the first botanists who paid attention to the general anatomy of epacrids. Although his sampling was outstanding (31 genera), his work focused on a limited number of wood anatomical characters of mostly juvenile wood samples. The best overall summary of the wood anatomy is given by Metcalfe and Chalk (1950). There are several other publications that deal with the wood anatomy of one or more epacrid species, such as the work of Carlquist (1977a) including remarks on the ecological wood anatomy of five epacrid genera, Meylan and Butterfield (1978) investigating three epacrid genera with SEM, Ilic (1991) showing pictures of two genera, Schweingruber (1992) discussing growth rings and growth zones of 43 epacrid samples, and Bell and Pate (1996) and Bell *et al.*

(1996) commenting on various characteristics related to fire response mechanisms within epacrids.

This work presents a detailed wood anatomical overview of the epacrids. Special emphasis is paid to a comparison of the wood anatomical variation with recent molecular phylogenies to reveal possible evolutionary patterns and to comment on the intrafamilial classification. Moreover, ecological conditions are taken into consideration to better interpret the anatomical variation observed.

MATERIALS AND METHODS

Wood samples of 44 specimens representing 34 species and 16 genera were investigated using light microscopy (LM) and scanning electron microscopy (SEM). The wood

TABLE 2. List of the wood samples studied with reference to the provenance, collector, and the diameter of the wood sample

Species	Provenance	Collector	Diameter (mm)
<i>Andersonia caerulea</i> R.Br.	Australia (near Northcliffe towards Windy Harbour)	C. H. Gittins 1735 (AQ 186757)	2.5
<i>A. sprengeioides</i> R.Br.	Australia (Albany)	C. T. White 5303 (AQ 186747)	6
<i>Cosmelia rubra</i> R.Br.	Australia	J. M. Powell 3143 (NSW 202688)	3.5
<i>Cyathodes glauca</i> Labill.	Australia (Tasmania)	Lhotsky 38 (K 11737)	32
<i>D. longifolium</i> R.Br.	New Zealand	M. v. Balgooy 4415 (L)	17
<i>D. longifolium</i> R.Br.	New Zealand	J. D. Hooker s.n. (K 11738)	35
<i>D. oliveri</i> Du Rietz	New Zealand (Deniston)	M. v. Balgooy 4500 (L)	18
<i>D. palustre</i> W.R.B.Oliv.	New Caledonia	Unknown (L)	Mature
<i>D. strictum</i> Hook.f.	New Zealand	H. J. Dentzman 2085 (MADw 5075)	Mature
<i>D. subulatum</i> Hook.f.*	New Zealand, Kanau	Unknown 4945	30
<i>D. traversii</i> Hook.f.	New Zealand	J. D. Enys 190 (K 11740)	Mature
<i>D. uniflorum</i> Hook.f.	New Zealand (near Lake Lyndon)	M. v. Balgooy 4321 (L)	12
<i>D. urvilleanum</i> A.Rich.	New Zealand (Campbell Island)	J. D. Hooker s.n., (K 11742)	50
<i>D. verticillatum</i> Labill.	New Caledonia	Unknown (MADw 14126)	Mature
<i>Epacris impressa</i> Labill.	South Australia	M. Nee 45466 (MADw 48036)	13
<i>E. impressa</i> Labill. var. <i>ovata</i> Benth.*	Unknown	H.K. 7	2
<i>E. miniata</i> Lindl.*	Unknown	Unknown	3
<i>Leptecophylla</i> sp.	Tahiti (Society Islands)	Grant 4397 (L)	27
<i>L. juniperina</i> (J.R.Frost. & G.Frost) C.M.Weiller	New Zealand	Unknown (K 11736)	58
<i>L. tameiameiae</i> (Cham. & Schldl.) C.M.Weiller	Hawaii (Pukeawe, Aalii Mahu)	Unknown (MADw 3336)	Mature
<i>L. tameiameiae</i> (Cham. & Schldl.) C.M.Weiller	Hawaii (Kauai)	Stern & Herbst 2939 (U 18556)	45
<i>Leucopogon cumbuliae</i> Labill.	New Caledonia	Unknown (MADw 14712)	Mature
<i>L. cumbuliae</i> Labill.	New Caledonia	Unknown (MADw 14339)	Mature
<i>L. fasciculatus</i> A.Rich.	New Zealand	McDonald (K 11743)	Mature
<i>L. lanceolatus</i> R.Br.*	Unknown	Unknown	2
<i>L. malayanus</i> Jack.	Borneo	Ogata 80 (L)	13
<i>L. parviflorus</i> Lindl.	South Australia (Eyres Peninsula, Port Lincoln)	W. Cain 58 (MADw 2278)	Mature
<i>L. richei</i> R.Br.	Australia	W. R. Guilfoyle, s.n. (K 11744)	110
<i>Monotoca elliptica</i> R.Br.	Australia (New South Wales)	Unknown (K 11747)	Mature
<i>M. elliptica</i> R.Br.	Australia	Unknown (K 11745)	170
<i>M. tamariscina</i> F.Muell.	Australia (Walpole)	B. Barnsley 781 (NSW 403177)	2
<i>Needhamiella pumilio</i> (R.Br.) L.Watson	Australia	J. M. Powell 2771 (NSW 203537)	2
<i>Oligarrhena micrantha</i> R.Br.	SW Australia (SW base of East Mount Barren)	A. N. Rodd & J. McCarthy 5103 (NSW 484132)	3
<i>Prionotes cerinthoides</i> R.Br.	Australia (Tasmania)	J. H. Hemsley 6546 (NSW 438221)	3
<i>P. cerinthoides</i> R.Br.	Australia (Tasmania)	A. Moscal 7369 (NSW 363729)	2.5
<i>R. continentis</i> B.L.Burt	Australia (Victoria, Mount Sterling)	Unknown (K 38484)	18
<i>R. dracophylla</i> R.Br.	Australia (Tasmania, Mount Wellington)	R. Melville 2394 (K 38443)	8
<i>R. pandanifolia</i> Hook.f.	Australia (Tasmania)	Unknown (K 11748)	40
<i>Sprengelia incarnata</i> Sm.	Australia (Blue Mountains National Park)	A. J. Whalen & G. Corsini 450 (NSW 500934)	3
<i>S. sprengeioides</i> (R.Br.) Druce	Australia (Queensland, Cooloola National Park)	J. M. Powell & J. Armstrong 947 (AQ 591963)	5
<i>Styphelia laeta</i> subsp. <i>latifolia</i> (R.Br.) J.M.Porter	Australia	R. Brown s.n. (K 11749)	140
<i>Trochocarpa laurina</i> R.Br.	NW New Guinea (Kebbar Valley, Nerto)	Unknown (L)	61
<i>T. laurina</i> R.Br.	New Guinea (Kebbar Valley)	van Royen & Sleumer 6750 (U 3650)	45

*Mature' means that the wood sample is derived from a mature stem, although the exact diameter could not be traced.

* Slides from the permanent slide collection at the Royal Botanic Gardens, Kew, UK.

anatomical terminology follows the 'IAWA list of microscopic features for hardwood identification' (IAWA Committee, 1989).

Since all three types of non-perforated tracheary elements, tracheids, fibre-tracheids and libriform fibres, are present in Ericaceae *s.l.*, and intermediate cell types frequently occur in this family (e.g. Baas, 1979), it may be difficult in some instances to determine the true nature of

a cell. We consider tracheids to be long and narrow cells, with dense pitting on both radial and tangential walls (approx. 15–50 pits per 100 µm of tracheid length). These pits are distinctly bordered and form two or three longitudinal rows on the radial and tangential walls. Tracheids are relatively rare in epacrids and have usually thin to thick walls. Fibre-tracheids on the other hand, represent the most common cell type of the ground tissue. They are somewhat

tracheids. They are narrow, mostly thin-walled, septate or non-septate, and show only few to very few, indistinctly to minutely bordered pits (sometimes also simple pits) on the tangential walls. Pit borders on the libriform fibres are 2–3 µm in size and their density ranges from less than one to four per 100 µm length. Sometimes only two or three pits are observed near the end of libriform fibres. For all measurements of tracheary elements, only clearly identifiable cells were taken into account.

Wood sections of about 25 µm were cut using a sliding microtome. Most of the material collected was derived from thick, mature stems, but wood from very narrow stems (about 2–3 mm in diameter) was examined for genera that produce very little secondary xylem (e.g. *Needhamiella*, *Oligarrhena* and *Prionotes*). Transverse sections (TS) were cut using two pieces of polystyrene foam to support the tiny samples. To make tangential (TLS) and radial (RLS) longitudinal sections of these thin stems, the sample was mounted using superglue on a rectangular piece of wood that was clamped in the microtome holder. The entire thickness of the wood sample could then be used to produce longitudinal sections. After bleaching, staining and dehydrating, tissues were mounted in Canada balsam. The techniques of Jansen *et al.* (1998) were followed to prepare samples for maceration and SEM. Wood features were plotted on trees using the program MacClade 4.01 (Maddison and Maddison, 2001). Graphics were made with CA CricketGraph III version 1.5.

The wood samples studied are listed in Table 2 with reference to the origin, collector, and the diameter of the wood sample.

WOOD DESCRIPTIONS

The material studied is described according to the classification *sensu* Crayn *et al.* (1998). For each genus examined, the nominator gives the number of species studied and the denominator is the total number of species. Numbers in parentheses are mean values. A summary of the most important results is presented in Table 3.

Prionoteae (*Prionotes* 1/1; Fig. 1A–E)

Growth rings with distinct boundaries (Fig. 1A). Diffuse-porous (Fig. 1A and B). Vessels predominantly solitary, sometimes in short radial or tangential multiples (Fig. 1B). Vessel outline angular to rounded (Fig. 1B). Vessel perforation plates exclusively scalariform (Fig. 1D), with 22–(34)–50 bars, intervessel pits opposite, 3–5 µm in diameter, non-vestured. Vessel-ray pits opposite to scalariform (Fig. 1E), 3–10 µm in diameter, with distinct borders. Helical thickenings absent. Vessel lumina 10–(15)–20 µm in tangential diameter, 320–(366)–440 vessels mm⁻², vessel elements 320–(457)–750 µm long. Tracheids common, 340–(460)–670 µm long, pits 3–4 µm in size, pit density on tangential walls 30–45/100 µm. Fibre-tracheids uncommon, fibre pits distinctly bordered, 3–4 µm in diameter, pit density on tangential walls 10–15/100 µm. Fibre-tracheids thin- to thick-walled (Fig. 1B), 380–(477)–600 µm long. Libriform fibres absent. Axial parenchyma scarce and

diffuse, mostly two cells per strand. Rays exclusively uniseriate (Fig. 1C), 180–(307)–480 µm high, consisting of upright ray cells, 13–(17)–22 rays mm⁻¹. Gummy deposits in ray cells. Few crystals observed in the pith of NSW 438221. Pith cells mostly angular, thin-walled (Fig. 1A).

OLIGARRHENEAE (*Oligarrhena* 1/1, *Needhamiella* 1/1; Fig. 1F–I)

Growth ring boundaries indistinct (Fig. 1G). Diffuse-porous (Fig. 1G). Vessels exclusively solitary with angular outlines (Fig. 1F and G). Vessel perforation plates simple (Fig. 1H), a few scalariform perforation plates with two to three bars present in *Oligarrhena* (Fig. 1I). Intervessel pits opposite to alternate, 2–4 µm in diameter, non-vestured, distinctly bordered. Vessel-ray pitting similar to intervessel pits, sometimes scalariform in *Needhamiella* and 7–9 µm in diameter. Helical thickenings absent. Tangential diameter of vessel lumina 6–(10)–13 µm in *Needhamiella* and 10–(14)–20 µm in *Oligarrhena*, 240–(268)–410 vessels mm⁻², length of vessel elements 170–(300)–410 µm. Tracheids present, 230–(305)–380 µm long, pits 3–4 µm in size, pit density on tangential walls 20–30/100 µm. Fibre-tracheids common, pits distinctly bordered, 3–4 µm in diameter, pit density on tangential walls 6–10/100 µm. Fibre-tracheids thick to very thick-walled (Fig. 1F and G), 300–(385)–500 µm long. Libriform fibres absent. Axial parenchyma sparse, diffuse, mostly two cells per strand. Rays exclusively uniseriate, 240–(477)–920 µm high in *Oligarrhena* and 100–(223)–320 µm high in *Needhamiella*, 17–(20)–24 rays mm⁻², composed of upright cells. Gummy deposits in ray cells. Crystals absent in wood and pith. Pith cells oval to angular in *Needhamiella*, oval to circular in *Oligarrhena*, walls remarkably thick (Fig. 1F).

COSMELIEAE (*Andersonia* 2/22, *Cosmelia* 1/1 and *Sprengelia* 2/4; Fig. 2A–G)

Growth ring boundaries indistinct in *Andersonia sprengelioides*, *Sprengelia* (Fig. 2C) and *Cosmelia*, and absent in *A. caerulea*. Wood diffuse-porous (Fig. 2C). Vessels predominantly solitary, sometimes in short tangential multiples in *Cosmelia* (Fig. 2B) and *Sprengelia*. Vessel outline angular (Fig. 2B and C). Perforations scalariform with 8–(25)–40 bars in *Sprengelia* (Fig. 2E) and *Cosmelia*, mainly simple in *Andersonia* (Fig. 2F), but few scalariform perforations with one to two bars in *A. sprengelioides*. Intervessel pits opposite, 2–5 µm in diameter, non-vestured, distinctly bordered. Vessel-ray pits opposite to scalariform (Fig. 2G), 3–10 µm in diameter, distinctly bordered. Helical thickenings absent. Vessel lumina 8–(13)–20 µm in tangential diameter, 320–(528)–780 vessels mm⁻², length of vessel elements 250–(483)–650 µm. Tracheids present, 340–(428)–560 µm long, pits 3–5 µm in size, pit density on tangential walls 20–30/100 µm. Fibre-tracheids common, with distinctly bordered pits, 3–5 µm, thin- to thick-walled (Fig. 2B and C), 340–(612)–1040 µm long, pit density on tangential walls 7–10/100 µm. Libriform fibres rare in all species, non-septate, with few indistinctly bordered pits, pit density <1–2/100 µm on tangential walls. Axial paren-

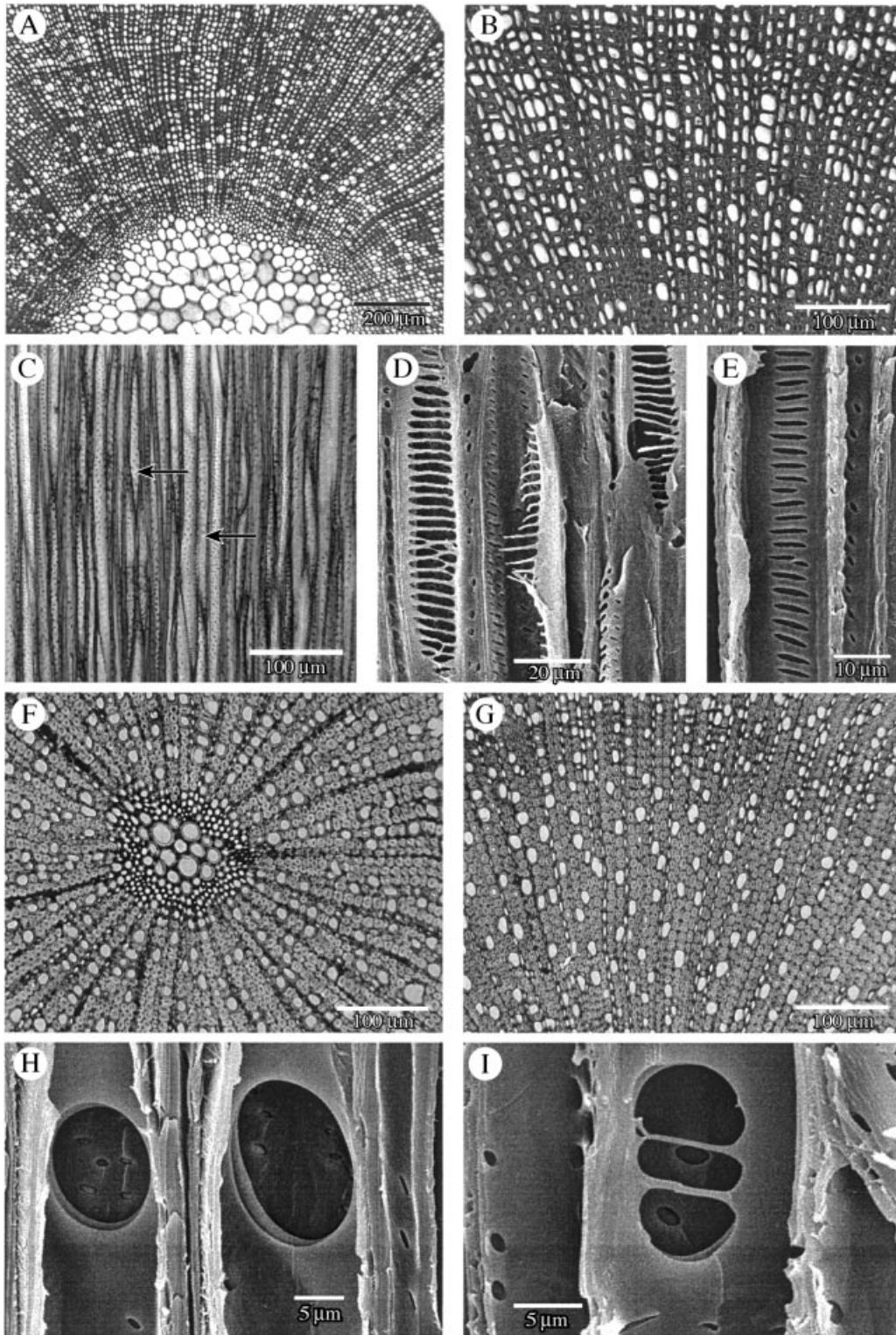


FIG. 1. A–E, *Prionotes cerinthoides*. A, Transverse section (TS), pith and wood. B, TS, indistinct growth rings, mainly solitary vessels. C, Tangential longitudinal section (TLS), narrow vessel elements and exclusively uniseriate rays (arrows). D, Radial longitudinal section (RLS), scalariform perforations with many bars. E, RLS, scalariform vessel-ray pitting. F, *Oligarrhena micrantha*: TS, thick-walled pith cells. G and H, *Needhamiella punilio*. G, TS, solitary vessels, thick- to very thick-walled fibres. H, RLS, two simple perforations. I, *O. micrantha*: RLS, scalariform perforation with two bars.

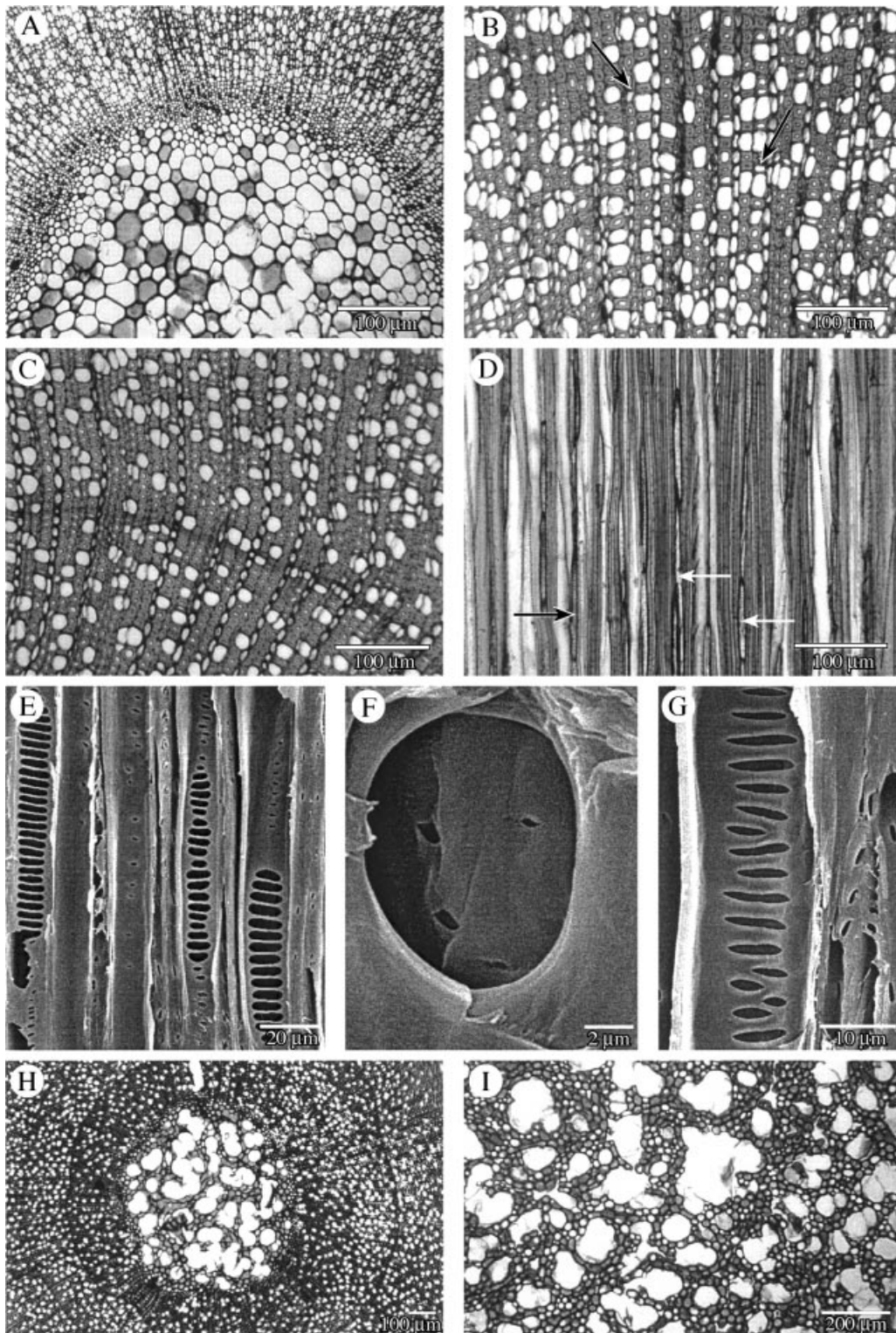


FIG. 2. A and B, *Cosmelia rubra*. A, TS, pith and wood. B, TS, vessels solitary or in small tangential multiples, scanty paratracheal parenchyma (arrows). C, *Sprengelia incarnata*: TS, narrow and mainly solitary vessels, exclusively uniseriate rays. D, *C. rubra*: TLS, exclusively uniseriate rays. E, *S. incarnata*: RLS, scalariform perforations with many bars. F, *Andersonia sprengelioides*: RLS, simple perforation plate. G, *S. incarnata*, RLS, scalariform vessel-ray pitting. H, *Dracophyllum subulatum*: TS, pith and wood. I, *Richea continentis*: TS, small pith cells scattered between larger, thin-walled pith cells.

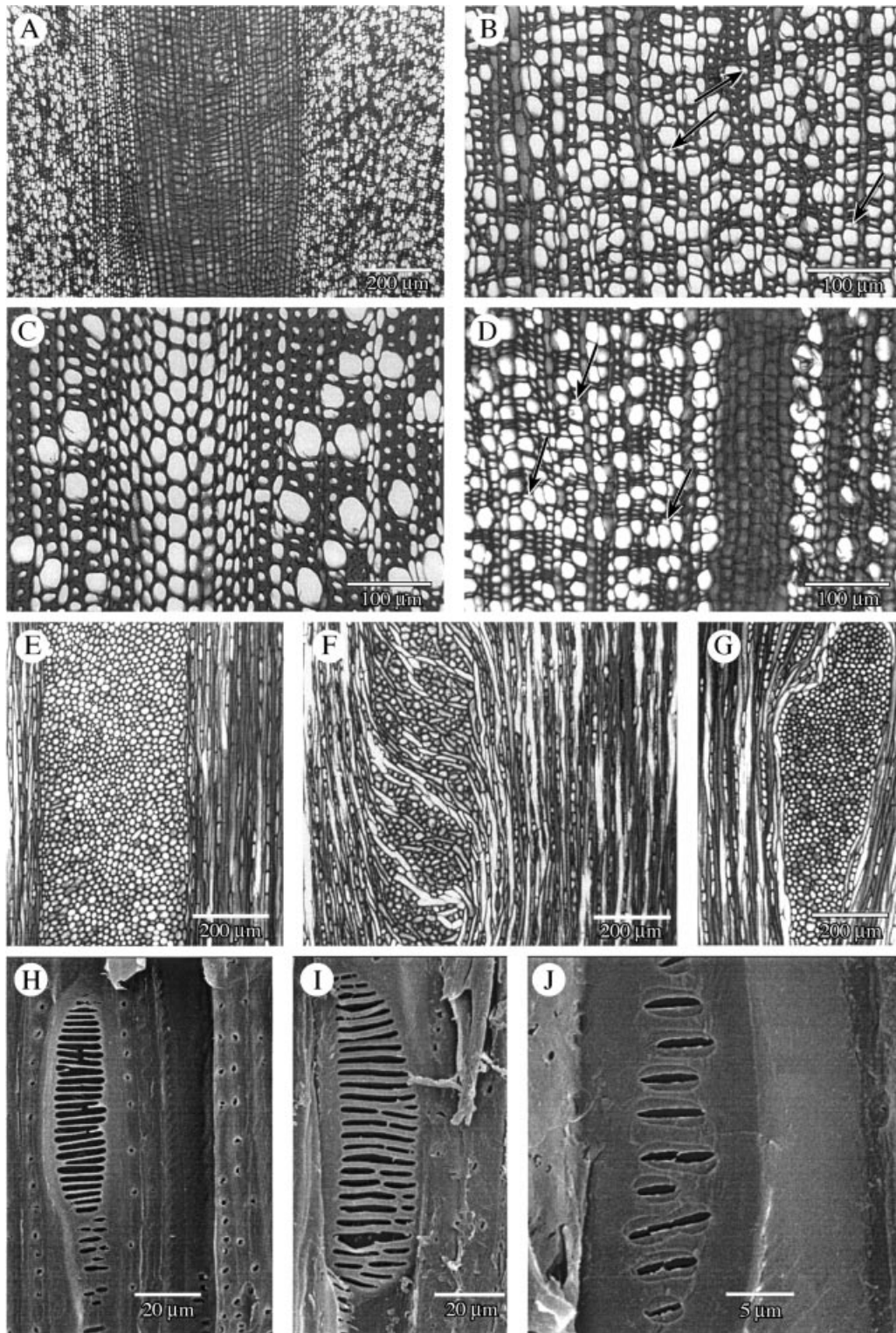


FIG. 3. A and B, *Dracophyllum strictum*. A, TS, very wide multiseriate ray. B, TS, vessels solitary or in small tangential groupings, scanty paratracheal parenchyma (arrows). C, *D. verticillatum*: TS, relatively wide vessels with low frequency. D, *Richea continentis*: TS, vessels narrow and dense, scanty paratracheal parenchyma (arrows). E, *D. strictum*: TLS, very wide multiseriate ray. F, *D. oliveri*: TLS, aggregate ray. G, *R. continentis*: TLS, very wide multiseriate ray. H, *D. uniflorum*: RLS: scalariform perforation. I, *R. pandanifolia*: RLS, scalariform perforation. J, *D. strictum*: RLS, opposite to scalariform vessel-ray pitting with distinct borders.

chyma very rare, paratracheal (Fig. 2B and C), two to three cells per strand. Rays exclusively uniseriate (Fig. 2D), 140–(442)–1000 μm high, composed of upright cells, 16–(20)–26 rays mm^{-1} . Gummy deposits in ray cells. Prismatic crystals and druses in pith parenchyma, no crystals in wood. Pith cells mostly angular, smaller cells scattered between larger cells, thin-walled (Fig. 2A).

Richeae (*Dracophyllum* 11/48, *Richea* 3/11; Figs 2H, I and 3A–J)

Growth ring boundaries distinct. Typically diffuse-porous (Fig. 3D), semi-ring-porous in *D. palustre*. Vessels mostly solitary, sometimes in short radial and/or tangential multiples of two to four (Fig. 3A–D). Vessel outline angular (Fig. 3B–D). Vessel perforation plates scalariform (Fig. 3H and I) with 8–(22)–78 bars. Intervessel pits opposite in *Richea*, and opposite to scalariform in *Dracophyllum*, pit size 3–5 μm in *Richea* and 3–7 μm in *Dracophyllum*, non-vestured. Vessel-ray pitting opposite to scalariform, 3–13 μm in diameter, distinctly bordered (Fig. 3J). Helical thickenings present in vessel element tails in *D. urvilleanum* and *D. verticillatum*, sometimes throughout body of vessel elements in *R. continentis*, absent in other species. Vessel lumina 8–(18)–40 μm in tangential diameter, 94–(387)–680 vessels mm^{-2} , 210–(452)–950 μm long. Tracheids sparsely present, 320–(454)–700 μm long, pit size 3–6 μm , pit density on tangential walls 25–30/100 μm . Tracheids lacking in *D. oliveri*, *D. palustre*, *D. uniflorum*, *D. urvilleanum* and *D. verticillatum*. Fibre-tracheids common, usually thin- to thick-walled, but sometimes also very thin- or very thick-walled, fibre length 270–(594)–1170 μm , pits distinctly bordered and 3–6 μm in diameter, pit density on tangential walls 7–10/100 μm . Libriform fibres uncommon, sometimes septate, and observed in *D. longifolium*, *D. traversii*, *D. urvilleanum* and *R. continentis*, pits 2–3 μm in size, pit density on tangential walls 1–4/100 μm . Axial parenchyma mostly scanty paratracheal (Fig. 3B–D), sometimes also diffuse to diffuse-in-aggregates, two–four cells per strand. Uniseriate rays very common, 150–(453)–1550 μm high, consisting of upright cells, 7–(15)–26 rays mm^{-1} . Multiseriate rays rare, 5- to 22-seriate (Fig. 3E–G), absent in *R. dracophylla*, 800–(2871)–12 500 μm high, consisting of mostly procumbent and square body ray cells and more than four marginal ray cells, up to one multiseriate ray mm^{-1} , and sometimes two rays mm^{-1} in *D. traversii*, sheath cells present in *D. verticillatum*. Aggregate rays in few species of *Dracophyllum* (Fig. 3F). Gummy deposits in ray cells. Prismatic crystals rare in multiseriate rays. Pith cells of two different types: small groups of larger cells with very thin walls clustered between smaller cells with thicker walls (Fig. 2H and I).

Epacrideae (*Epacris* 2/35; Fig. 4A–E)

Growth ring boundaries indistinct or distinct (Fig. 4B). Diffuse-porous (Fig. 4B). Vessels exclusively solitary, vessel outline angular. Vessel perforation plates scalariform with 5–11 bars (Fig. 4D and E). Intervessel pits opposite to

alternate, 2–4 μm in size, non-vestured. Vessel-ray pits similar to intervessel pits in size and shape. Helical thickenings sometimes present, throughout body of vessel elements or only in vessel element tails. Tangential diameter of vessel lumina 12–(16)–22 μm , 215–(242)–265 vessels mm^{-2} , vessel elements 360–(475)–590 μm long. Tracheids not observed. Fibre-tracheids common, thin- to thick- to very thick-walled (Fig. 4B), 420–(661)–780 μm long with distinctly bordered pits, pits 3–4 μm in diameter, pit density on tangential walls 7–10/100 μm . Libriform fibres uncommon, septate, pits 2–3 μm in size, pit density on tangential walls 1–2/100 μm . Axial parenchyma rare, diffuse, two to three cells per parenchyma strand. Rays exclusively uniseriate (Fig. 4C), 250–(593)–850 μm high, consisting of upright cells, 9–(12)–13 rays mm^{-1} . Gummy deposits in ray cells. Crystals absent. Prismatic crystals in pith of *E. impressa*. Pith cells mostly angular, sometimes circular, thin-walled (Fig. 4A).

STYPHELIEAE (*Cyathodes* 1/3, *Leptecophylla* 2/12, *Leucopogon* 6/150, *Monotoca* 2/11, *Styphelia* 1/12, *Trochocarpa* 1/12; Figs 4F–I and 5A–I)

Growth rings indistinct (Fig. 4G), but distinct in *Monotoca elliptica* (K 11747). Diffuse-porous. Vessels mostly solitary (Fig. 4G–I), sometimes in short tangential multiples in *Leptecophylla* and in short radial multiples in *Monotoca elliptica*, *Leucopogon fasciculatus*, and in *Leptecophylla juniperina*. Vessel outline angular (Fig. 4G–I). Vessel perforation plates mostly simple (Fig. 5C and E), 10 % of the vessel perforations scalariform with one to three bars in *Leptecophylla* sp., 40 % scalariform with 1–17 bars in *Trochocarpa laurina*, 60 % scalariform with two to five bars in *Leucopogon fasciculatus*, 60 % scalariform with 2–11 bars in *Styphelia laeta*, 55–70 % scalariform with one to ten bars in *M. elliptica* and 75 % scalariform with three to seven bars in *M. tamariscina*. Intervessel pits mostly alternate in *Cyathodes*, *Leptecophylla* and *Trochocarpa*, alternate to opposite in *Monotoca*, *Styphelia* and *Leucopogon*, and sometimes also scalariform in *Leucopogon fasciculatus* and *L. malayanus*. Intervessel pits 2–5 μm in size, distinctly bordered, but scalariform pits in *L. malayanus* up to 8 μm . Vessel-ray pits generally similar to intervessel pits in arrangement, mainly alternate and sometimes opposite in *Cyathodes*, *Leptecophylla*, *Leucopogon* (Fig. 5B) and *Trochocarpa*, opposite to alternate in *Styphelia laeta* and *M. elliptica* (Fig. 5F), and sometimes also rarely scalariform in species of *Cyathodes*, *Monotoca* and *Leucopogon*. Vessel-ray pits 2 μm in diameter in *Leucopogon*, *Leptecophylla*, *Monotoca* and *Trochocarpa*, large scalariform pits up to 16 μm in *Leucopogon malayanus*. Helical thickenings only in vessel element tails in *Leucopogon parviflorus*, *L. richei* and *Trochocarpa laurina*, throughout the body of vessel elements in *Leptecophylla juniperina* (Fig. 5C) and *L. tameia-meiae*; sometimes with grooves on the inner vessel walls of *Monotoca* (Fig. 5F). Tangential diameter of vessel lumina 15–(33)–60 μm , 14–(115)–440 vessels mm^{-2} , vessel element lengths 180–(432)–950 μm . Tracheids in all species, 250–(572)–1060 μm long, pits 3–5 μm in size, pit density on

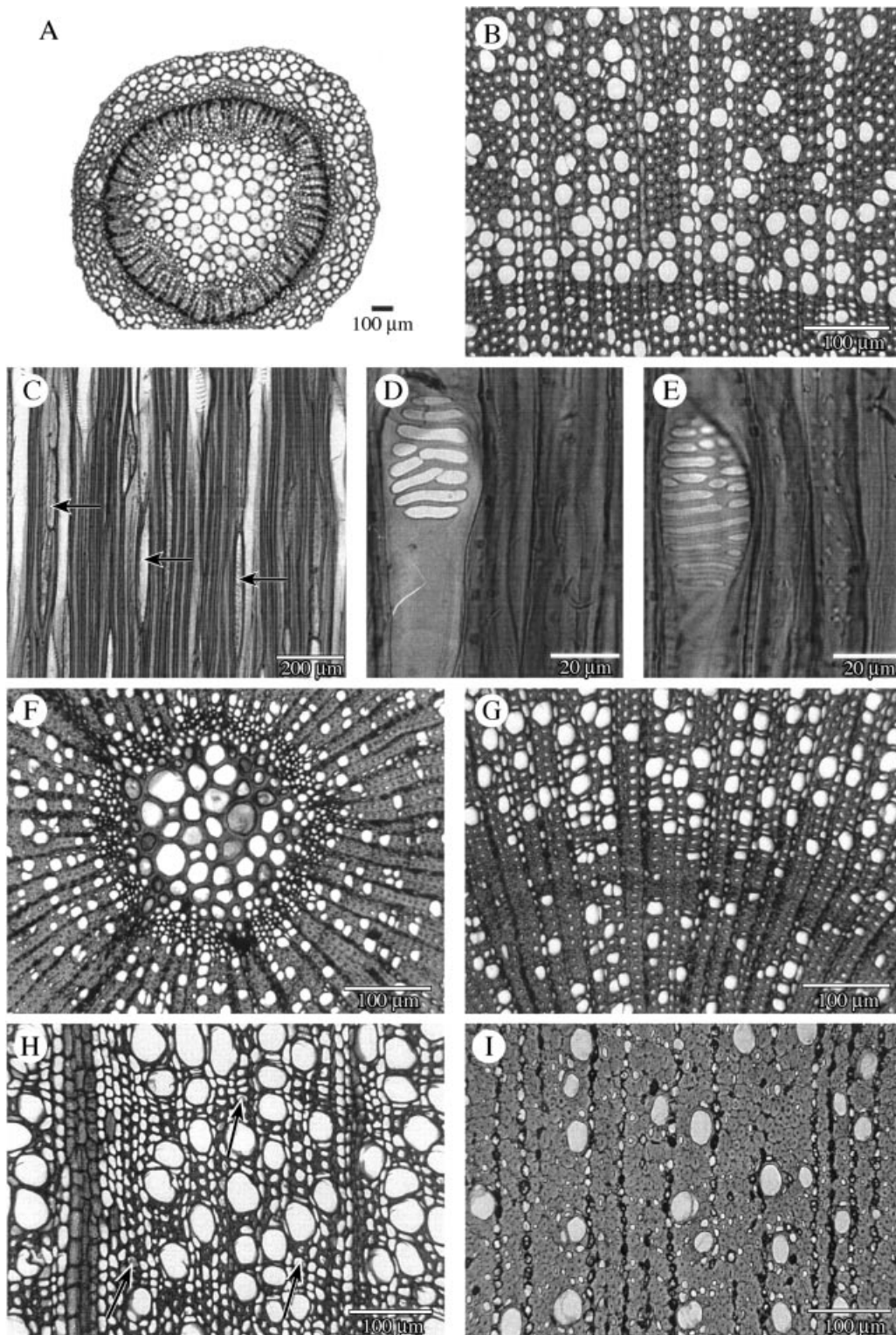


FIG. 4. A, *Epacris miniata*: TS, young stem. B–E, *E. impressa*. B, TS, distinct growth ring, solitary vessels. C, TLS, exclusively uniseriate rays (arrows). D and E, RLS, irregular scalariform perforation plate. F and G, *Monotoca tamariscina*. F, TS, thick-walled pith cells. G, TS, solitary vessels. H, *Leptocophylla tameiameiae*: TS, vessels wide and solitary, axial parenchyma diffuse-in-aggregates (arrows). I, *Cyathodes glauca*: TS, vessels solitary, very thick fibre walls, diffuse-in-aggregates axial parenchyma.

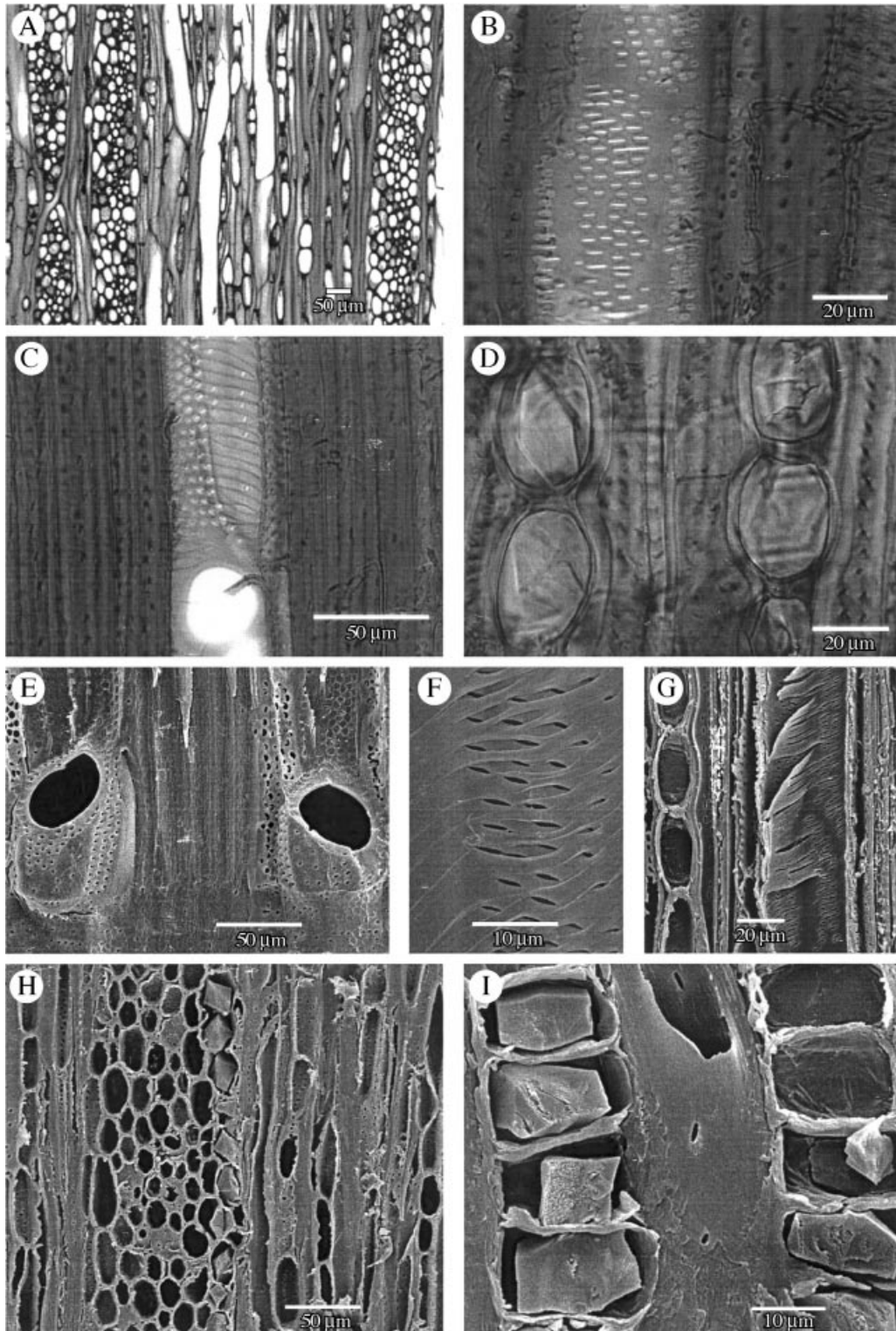


FIG. 5. A, *Monotoca elliptica*: TLS, uni- and multiseriate rays. B, *Leucopogon richei*: RLS, mainly alternate vessel-ray pitting with distinct borders. C, *Leptecophylla juniperina*: RLS, simply perforated vessel with helical thickenings. D, *Leucopogon parviflorus*: RLS, crystals in axial parenchyma cells showing thickened walls. E, *Leucopogon fasciculatus*: RLS, two simple perforations. F, *Monotoca elliptica*: RLS, grooves interconnecting alternate vessel-ray pits. G, *Trochocarpa laurina*: RLS, axial parenchyma cells with thickened walls (crystals removed). H, *L. richei*: TLS, crystal bearing axial parenchyma strand next to multiseriate ray. I, *Leptecophylla* sp.: RLS, crystals in chambered axial parenchyma cells.

tangential walls 20–30/100 μm . Fibre-tracheids common, with distinctly bordered pits, thin- to thick-walled (Fig. 4G and H), very thick-walled in *Cyathodes glauca* (Fig. 4I), 450–(823)–1300 μm long, pits 3–5 μm in diameter, pit density on tangential walls 6–10/100 μm . Libriform fibres sometimes present in *Monotoca*, *Leucopogon parviflorus*, *L. richei* and *Cyathodes*, septate or non-septate, pits 2–3 μm in size, pit density on tangential walls 1–4/100 μm . Axial parenchyma common, diffuse-in-aggregates (Fig. 4H and I), two to four cells per strand, up to five cells in *Styphelia laeta*. Uniseriate rays common (Fig. 5A), 150–(544)–1100 μm high, homogeneous consisting of upright cells, 4–(9)–23 mm^{-1} . Multiseriate rays 3–5-seriate (Fig. 5A), 7–9-seriate in *L. richei*, and 9–17-seriate in *Styphelia laeta*, 350–(1400)–4100 μm high, procumbent and square body ray cells with one to over four rows of upright marginal cells, 0–(3)–6 mm^{-1} , very few multiseriate rays in *Monotoca tamariscina*, sheath cells in all species and mostly indistinct. Gummy deposits in ray cells (Fig. 4I). Large prismatic crystals in chambered axial parenchyma cells near multiseriate rays (Fig. 5D, G–I), crystals present in pith cells of *L. lanceolata*, crystals absent in *Cyathodes glauca* and in *M. tamariscina*. Pith cells oval to circular with unusually thick walls in *L. lanceolata*, pith cells angular to oval with thin walls in *Styphelia malayana*, pith cells round to angular with remarkably thick walls in *M. tamariscina* (Fig. 4F).

DISCUSSION

Characteristic features of the wood structure of epacrids

A typical epacrid wood shows growth rings, diffuse porosity and solitary, narrow vessels usually ranging from 10 to 40 μm in tangential diameter. The narrowest vessels are only 6 μm in *Needhamiella pumilio*, while vessels up to 60 μm occur in several species of Styphelieae. A similar variability is found with respect to vessel density, which usually ranges from 50 to 450 vessels per mm^2 . Extremely high values (more than 500 per mm^2) occur in Richeeae and Cosmelieae. The length of vessel elements is commonly between 250 and 600 μm . Vessels have scalariform or simple perforation plates; both types are found in *Andersonia*, *Leptecophylla*, *Leucopogon*, *Monotoca*, *Oligarrhena*, *Styphelia* and *Trochocarpa*, although one type usually dominates. In general, intervessel pits are distinctly bordered, and opposite to scalariform in species with scalariform perforations, or opposite to alternate in species with simple perforations. Vessel-ray pitting is similar to intervessel pitting. The fibre-tracheids are characteristically non-septate (Butterfield and Meylan, 1976), with distinctly bordered pits and often thick- to very thick walls. Tracheids are generally present. Few septate or non-septate thin-walled libriform fibres with few simple to indistinctly bordered pits occur in several genera. The axial parenchyma is sparsely diffuse with a tendency to scanty paratracheal in Richeeae, Cosmelieae and in *M. tamariscina*, but in Styphelieae the most common axial parenchyma type is diffuse-in-aggregates. Uniseriate rays consisting of upright cells are always present and mostly occur in combination with heterocellular, multiseriate rays, which

consist of procumbent to square body ray cells and one or several rows of upright or square marginal ray cells. Exclusively uniseriate rays are present in *Epacris* and in the tribes Cosmelieae, Oligarrheneae and Prionoteae. Multiseriate rays are in general three to ten cells wide. In Richeeae, however, more than 20-seriate rays are observed. The height of uniseriate rays is generally between 200 and 800 μm , while multiseriate rays are much higher (mostly between 600 and 3500 μm), with very tall rays in species of Richeeae and *Leucopogon*. Gummy deposits (possibly tannins) are frequently observed in ray cells. Crystals occur in chambered axial parenchyma cells of Styphelieae (except in *Cyathodes glauca* and *Monotoca tamariscina*), but only occur in ray cells of three species belonging to the tribe Richeeae.

In general, the present results agree very well with the family description presented by Metcalfe and Chalk (1950), and only small differences can be noticed. Features in the wood of epacrids that were not observed in this study are the presence of horizontal resin plates in *Dracophyllum*, and secretory cells in unlignified tissues of several genera. Furthermore, the occasional occurrence of septate libriform fibres is not restricted to *Lysinema*, *Monotoca*, *Sprengelia* and *Epacris*, but has also been found in several other taxa of Cosmelieae, Richeeae and Styphelieae. Although we did not obtain fresh material which would be necessary to observe living libriform fibres, we suggest that epacrids retain their living protoplast in the few thin-walled fibres with few indistinctly bordered pits. There are no reports of living protoplasts in the literature with respect to epacrids, but this feature has been observed in similar libriform fibres of the sister group Vaccinioideae (Braun, 1961; Fahn and Leshem, 1962; Luteyn, 1983; pers. obs.). Meylan and Butterfield (1978) observed uniseriate and 2–3-seriate rays in *Dracophyllum longifolium* and *D. traversii* as well as very conspicuous rays, although the narrow multiseriate rays were not reported in this study. Moreover, we did not observe sclerosed walls of the crystalliferous cells in *Monotoca* and *Trochocarpa* (Chattaway, 1956).

Wood anatomical comparison with other Ericaceae s.l.

The wood structure of the epacrids shows many similarities to that of other Ericaceae *s.l.* Examples are the presence of diffuse porosity, narrow and solitary vessels with an angular vessel outline, high vessel frequency, scalariform and/or simple perforations, tracheids, distinctly bordered fibre pits (fibre-tracheids), sparsely apotracheal to paratracheal axial parenchyma, and the combination of uniseriate rays with less common multiseriate rays.

It is noteworthy that the wood anatomy of the epacrids (subfamily Styphelioideae) especially corresponds with that of subfamily Vaccinioideae, to which epacrids are closely related according to molecular data (Kron *et al.*, 2002). One feature in particular may support the relationship between both groups, namely the occurrence of wide and high multiseriate rays, both of which are nearly absent in other taxonomic groups of the family. In addition, libriform fibres occur sporadically in both subfamilies, although these fibres are also observed in the distantly related subfamily

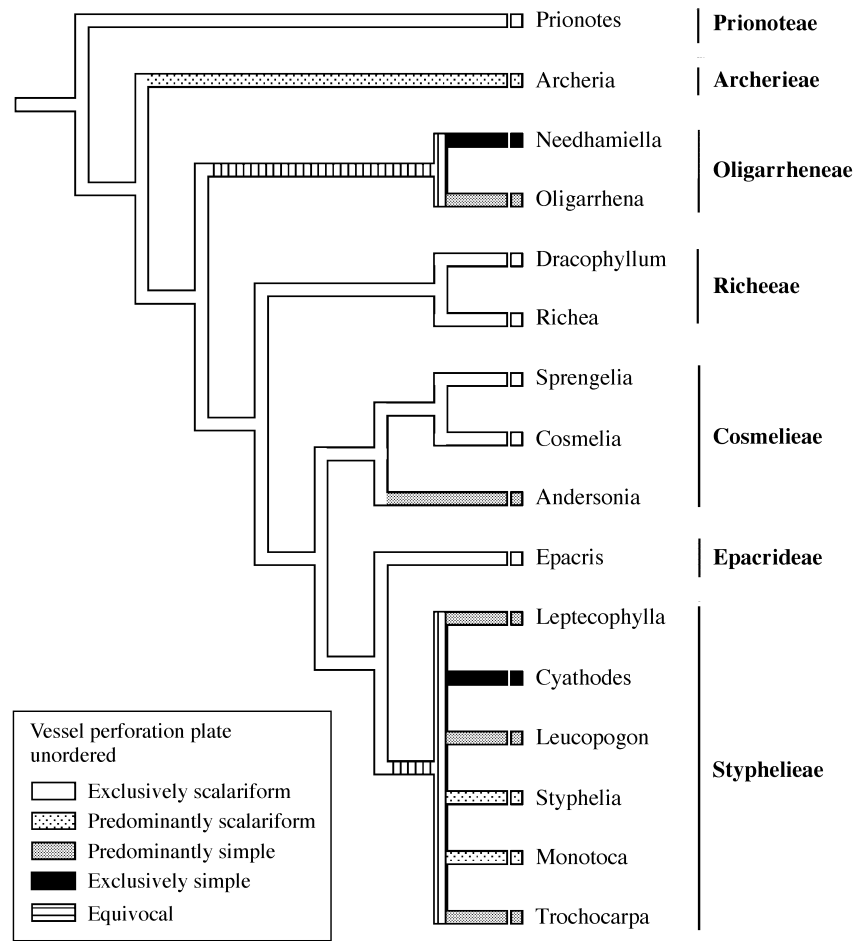


FIG. 6. Type of vessel perforation plates in the epacrid genera based on the molecular phylogenetic studies of Crayn *et al.* (1998) and Crayn and Quinn (2000).

Arbutioideae (pers. obs.). A feature that is also shared by Styphelioideae, Vaccinioideae and Arbutioideae appears to be the presence of crystal-bearing axial parenchyma cells (pers. obs.).

The distribution of axial parenchyma may be used to distinguish between Vaccinioideae and Styphelioideae, since all Vaccinioideae genera are characterized by scanty paratracheal parenchyma, whereas epacrids mostly have diffuse(-in-aggregates) axial parenchyma, except for Cosmelieae and Richeeae. However, these two tribes can be readily distinguished from Vaccinioideae by the width of their rays (exclusively uniseriate and very wide multiseriate rays, respectively). In Vaccinioideae, extremely narrow (i.e. exclusively uniseriate) or wide (>15-seriate) rays do not occur in the secondary xylem of mature stems (Metcalf and Chalk, 1950; pers. obs.).

Systematic and phylogenetic aspects

Although several genera cannot be distinguished clearly from each other based on wood anatomical features alone, the secondary xylem of epacrids provides useful information for confirming or negating already proposed relation-

ships owing to the consistency of several characters at the tribal level (Crayn *et al.*, 1998). Although tribal relationships are not yet completely understood, we have plotted the four most important wood anatomical features within epacrids on a tree that is based on the molecular results presented by Crayn and co-workers (Crayn *et al.*, 1998; Crayn and Quinn, 2000), and which shows only the genera included in this study together with the genus *Archeria*. These four taxonomically significant wood features are: type of perforation plate (Fig. 6); distribution of axial parenchyma (Fig. 7); width of rays (Fig. 8); and the presence and location of prismatic crystals (Fig. 9). A discussion of the wood anatomical variation within and between the various tribes is presented below.

According to *rbcL* data, the tribes Prionoteae and Archerieae take the most basal position within Styphelioideae, although the primitive status of the Archerieae is doubtful based on *matK* sequence data. Exclusively scalariform vessel perforation plates with many bars in *Prionotes* and predominantly scalariform perforations in *Archeria* (Fig. 6) may indicate their primitive position, although the type of vessel perforation plates may also be associated with ecological aspects (see below).

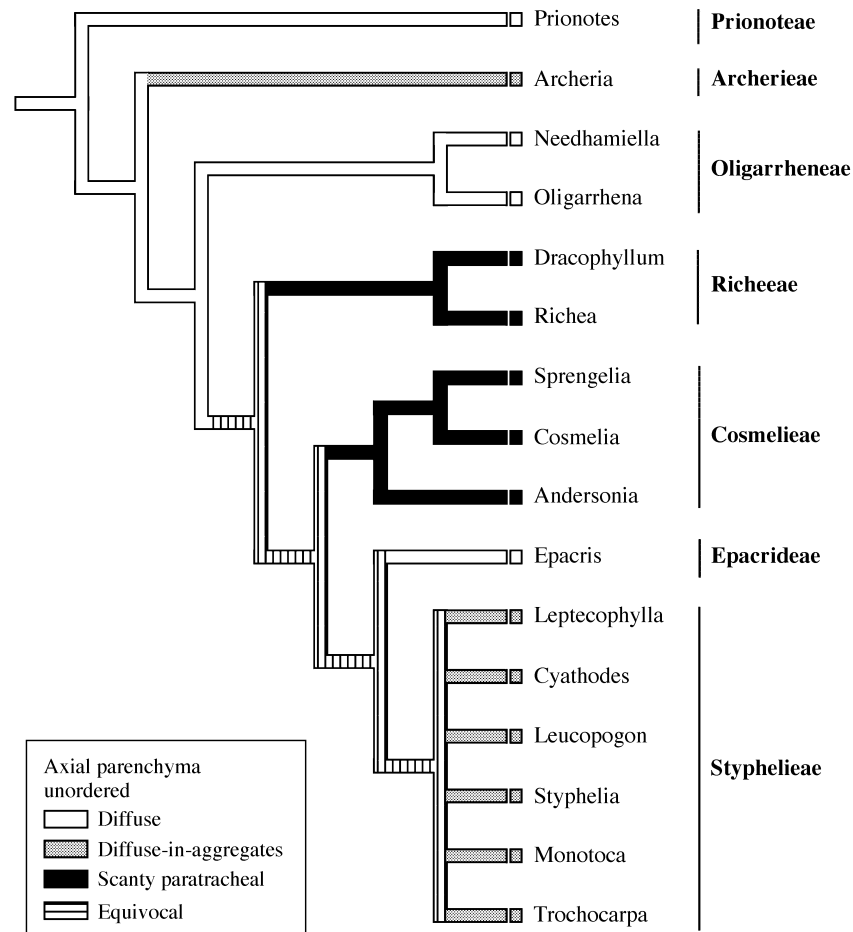


FIG. 7. Main axial parenchyma types in the epacrid genera based on the molecular phylogenetic studies of Crayn *et al.* (1998) and Crayn and Quinn (2000).

Furthermore, Metcalfe and Chalk (1950) recorded ‘numerous bars’ in the perforations of the genus *Lebetanthus* (Prionoteae). *Prionotes* has rather long vessel elements, opposite to scalariform intervessel and vessel-ray pitting, sporadic diffuse axial parenchyma (Fig. 7) and exclusively uniseriate rays (Fig. 8), which appear to be primitive features within epacrids. The high proportion of tracheids and relatively low proportion of fibre-tracheids in this genus may be the result of its climbing habit, a condition that is not found elsewhere in epacrids. Although wood of *Archeria* was not available to us, the data presented by Meylan and Butterfield (1978) show that most features agree with *Prionotes*, which could reveal its primitive status. The only noteworthy differences in *Archeria* are the axial parenchyma distribution, which is diffuse, diffuse-in-aggregates and scanty paratracheal, and the occasional occurrence of simple perforations and biseriate rays (Figs 6–8).

The wood anatomical structure of the two genera of the Oligarrheneae, *Oligarrhena* and *Needhamiella*, is very similar. Characteristic features include very narrow vessel elements with mainly simple perforation plates (Fig. 6), opposite to alternate vessel pitting, sparsely diffuse axial

parenchyma (Fig. 7), exclusively uniseriate rays (Fig. 8) and remarkably thick pith parenchyma walls. The presence of mainly simple perforations and alternate vessel pitting, two features that are also seen in the former relatives of Styphelieae, could point to an advanced taxonomic position within the subfamily. However, this is not demonstrated by *rbcL* or by *matK* data.

According to the latest *rbcL* data, the tribe Oligarrheneae should be enlarged by the inclusion of *Monotoca tamariscina*, a former member of Styphelieae, which is strongly nested near *Oligarrhena* and *Needhamiella* (E. Brown, pers. com.). Considering wood anatomy, the inclusion of *M. tamariscina* reduces the homogeneity of Oligarrheneae owing to the presence of a high percentage of scalariform perforation plates, mainly opposite vessel-ray pits, and sparse, scanty paratracheal axial parenchyma. However, these differences are far from obvious: perforation plates can be influenced by environmental factors (see ecological aspects), and alternate vessel pitting and sparse axial parenchyma are also observed in *M. tamariscina*. Furthermore, it is plausible that *M. tamariscina*, unlike *M. elliptica*, does not fit within Styphelieae because of the

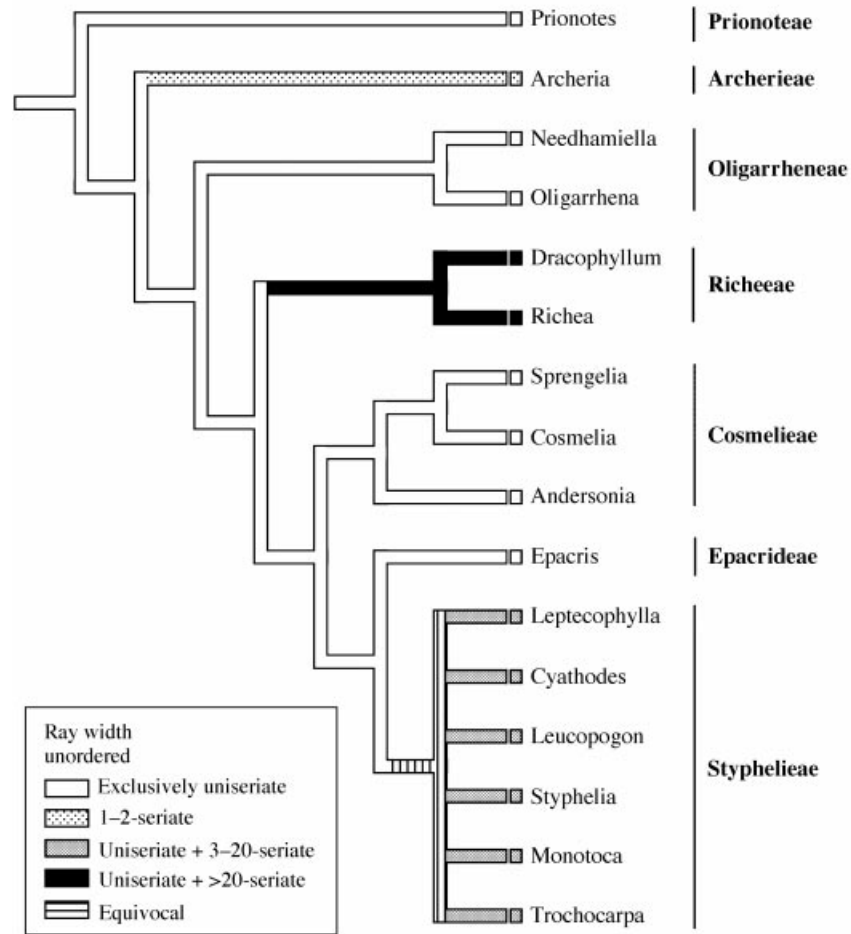


FIG. 8. Ray width in the epacrid genera based on the molecular phylogenetic studies of Crayn *et al.* (1998) and Crayn and Quinn (2000).

lack of crystals in chambered axial parenchyma cells, and the sparsely axial parenchyma. Moreover, some quantitative characters in *M. tamariscina*, such as the tangential vessel diameter, vessel frequency and height of multiseriate rays, clearly differ from those of other Styphelieae, although this may also be related to the narrow stem from which the wood sample was taken.

Cosmelieae and Richeeae are characterized by a scanty paratracheal distribution of axial parenchyma (Fig. 7) and a very high vessel density. However, the two tribes can easily be distinguished from each other by the presence of very wide and high multiseriate rays and the sparse occurrence of prismatic crystals in ray cells of Richeeae (Figs 8 and 9). Furthermore, *Richea* and *Dracophyllum* have a peculiar pith parenchyma consisting of small cells with thickened walls and groups of large cells with very thin walls, which is also observed in *Andromeda* and *Zenobia* (Andromedeae *s.s.*, Vaccinioideae; pers. obs.). The three genera constituting the Cosmelieae share exclusively uniseriate rays and pith parenchyma cells with prismatic crystals and, to a lesser extent, druses. Nevertheless, similar crystals in the pith are also reported in other epacrid genera such as *Dracophyllum*, *Richea*, *Epacris*, *Prionotes*, *Leucopogon* and *Coleanthera*,

and more observations on mineral inclusions in different plant tissues are required to investigate their systematic significance (Curtis, 1941; Metcalfe and Chalk, 1950). A possible sister relationship of Cosmelieae with Styphelieae, which is based on *matK* data (Kron *et al.*, 2002), is wood anatomically unlikely owing to major differences in the wood structure, for instance vessel pitting, the structure of rays and the presence/absence of crystals.

Although molecular data do not show a relationship between Epacrideae and Oligarrheneae, several characters in the secondary xylem of *Epacris* indicate similarities with *Oligarrhena* and *Needhamiella*, namely opposite to alternate intervessel pitting, diffuse axial parenchyma, exclusively uniseriate rays and absence of prismatic crystals in the wood (Figs 7–9). Two characters that seem to differentiate the two clades are the structure of the perforation plate (Fig. 6) and the thickness of the pith parenchyma walls. Metcalfe and Chalk (1950) described perforation plates in *Woollisia* (Epacrideae) as exclusively scalariform with more than 20 bars, but as predominantly simple in *Lysinema* (Epacrideae). Although *Archeria* has previously been placed within Epacrideae, wood anatomical features contradict this close relationship because of the opposite

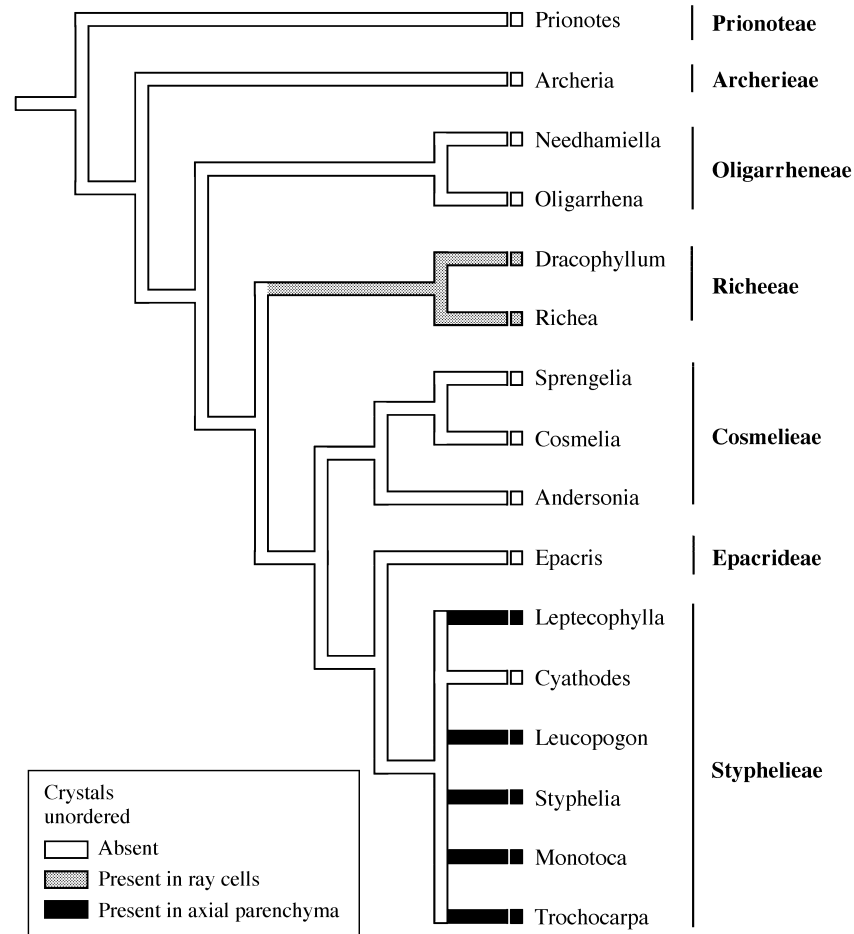


FIG. 9. Presence and location of prismatic crystals in the epacrid genera based on the molecular phylogenetic studies of Crayn *et al.* (1998) and Crayn and Quinn (2000).

vessel pitting, various axial parenchyma distribution and the occasional occurrence of biseriata rays in *Archeria* (Watson, 1967; Meylan and Butterfield, 1978; Powell *et al.*, 1996). The latter character, however, is also reported by Etienne (1917) in *Lysinema* (tribe Epacrideae). More genera of Epacrideae need to be examined to reveal the diversity in wood anatomy within the tribe and to make further conclusions about tribal relationships.

There is significant wood anatomical evidence to suggest that Styphelieae is the most advanced tribe within epacrids. Simple vessel perforation plates are common in this group, but some species have simple perforation plates in combination with the sporadic occurrence of scalariform perforation plates with generally few bars, for instance in *Leptecophylla*, *Leucopogon* and *Trochocarpa* (Fig. 6). On the other hand, *Pentachondra* has exclusively scalariform vessel perforation plates (Metcalf and Chalk, 1950). The relatively high number (10–20+) bars in the scalariform perforations of *Pentachondra* may form an additional ‘non-styphelian’ character alongside other morphological features. However, scalariform perforation plates in *Pentachondra* may also have a functional explanation

since this genus grows in subalpine to alpine habitats (see below). Several authors have suggested maintaining *Pentachondra* as sister genus to the remaining Styphelieae (Smith-White, 1948, 1955; Watson, 1962; Weiller *et al.* 1994; Crayn *et al.*, 1998). Other wood anatomical features that characterize the tribe Styphelieae include relatively wide vessel elements, alternate vessel pitting, diffuse-in-aggregates axial parenchyma, and uniseriate rays occurring together with multiseriate rays containing sheath cells (Figs 7 and 8). Most remarkable is the presence of large prismatic crystals in chambered axial parenchyma cells in nearly all species of the Styphelieae studied (Fig. 9). This feature is also present in *Acrotliche*, which is included in this tribe (Metcalf and Chalk, 1950).

Ecological and functional considerations

As mentioned in the Introduction, epacrids occur in a wide range of habitats and climates, and these environmental conditions need to be considered when interpreting the secondary xylem of this group. It is impossible to determine detailed ecological trends on the basis of field notes on

TABLE 4. Survey of ecological data and selected wood anatomical features for the species studied

Species	Tropical	Temperate	Lowland	Montane/alpine	Long dry period	Frost present	Growth rings distinct	Scalariform perforations (%)	Number of bars per plate	Vessel diameter (µm)	Vessel density (/mm ²)	Vessel element length (µm)	V-value	M-value
<i>Andersonia caerulea</i>	-	+	+	-	+	-	-	0	0	8 (12) 18	460 (505) 540	420 (537) 650	0.02	12
<i>A. sprengelioides</i>	-	+	+	-	+	-	-	5	1-2	10 (12) 18	360 (458) 540	270 (340) 430	0.03	9
<i>Cosmelia rubra</i>	-	+	+	-	+	-	-	100	19 (27) 34	8 (13) 20	480 (552) 640	410 (575) 740	0.02	13
<i>Cyathodes glauca</i>	-	+	?	?	-	+	-	0	0	20 (24) 30	66 (76) 82	300 (378) 450	0.32	119
<i>Dracophyllum longifolium</i> ¹	-	+	?	?	-	+	+	100	11 (17) 25	10 (13) 20	480 (557) 680	210 (370) 480	0.02	9
<i>D. longifolium</i> ²	-	+	?	?	-	+	+	100	15 (20) 25	15 (21) 25	260 (286) 321	230 (451) 600	0.07	33
<i>D. oliveri</i>	-	+	-	+	-	+	+	100	21 (25) 30	8 (15) 20	396 (507) 670	280 (440) 520	0.03	13
<i>D. palustre</i>	+	-	+	-	-	-	+	100	9 (19) 30	12 (16) 20	280 (318) 400	220 (379) 510	0.05	19
<i>D. strictum</i>	-	+	?	?	-	+	+	100	16 (32) 54	15 (19) 21	420 (518) 610	420 (616) 800	0.08	26
<i>D. subulatum</i>	-	+	-	+	-	+	+	100	8 (16) 27	10 (17) 20	125 (208) 368	?	0.08	?
<i>D. traversii</i>	-	+	-	+	-	+	+	100	17 (24) 30	15 (19) 25	140 (176) 210	330 (444) 630	0.08	25
<i>D. uniflorum</i>	-	+	?	?	-	+	+	100	13 (16) 20	9 (13) 20	440 (550) 680	280 (415) 530	0.02	48
<i>D. verticillatum</i>	+	-	?	?	-	-	-	100	24 (45) 78	25 (32) 40	94 (125) 172	680 (790) 950	0.26	202
<i>Epacris impressa</i>	-	+	+	-	+	-	-	100	5 (8) 11	12 (16) 22	215 (242) 265	360 (475) 590	0.07	31
<i>Leptecophylla</i> sp.	+	-	-	+	+	-	-	10	1 (2) 3	15 (25) 30	130 (176) 220	180 (347) 440	0.14	49
<i>L. juniperina</i>	-	+	?	?	-	+	-	0	0	20 (31) 40	54 (79) 110	370 (618) 950	0.39	243
<i>L. tameiameia</i> ¹	+	-	-	+	?	-	-	0	0	25 (32) 40	66 (116) 141	330 (433) 540	0.19	62
<i>L. tameiameia</i> ²	+	-	-	+	?	-	-	0	0	25 (35) 45	145 (187) 210	220 (333) 500	0.28	119
<i>Leucopogon cumbulifolia</i> ¹	+	-	?	?	-	-	-	0	0	35 (41) 60	34 (46) 62	280 (456) 600	0.89	406
<i>L. cumbulifolia</i> ²	+	-	?	?	-	-	-	0	0	25 (35) 40	34 (44) 54	270 (396) 550	0.80	315
<i>L. fasciculatus</i>	-	+	?	?	-	+	-	60	2 (4) 5	25 (35) 45	14 (28) 42	270 (447) 560	1.25	559
<i>L. malayanus</i>	+	-	?	?	-	-	-	0	0	30 (36) 45	58 (97) 112	300 (413) 550	0.37	153
<i>L. parviflorus</i>	-	+	+	-	+	+	-	0	0	25 (38) 50	?	160 (366) 490	?	?
<i>L. richei</i>	-	?	+	-	?	?	-	0	0	20 (31) 40	58 (63) 75	280 (360) 450	0.49	177
<i>Monotoca elliptica</i> ¹	-	+	?	?	?	?	+	70	3 (5) 10	25 (33) 40	82 (96) 108	350 (473) 620	0.34	163
<i>M. elliptica</i> ²	-	+	?	?	?	?	-	55	1 (3) 5	20 (27) 40	74 (88) 104	250 (329) 430	0.31	101
<i>M. tamariscina</i>	-	+	+	-	+	-	-	75	3 (5) 7	15 (19) 26	340 (378) 440	320 (448) 570	0.05	23
<i>Needhamiella pumilio</i>	-	+	+	-	+	-	-	0	0	6 (10) 13	240 (268) 280	170 (280) 400	0.04	10
<i>Oligarrhena micrantha</i>	-	+	+	-	+	-	-	5	1-2	10 (14) 20	210 (267) 300	260 (321) 410	0.05	17
<i>Prionotes cerinthoides</i> ¹	-	+	-	+	-	+	+	100	24 (38) 50	10 (16) 20	295 (355) 440	350 (481) 750	0.05	22
<i>P. cerinthoides</i> ²	-	+	-	+	-	+	+	100	22 (30) 50	10 (15) 20	320 (378) 440	320 (433) 570	0.04	17
<i>Richea continentis</i>	-	+	-	+	-	+	+	100	8 (15) 20	10 (16) 29	350 (401) 580	230 (352) 550	0.03	12
<i>R. dracophylla</i>	-	+	-	+	-	+	+	100	11 (16) 22	10 (12) 17	365 (396) 420	250 (371) 520	0.03	11
<i>R. pandanifolia</i>	-	+	-	+	-	+	+	100	17 (24) 29	15 (24) 30	250 (361) 480	300 (499) 750	0.07	33
<i>Sprengelia incarnata</i>	-	+	-	+	-	+	+	100	18 (21) 26	8 (12) 18	620 (675) 780	250 (447) 600	0.02	8
<i>S. sprengelioides</i>	-	+	?	?	-	?	-	100	12 (26) 40	10 (15) 20	320 (448) 560	430 (514) 650	0.03	17
<i>Styphelia laeta</i> subsp. <i>latifolia</i>	-	+	?	?	?	?	-	60	2 (5) 11	22 (41) 60	76 (86) 95	350 (464) 570	0.48	221
<i>Trochocarpa laurina</i> ¹	+	-	-	+	-	-	-	40	1 (5) 14	25 (38) 58	60 (85) 102	400 (613) 750	0.45	274
<i>T. laurina</i> ²	+	-	-	+	-	-	-	40	8 (12) 17	25 (42) 60	50 (69) 90	220 (467) 650	0.45	284

Ecological data based on Bentham (1869), Alan (1961), Burrows *et al.* (1979), George *et al.* (1979), Specht (1979a, b), Specht and Womersley (1979)

+, Present; -, absent; ?, unknown.

Numbers after the name of specimens of the same species refer to the order used in Table 2.

Mean values are shown in parentheses.

A 'long dry period' is considered to last for at least a few months per year; 'frost present' means that the species experiences at least 10 d of frost per year.

herbarium or xylarium labels accompanying the wood samples studied. Therefore, various floras and other floristic resources were consulted for each species to gather ecological information, including altitude, latitude, the annual amount of precipitation and the presence or absence of frost. However, the ecological ranges of some species are too large to determine exact parameters. Furthermore, a relatively small number of species has been analysed in the present study. Despite these shortcomings, some general trends in the wood of epacrids can be deduced from our data.

The ecological data of most species are presented in Table 4 together with selected wood anatomical features that may be susceptible to varying ecological factors.

Diffuse-porous wood is found in nearly all epacrids. Growth rings are generally present, but distinct growth rings are especially common in *Dracophyllum*, *Prionotes* and *Richea*, three genera that are mainly found in non-tropical, montane to (sub)alpine regions (Burrows *et al.*, 1979; Specht, 1979). This can be explained by the cooler winter temperatures in non-tropical higher areas, which result in

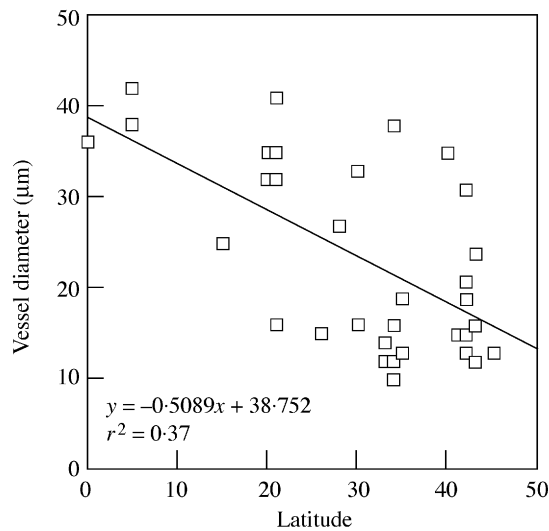


FIG. 10. Scatter plot of mean vessel diameter and latitude for the epacrids studied with linear curve fit.

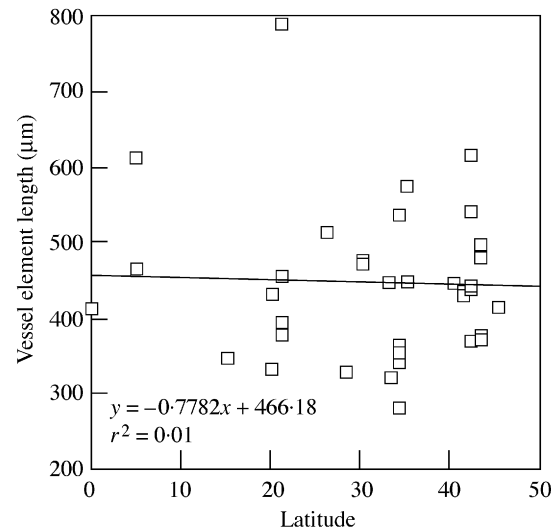


FIG. 12. Scatter plot of mean vessel element length and latitude for the epacrids studied with linear curve fit.

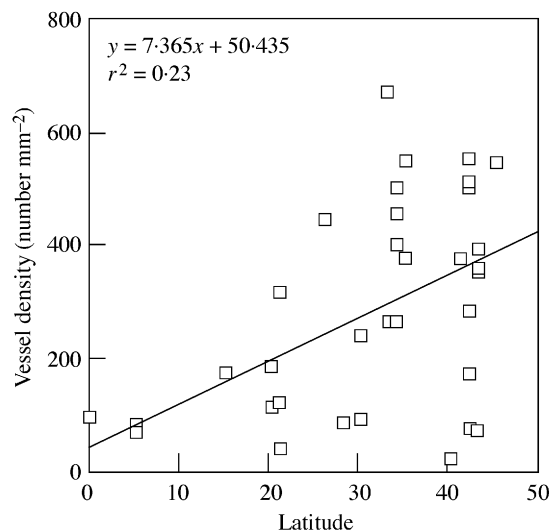


FIG. 11. Scatter plot of mean vessel density and latitude for the epacrids studied with linear curve fit.

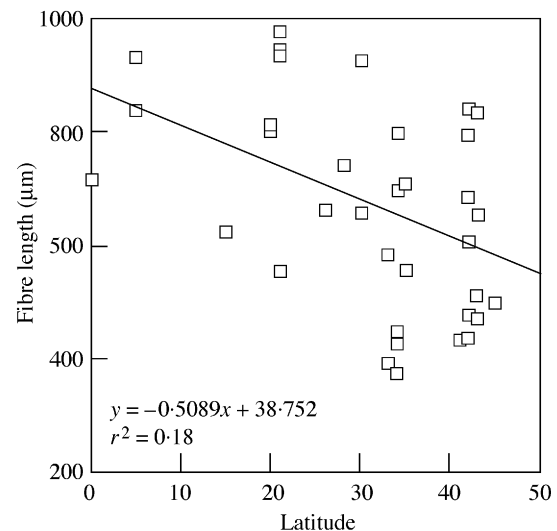


FIG. 13. Scatter plot of mean fibre length and latitude for the epacrids studied with linear curve fit.

seasonal changes in xylem formation. These results support the data of Schweingruber (1992), who concluded that many (non-tropical) Australian epacrids growing in montane or alpine sites show distinct growth rings, whereas other Australian epacrids have less distinct growth zones.

In Figs 10–14 the mean value of vessel diameter, vessel density, vessel element length, fibre length and the frequency of scalariform perforation plates are plotted against latitude of provenance, which can be considered as a rough indicator of macroclimatic conditions (e.g. Baas, 1973, 1986; Van der Graaf and Baas, 1974; van den Oever *et al.*, 1981; Noshiro and Baas, 2000). The results obtained agree with general latitudinal trends established for various other woody plant groups. As could be expected, the tangential vessel diameter and vessel density shows a

negative correlation with increasing latitudinal ranges, while vessel density illustrates the opposite correlation ($r^2 = 0.37$ and 0.23 , respectively). The frequency of scalariform perforations shows a weaker latitudinal trend ($r^2 = 0.19$), but this picture is probably blurred by altitudinal conditions (see below). Furthermore, fibre length shows a negative correlation with latitude ($r^2 = 0.18$), although vessel element length in epacrids (Fig. 12) does not demonstrate any significant correlation with latitude of provenance ($r^2 = 0.01$).

In addition to these latitudinal trends, it should be emphasized that several other factors interfere with the trends shown in Figs 10–14, including: (1) a different sampling of the material studied, i.e. variable stem thickness and maturity; (2) impact of frost; (3) availability and amount

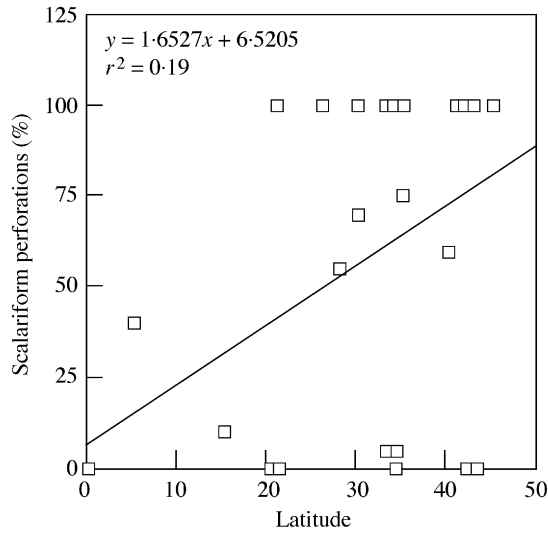


FIG. 14. Scatter plot of percentage of scalariform perforations and latitude for the epacrids studied with linear curve fit.

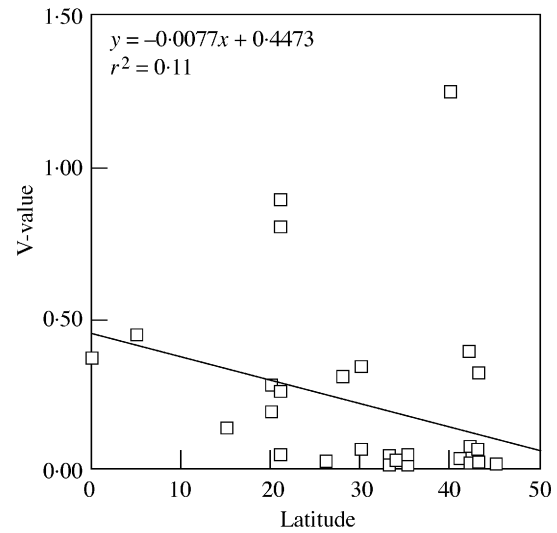


FIG. 16. Scatter plot of V-value and latitude for the epacrids studied with linear curve fit.

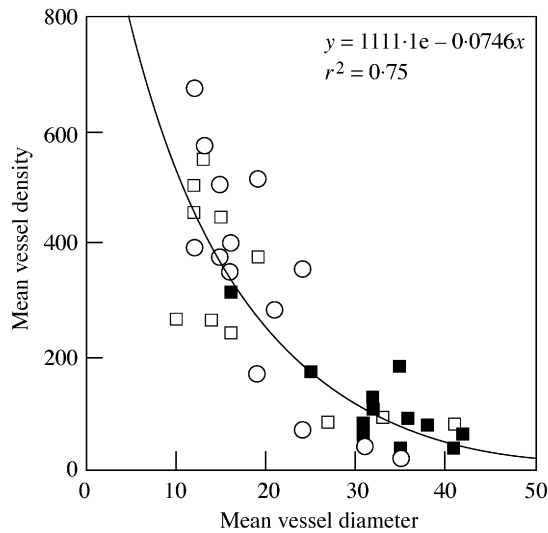


FIG. 15. Scatter plot of mean vessel density and mean vessel diameter for the tropical (black symbols) and temperate (white symbols) epacrids studied with exponential curve fit. Species that definitely experience a minimum of 10 d of frost per year are marked with a circle.

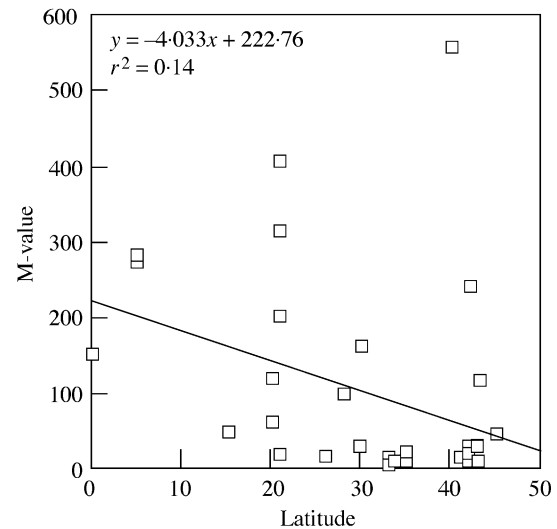


FIG. 17. Scatter plot of M-value and latitude for the epacrids studied with linear curve fit.

of precipitation; (4) effect of altitude (see also above); and (5) difference in fire response mechanisms.

When wood sections derived from very thin stems (2–3 mm in size) are compared with sections of much thicker samples, different quantitative wood features between the juvenile and mature wood may be expected. However, most of the thin epacrid wood samples studied are derived from tiny shrubs that must grow for several years to produce narrow stems of a few millimetres thick. Therefore, these narrow wood samples are not considered to be juvenile. Since the wood samples of *L. lanceolatus* and *E. miniata* are clearly juvenile, they are omitted from all scatter plots.

The vessel diameter is narrow in most epacrids (<30 μm) and shows a negative correlation with vessel frequency ($r^2 = 0.75$; Fig. 15). The functional significance of the narrow vessel diameter and high vessel frequency in the wood of most epacrids can largely be explained in terms of increased safety of the ascent of sap as a reaction to freeze-thaw cycles. Indeed, many epacrids that have a very narrow vessel diameter grow in temperate, montane to (sub)alpine regions (e.g. *Dracophyllum*, *Richea* and *Prionotes*), i.e. in areas with at least 10 d of frost per year (Fig. 15; Burrows *et al.*, 1979; Specht, 1979). The correlation between freeze-thaw cycles and vessel diameter was supported experimentally by Feild and Brodrigg (2001). They found a positive

relationship between loss of hydraulic conductivity due to a single freeze–thaw cycle and the average vessel diameter of 12 species from a treeline mixed-conifer heath in Tasmania. The wood of *Richea scoparia* Hook.f. proved to be well adapted to its environment because of the small loss of hydraulic conductivity induced by freeze–thaw cycles, while this loss was much higher in non-epacrid species with much wider vessels. The explanation for this is the greater likelihood of freeze–thaw cavitation in plants with wider vessels because of smaller adhesion forces between the water column and the larger vessel wall. The trade-off between conduit diameter and susceptibility to cavitation has also been suggested by Zimmermann and Brown (1971), Sperry and Sullivan (1992), Sperry *et al.* (1994) and Davis *et al.* (1999). Moreover, the presence of narrow tracheids (and to a lesser extent fibres with distinctly bordered pits) also contributes to the safety of water transport in this family.

To determine the susceptibility of secondary xylem to embolism, Carlquist (1977b) introduced the concept of vulnerability ('V' = mean vessel diameter divided by mean vessel frequency). Consequently, very small vessel diameters correspond with low V-values (<1), which reflect high conductive safety, while high V-values (>3) are indicative of species showing a high conductive efficiency. Table 4 shows that species of Styphelieae have the highest V-values (mostly between 0.3 and 0.8) because of their relatively wide vessels and low vessel densities. The presence of frost does not always seem to have an effect on the V-index. For example, temperate Styphelieae, some species of which experience at least 10 d of frost per year, and the montane tropical Styphelieae, which hardly ever experience any frost, have the same mean V-index (0.45). Moreover, very low V-values resulting from narrow vessels are found in *Monotoca tamariscina* (V = 0.05), Oligarrheneae (V = 0.04) and in *C. rubra* (V = 0.02), which all have narrow stems (2–4 mm in size) and grow in the wet tip of south-west Australia where frost is very rare.

Although epacrids are not found in very dry deserts or semi-deserts, Australian lowland species in particular experience a long period of drought. To measure the amount of water available to plants, Carlquist (1977b) introduced the mesomorphy-index ('M' = V multiplied by mean vessel element length). Low M-values (<100) characterize plants that grow in dry (xeric) environments or in regions with a long dry period lasting several months, whereas higher M-values are typical of plants growing in wetter (mesic) habitats. For the Styphelieae studied, which mostly grow in mesic habitats, M-values demonstrate well the mesic factor. Another example is *Dracophyllum verticillatum*, the only representative of Richeeae, which grows in the tropical habitat of New Caledonia and has a relative high M-value (202). *D. palustre*, however, another New Caledonian representative, has much lower M-values similar to those of temperate *Dracophyllum* species. On the other hand, the typical low M-values of Richeeae and Prionoteae seem to contradict their common distribution in mesic montane areas. A possible explanation for these low M-values may be the impact of frost in these regions, which may reduce the vessel diameter markedly.

The V- and M-indices have been criticized by several authors (e.g. Van Vliet, 1979; van den Oever *et al.*, 1981; Baas, 1986), although others have demonstrated their usefulness in various plant groups (e.g. Carlquist, 1977b; Carlquist and Hoekman, 1985; Patterson and Tanowitz, 1989). As mentioned above, these indices are congruent with the ecology of some species studied, but in other species they provide no support. For the epacrids as a whole, the V- and M-indices show a weak correlation with the latitude of provenance ($r^2 = 0.11$ and 0.14 , respectively; Figs 16–17), although the mean values of tropical species are significantly higher (V = 0.4; M = 196) than those of the temperate representatives (V = 0.14; M = 60).

Based on our fragmentary altitudinal data, we were unable to link wood anatomical data with altitudinal ranges, although effects of altitude may play an important role (Baas, 1973; Van der Graaf and Baas, 1974; van den Oever *et al.*, 1981). This can be illustrated by the impact of altitude on the type of vessel perforation plates. For example, most tropical Styphelieae are characterized by simple or mixed simple/scalariform vessel perforations with few bars, which cause less resistance to flow than scalariform perforations with many bars. Indeed, simple perforations are favoured in regions where moments of peak transport are needed, and this is certainly the case in the tropical lowlands. Some epacrids growing in higher tropical areas, however, show more scalariform perforations owing to the cooler temperatures and hence the lower transpiration rates (e.g. Carlquist, 1975; Baas *et al.*, 1983; Baas, 1986; Carlquist, 2001). On the other hand, montane and (sub)alpine plants in temperate regions generally show scalariform perforation plates with numerous bars (e.g. *Dracophyllum*, *Pentachondra*, *Prionotes* and *Richea*), which might prevent freeze-induced air bubbles to fuse, thus avoiding dysfunctioning of a vessel (Zimmermann, 1983). Nevertheless, there are several counter examples, such as the closely related *Andersonia* and *Cosmelia* species. Although these grow in the same region (the temperate southern tip of west Australia), *Andersonia* is characterized by predominantly simple perforations, and *Cosmelia* by scalariform perforations with many bars.

Bell *et al.* (1996) and Verdaguer and Ojeda (2002) found that differences in growth form and root anatomy, especially with respect to ray width and starch supply, are related to different fire response mechanisms of plants (seeders *vs.* resprouters). Seeder plants are killed by fire and survive only through their seeds, whereas resprouters are able to sprout from the root crown when fires (or other major disturbances) destroy their above-ground parts. Within epacrids, several genera that can be considered as seeders appear to show uni- or biseriolate rays in their stem (e.g. *Andersonia*, *Needhamiella*, *Oligarrhena* and *Cosmelia*), whereas the multiseriate rays of more than three cells wide in Richeeae and Styphelieae may represent some resprouters (e.g. *Conostephium* and *Styphelia*) (Bell and Pate, 1996; Bell *et al.*, 1996). However, this relationship should be interpreted with caution until more fieldwork has been conducted.

In conclusion, certain wood anatomical characteristics in epacrids can largely be interpreted as being the result of an

adaptive evolution to different environmental conditions. This is most probably the case for various (dis)continuous vessel features. In general, the small vessel diameter and the high vessel frequency within epacrids result in low V- and M-values, which reflect their safe water transport mechanism in heathlands with long xeric periods or in mesic montane to (sub)alpine climates where freeze–thaw cycles occur. Most Styphelieae that grow in wet, temperate to tropical areas show a tendency to a higher conductive xylem sap transport by the presence of wider vessels with mostly simple perforation plates, resulting in higher V- and M-values.

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