

---

CSIRO PUBLISHING

---

# Australian Systematic Botany

Volume 10, 1997  
© CSIRO Australia 1997



An international journal devoted to the taxonomy,  
biogeography and evolution of all plant groups

[www.publish.csiro.au/journals/asb](http://www.publish.csiro.au/journals/asb)

All enquiries and manuscripts should be directed to

*Australian Systematic Botany*

**CSIRO PUBLISHING**

PO Box 1139 (150 Oxford St)

Collingwood

Vic. 3066

Australia

Telephone: 61 3 9662 7624

Facsimile: 61 3 9662 7611

Email: [deborah.penrose@publish.csiro.au](mailto:deborah.penrose@publish.csiro.au)



Published by **CSIRO PUBLISHING**  
for CSIRO Australia and  
the Australian Academy of Science



## Relationships and Generic Concepts within Styphelieae (Epacridaceae)

Jocelyn M. Powell<sup>A</sup>, David A. Morrison<sup>B</sup>, Paul A. Gadek<sup>C</sup>,  
Darren M. Crayn<sup>C</sup> and Christopher J. Quinn<sup>CD</sup>

<sup>A</sup>National Herbarium of New South Wales, Royal Botanic Gardens,  
Sydney, NSW 2000, Australia.

<sup>B</sup>Department of Applied Biology, University of Technology, Sydney,  
PO Box 123, Broadway, NSW 2007, Australia.

<sup>C</sup>School of Biological Science, University of New South Wales,  
Sydney, NSW 2052, Australia.

<sup>D</sup>Corresponding author; email: chris.quinn@unsw.edu.au

### Abstract

A morphological data base of 30 characters has been assembled for 33 terminal taxa in the tribe Styphelieae sensu Powell *et al.* (1996), as well as four outgroup taxa representing the other major affinity groups previously identified within the Epacridaceae on morphological and molecular data. Heuristic and bootstrap analyses provided strong support for the tribe, but indicated a need to modify several long-established generic concepts. Four genera are shown here to be polyphyletic. Six new monotypic genera should be segregated from *Astroloma*. *Brachyloma* should be divided into three segregates. Two distinct affinity groups warranting generic status were identified within *Cyathodes*. The separation of the monotypic Western Australian genus, *Croninia*, from *Leucopogon* s.l. is supported, and four other separate entities are here recognised: four species from section *Heteranthus* Benth. should be united with *Lissanthe*, and the other three segregates warrant generic status. In addition, *Monotoca* is paraphyletic, and should be redefined to incorporate *Oligarrhena*, while a new genus, 'Pseudactinia', is required to accommodate two new species from Western Australia. There seems little justification for maintaining the distinction between *Trochocarpa* and *Decatoca*. The pattern of intergeneric relationships resolved suggests that *Astroloma* s.l., *Coleanthera*, *Conostephium*, *Croninia*, *Melichrus*, *Styphelia* and much of *Leucopogon* s.l. constitute an affinity group, and that *Brachyloma* s. str. and *B. scortechinii* are basal within the tribe, but there is only weak support for these aspects of the topology within the data.

### Introduction

Recent morphological and molecular studies have shown the Epacridaceae sensu Crayn *et al.* (1996) to be a monophyletic assemblage embedded within the Ericaceae s.l. (e.g. Anderberg 1993; Judd and Kron 1993; Kron and Chase 1993; Kron 1996); however, further work is required before the taxonomic treatment of the entire order can be finalised. Recent intensive studies of Epacridaceae have demonstrated the existence of several robust lineages within Epacridaceae, the largest of which is the Styphelieae (including *Needhamiella* and *Oligarrhena*; Powell *et al.* 1996). While all genera in the family were included in that study, representation of the Styphelieae clade was greatly reduced in the final analysis because of the marked uniformity of the tribe in the data base employed. Evidence of the strength of this Styphelieae clade has also been obtained from molecular studies (Crayn *et al.* 1996; unpublished data).

*Choristemon* (Williamson 1924), a monotypic genus from Victoria, which is characterised by free filaments inserted below the ovary and the anthers dorsifixed near the base and two-locular, is known only from the type specimen, and is considered extinct (J. Willis, pers. comm.). It is virtually identical to *Leucopogon virgatus* in habit and foliage, and it seems likely that the differences in floral structure may be due to malformation: the anthers,

for example, are empty of pollen and staminode-like. Hence, this dubious monotypic genus was excluded from the analyses.

To date, both morphological and molecular studies have provided strong support for several tribal groups within the family, but have provided only weakly supported and conflicting patterns of relationship between these tribes. In the morphological analysis, Styphelieae were placed as sister to a clade comprising Richeae plus Cosmelieae, while the remaining genera (Epacrideae) constituted a basal paraphyletic assemblage (Powell *et al.* 1996). Molecular analyses have supported the monophyly of the first three tribes, but have given a very different and much more highly resolved set of relationships for the genera assigned to Epacrideae (Crayn *et al.* 1996). *Lebetanthus* was excluded from the family, and all but two of the remaining genera were shown to constitute a relatively derived clade that was the sister group of Styphelieae, while *Prionotes* occupied a quite separate position at the base of the Epacridaceae clade. Work in progress shows *Archeria* also to be relatively basal (Crayn, unpublished data). Hence, the following outgroups were included: *Epacris* (Epacrideae), *Richea* (Richeae), *Sprengelia* (Cosmelieae) and *Archeria*. The last of these was used to root the analyses. Problems of homology arose in some characters when more distant outgroups were selected, for example from subfamily Vaccinioideae of Ericaceae.

This paper presents a morphologically based analysis of relationships within this tribe, and in particular, presents a reassessment of some generic concepts; it is the culmination of studies on the family over a number of years by one of us (J. M. P.).

## Materials and Methods

As far as possible, all species (including some undescribed species) were scored using a wide range of specimens. In most cases, genera or subgenera, as currently circumscribed, were treated as terminal taxa. In some cases, however, these taxa proved to be heterogeneous for several characters, and therefore were split into smaller more homogeneous groups of species. The terminal taxa and the species scored within each are given in Table 1.

### Definition of Characters

The following characters were found to provide scorable variation across the ingroup.

#### (1) *Pherophylls subtending inflorescences*

Three states are recognised within the ingroup: persistent 'mature-type leaves' indistinguishable from other leaves on the plant (1/0); deciduous mature-type leaves that fall after flowering (1/1); or caducous 'early seasonal leaves' readily distinguished by their obovate shape and hyaline margin, which fall before or during flowering (1/2). Some species of *Brachyloma* and *Monotoca* are polymorphic, the first inflorescences being borne in the axils of caducous 'early seasonal leaves', whereas later ones are formed in the axils of persistent 'mature-type leaves'.

#### (2) *Flower pedicel*

In the majority of Styphelieae the bracts and bracteoles clothe the peduncle immediately below the sepals (2/0); in others the flowers are pedicellate above the bracteoles (2/1).

#### (3) *Flowering shoots*

Single flowers or inflorescences are borne on indeterminate or determinate flowering shoots. In the first case, the shoot is terminated by a non-floral bud that gives rise to continued vegetative growth after the flowering season (3/0); in the second, the terminal bud of the flowering shoot remains dormant or is non-functional, and vegetative growth is initiated from below the flowering shoot (3/1).

#### (4) *Floral bracts*

Flowers may be subtended by numerous bracts or bracteoles (4/0), by a single bract and a pair of bracteoles (4/1), or by a pair of bracteoles only (4/2).

#### (5) *Structure of bracteoles*

Bracteoles may be non-keeled, often with conspicuous striate venation (5/0), or keeled, having a strongly thickened midrib (5/1).

*(6) Inflorescence rudiment*

Reduction of inflorescences, eventually leading to single flowers, is evidenced within the family both by empty bracts towards the base of the peduncle and the presence of floral rudiments at the apex of the inflorescence. The latter may be simply a non-expanded bud more or less enclosed within the subtending bract (6/0) (a rudiment; Bentham 1869), or a flattened, expanded bract-like structure or false-bract (6/1) (Watson 1964; Powell, unpublished data).

*(7) Staminal position*

In most Epacridaceae, corolla lobes are erect to spreading and filaments are short, so the anthers are at most half-exserted (7/0). Alternatively, the filaments may be long and erect, so that the anthers are fully exserted well beyond the corolla (7/1), or reflexed so that the anthers are exserted between the lobes to lie parallel to or below the throat (7/2).

*(8) Aestivation*

Corolla lobes may be valvate (8/3), induplicate-valvate (8/4) or imbricate in the bud. There is some variation in the expression of the imbricate state; in some species of *Brachyloma*, the lobes are imbricate overall in the bud and remain basally so when the flowers open (8/0), while in others, they are imbricate mainly at the base, the apices appearing more or less valvate in bud (8/1); in *Trochocarpa* and *Decatoca*, the lobes are only distally imbricate (8/2).

*(9) Corolla tube hairs*

These may be ornamented (Powell 1993) (9/0), smooth (9/1) or glandular (9/2).

*(10) Corolla pads*

Hairs within the corolla tube may arise directly from surface cells (10/0). In some species of *Brachyloma*, the hairs near the throat are associated with a flap of tissue attached near the base of the lobes (10/1), whereas in some other taxa, thick flaps of tissue near the base of the tube carry the hairs (10/2).

*(11) Filaments*

These may be terete and more or less filiform (11/0), broad and flat (11/1), or thick and tapering (11/2).

*(12) Apparent anther apex*

The anthers become inverted during development in the family (Copeland 1954). The apex may be emarginate (12/0), deeply or shortly bifurcate (12/1), or have a sterile tip above the thecae (12/2).

The Styphelieae show a considerable range of pollen and aperture types that have been discussed by Smith-White (1955, 1959), Rao (1961), Franks and Watson (1963) and McGlone (1978). Some of this variation is scored in characters 13 and 14.

*(13) Pollen type*

Pollen may be shed either as tetrads (13/0) or monads of the S type (Smith-White 1948) (13/1).

*(14) Aperture type*

Pollen may be tricolporate (type CP3) (14/0), type CP4 (14/1), type CP6 (14/2), type P1 (monoporate, 14/3), type P6 (14/4), types P8–10 (14/5), annular-porate (Powell 1993) (14/6), or multiporate (14/7).

*(15) Floral nectary*

Present (15/0); absent (15/1).

*(16) Style*

The length of the ovary plus style less than half the length of the corolla tube (16/0), or nearly equal to or longer than the tube (16/1).

**Table 1. Description of terminal taxa and the representative species scored**

Distribution: NSW, New South Wales; Qld, Queensland; SA, South Australia; Tas., Tasmania; Vic., Victoria; WA, Western Australia; Au, widespread in Australia; NC, New Caledonia; NG, New Guinea; NZ, New Zealand. (–, taxon unrepresented)

Terminal taxon	Total spp.	Notes	Representatives scored	Distribution
<i>Acrotiche</i>	14		<i>A. affinis</i> DC., <i>A. cordata</i> (Labill.) R.Br., <i>A. depressa</i> R.Br., <i>A. fasciculiflora</i> (Regel) Benth., <i>A. halmaturina</i> B.Paterson, <i>A. patula</i> R.Br., <i>A. serrulata</i> R.Br.	Qld, NSW, SA, Tas., Vic., WA
<i>Astroloma</i> A	13	most of sect. <i>Stomarrhena</i> <sup>A</sup>	<i>A. compactum</i> R.Br., <i>A. drummondii</i> Sond., <i>A. epacridis</i> (DC.) Druce, <i>A. humifusum</i> (Cav.) R.Br., <i>A. macrocalyx</i> Sond., <i>A. microcalyx</i> Sond., <i>A. pallidum</i> R.Br., <i>A. prostratum</i> R.Br., <i>A. serratifolia</i> (DC.) Druce	WA (NSW, SA, Tas.)
<i>A. xerophyllu</i>	1	ex sect. <i>Stomarrhena</i>	<i>A. xerophyllum</i> Sond.	WA
<i>A. stomarrhena</i>	1	ex sect. <i>Stomarrhena</i>	<i>A. stomarrhena</i> Sond.	WA
<i>A. pinifolium</i>	1	ex sect. <i>Stenanthera</i> <sup>A</sup>	<i>A. pinifolium</i> (R.Br.) Benth.	NSW, Vic., Tas.
<i>A. ciliatum</i>	1	ex sect. <i>Stomarrhena</i>	<i>A. ciliatum</i> (Lindl.) Druce	WA
<i>A. conostephioides</i>	1	ex sect. <i>Pentataphrus</i> <sup>A</sup>	<i>A. conostephioides</i> (Sond.) Benth.	SA, Vic.
<i>Astroloma</i> G	1	ex sect. <i>Pentataphrus</i>	<i>A. baxteri</i> DC.	WA
<i>Brachyloma</i> A	3		<i>B. concolor</i> Benth., <i>B. ericoides</i> (Schldl.) Sond., <i>B. preissii</i> Sond.	SA, Vic., WA
<i>Brachyloma</i> B	3		<i>B. ciliatum</i> (R.Br.) Benth., <i>B. daphnoides</i> (Sm.) Benth., <i>B. depressum</i> (F.Muell.) Benth.	Qld, NSW, SA, Tas., Vic.
<i>B. scortechinii</i>	1		<i>B. scortechinii</i> F.Muell.	Qld, NSW
<i>Coleanthera</i>	3		<i>C. coelophylla</i> (DC.) Benth., <i>C. myrtoides</i> Stschégl., <i>C. virgata</i> Stschégl.	WA
<i>Conostephium</i>	7		<i>C. drummondii</i> (Stschégl.) C.Gardner, <i>C. marchantiorum</i> A.Strid, <i>C. minus</i> Lindl., <i>C. pendulum</i> Benth., <i>C. preissii</i> Sond.	WA
<i>Cyathodes</i> A	16		<i>C. juniperina</i> (Forst.) Druce, <i>C. parvifolia</i> R.Br., <i>C. pendulosa</i> Jarman, <i>C. abietina</i> R.Br., <i>C. dealbata</i> R.Br., <i>C. divaricata</i> J.D.Hook., <i>C. glauca</i> Labill., <i>C. straminea</i> R.Br.	Qld, NSW, SA, Tas., Vic., WA, NZ
<i>Cyathodes</i> B	3		<i>C. empetrifolia</i> Hook.f., <i>C. nitida</i> Jarman, <i>C. petiolaris</i> (DC.) Druce	NZ, Tas.
<i>Cyathopsis</i>	1		<i>C. floribunda</i> Brongn. & Gris.	NC
<i>Decatoca</i>	1		<i>D. spencerii</i> F.Muell.	NG

<i>Leucopogon</i> A ( <i>Leucopogon</i> s. str.)	82	sect. <i>Perojoa</i> and sect. <i>Heteranthesis</i> <sup>A</sup> p.p.	<i>L. amplexicaulis</i> (Rudge) R.Br., <i>L. australis</i> R.Br., <i>L. capitellatus</i> DC., <i>L. lanceolatus</i> (Sm.) R.Br., <i>L. microphyllus</i> (Cav.) R.Br., <i>L. parviflorus</i> (Andrews) Lindl., <i>L. revolutus</i> R.Br., <i>L. verticellatus</i> R.Br. <i>L. kingianus</i> (F.Muell.) C.Gardner	Au, NZ, NC, Malaysia
<i>L. kingianus</i> ( <i>Croninia</i> )	1			WA
<i>Leucopogon</i> C (‘ <i>Gynoconus</i> ’)	8	short-styled spp. of sect. <i>Pleuranthus</i> <sup>A</sup>	<i>L. appressus</i> R.Br., <i>L. attenuatus</i> Cunn., <i>L. confertus</i> Benth., <i>L. cymbiformis</i> DC., <i>L. flexifolius</i> R.Br., <i>L. leptospermoides</i> R.Br., <i>L. pogonocalyx</i> Benth., <i>L. tamminensis</i> E.Pritzel	Qld, NSW, WA
?			<i>L. acuminatus</i> R.Br., <i>L. alittii</i> F.Muell., <i>L. biflorus</i> R.Br., <i>L. blepharolepis</i> F.Muell., <i>L. brevicuspis</i> Benth., <i>L. breviflorus</i> F.Muell., <i>L. clelandii</i> Cheel, <i>L. conchifolius</i> A.Strid, <i>concinus</i> Benth., <i>L. conostephioides</i> DC., <i>L. cordifolius</i> Lindl., <i>L. corynocarpus</i> Sond., <i>L. crassiflorus</i> (F.Muell.) Benth., <i>L. crassifolius</i> Sond., <i>L. cuspidatus</i> R. Br., <i>L. deformis</i> R.Br., <i>L. dielsianus</i> E.Pritzel, <i>L. ericoides</i> (Sm.) R.Br., <i>L. esquamatus</i> R.Br., <i>L. exolasius</i> (F.Muell.) Benth., <i>L. flavescens</i> Sond., <i>L. fletcheri</i> Maiden & Betche, <i>L. fraseri</i> Cunn., <i>L. glaucifolius</i> W.Fitzg., <i>L. hamulosus</i> E.Pritzel, <i>L. hispidus</i> E.Pritzel, <i>L. imbricatus</i> R.Br., <i>L. insularis</i> DC., <i>L. juniperinus</i> R.Br., <i>L. leptanthus</i> Benth., <i>L. margarodes</i> R.Br., <i>L. mitchellii</i> Benth., <i>L. multiflorus</i> R.Br., <i>L. muticus</i> R.Br., <i>L. neoanglicus</i> Benth., <i>L. nutans</i> E.Pritzel, <i>L. obtectus</i> Benth., <i>L. ovalifolius</i> Sond., <i>L. oxycedrus</i> Sond., <i>L. pendulus</i> R.Br., <i>L. planifolius</i> Sonder, <i>L. pleurandroides</i> F.Muell., <i>L. propinquus</i> R.Br., <i>L. pubescens</i> S.Moore, <i>L. racemosus</i> DC., <i>L. recurvisepalus</i> C.T.White, <i>L. riparius</i> Wakef., <i>L. rotundifolius</i> R.Br., <i>L. rufus</i> Lindl., <i>L. rupicolius</i> C.T.White, <i>L. setiger</i> R.Br., <i>L. sonderensis</i> J.H.Willis, <i>L. strictus</i> R.Br., <i>L. strongylophyllus</i> F.Muell., <i>L. woodsii</i> F.Muell., <i>L. sp. aff. fletcheri</i> .	Qld, NSW, SA, Tas., Vic., WA, NC
<i>Leucopogon</i> D (‘ <i>Axonanthus</i> ’)	60	long-styled spp. of sect. <i>Pleuranthus</i>		
<i>Leucopogon</i> E	4	sect. <i>Heteranthus</i> <sup>A</sup> p.p.	<i>L. pedicellatus</i> C.T.White, <i>L. pleiospermus</i> (F.Muell.) Benth., <i>L. pleuriloculatus</i> F.Muell., <i>L. rubicundus</i> (F.Muell.) Benth.	Qld, NSW, WA
<i>Lissanthe</i>	6		<i>L. sapida</i> R.Br., <i>L. strigosa</i> (Sm.) R.Br.	Qld, NSW, SA, Tas., WA
<i>Melichrus</i>	4		<i>M. adpressus</i> DC., <i>M. erubescens</i> DC., <i>M. procumbens</i> (Cav.) Druce, <i>M. urceolatus</i> R.Br.	Qld, NSW, Vic.

**Table 1.** (continued)

Terminal taxon	Total spp.	Notes	Representatives scored	Distribution
<i>Monotoca</i> A	7		<i>M. empetrifolia</i> R.Br., <i>M. glauca</i> (Labill.) Druce, <i>M. ledifolia</i> DC., <i>M. rotundifolia</i> J.H.Willis, <i>M. scoparia</i> (Sm.) R.Br., <i>M. submutica</i> (Benth.) Jarman, Sp. A ('aristata')	Qld, NSW, SA, Tas., Vic.
<i>Monotoca</i> B	3		<i>M. leucantha</i> E.Pritzel, <i>M. oligarrhenoides</i> F.Muell., <i>M. tamariscina</i> F.Muell.	WA
<i>Monotoca</i> C	1		<i>M. elliptica</i> (Sm.) R.Br.	Qld, NSW, Tas., Vic.
<i>Needhamiella</i>	1		<i>N. pumilio</i> (R.Br.) Watson	WA
<i>Pentachondra</i>	3		<i>P. ericaefolia</i> J.D.Hook., <i>P. involucrata</i> R.Br., <i>P. pumila</i> (Forst. & Forst.) R.Br.	Au, NZ
'Pseudoactinia'	1		Sp. A, Sp. B	WA
<i>Oligarrhena</i>	1		<i>O. micrantha</i> R.Br.	WA
<i>Styphelia</i> A	12		<i>S. adscendens</i> R.Br., <i>S. laeta</i> R.Br. <i>S. longifolia</i> R.Br., <i>S. viridis</i> Andrews, <i>S. triflora</i> Andrews, <i>S. tubiflora</i> Smith, <i>S. exarrhena</i> (F.Muell.) F.Muell., <i>S. intertexta</i> A.S.George, <i>S. pulchella</i> (Sond.) F.Muell., <i>S. tenuiflora</i> Benth.	Qld, NSW, SA, Tas., Vic., WA
<i>Trochocarpa</i>	10	subg. <i>Trochocarpa</i> <sup>B</sup>	<i>T. clarkei</i> (F.Muell.) F.Muell., <i>T. disticha</i> (Labill.) Spreng., <i>T. gunnii</i> (J.D.Hook.) Benth., <i>T. laurina</i> R.Br., <i>T. thymifolia</i> (R. Br.) Spreng.	Qld, NSW, Malaysia
	2	subg. <i>Pseudocyathodes</i> <sup>B</sup>	–	NG

<sup>A</sup>Bentham 1869.<sup>B</sup>Sleumer 1964.

(17) *Locule number*

This varies from 1–10 (11?), and infrageneric variation in some taxa is considerable; since precise coding of the number proved highly homoplastic, only three states are recognised: uniformly five (17/0); less than five (17/1); or greater than five (17/2).

(18) *Fruit type*

Fruit may be capsular (18/0), drupes with a single pyrene (18/1), or drupaceous with two or more separate pyrenes (18/2). In *Acrotriche*, there is a single pyrene that breaks into unilocular segments under pressure; this is scored as state 1.

(19) *Leaf venation*

Two states are recognised: actinodromous venation, comprising both parallel and reticulate elements, often 3–5 primary central parallel veins together with secondary veins branching from the outer pair and becoming reticulate towards the margin (19/0); or strictly parallelodromous venation (19/1)

(20) *Corolla tube indumentum*

The corolla tube may be glabrous (20/0) or hairy (20/1).

(21) *Number of corolla lobes*

Five (21/0); four (21/1).

(22) *Number of ovules per locule*

Numerous (22/0); one (22/1).

(23) *Placentation*

Axile (23/0); apical (23/1).

(24) *Number of stamens*

The number of stamens is either equal to the number of corolla lobes (24/0), or two (24/1).

(25) *Calyx and floral bracts*

These may be non-coloured (25/0) or coloured (25/1).

(26) *Hairiness of corolla lobes*

The adaxial surface of the corolla lobes may be glabrous apart from hairs at the throat (26/0), generally hairy (26/1), or have hairs restricted to the mid-line (26/2), or to an apical tuft (26/3).

(27) *Anther coherence*

Anthers may be free (27/0), or cohere around the style (27/1).

(28) *Filaments*

Anther filaments may be glabrous (28/0), or hairy (28/1).

(29) *Shape of stigma*

The stigma may be lobed (29/0) or capitate (29/1).

(30) *Corolla lobes*

These may be erect or spreading (30/0), or distinctly revolute (30/1).

Scoring these characters for the 33 ingroup terminal taxa and four outgroups yielded the data base in Table 2. Several additional autapomorphies not included in the analysis are available to augment the definitions of the terminal taxa (Table 3).

Heuristic parsimony analyses were performed in PAUP (Swofford 1993) set for TBR branch-swapping. Branch lengths for trees were calculated using the ACCTRAN optimisation; only unambiguous character-state changes were recorded on the branches in the final figures. Support for

**Table 2. Data matrix used in the analysis of Styphelieae**  
Polymorphisms shown in parentheses; –, inapplicable character. For description of characters, see text

Taxon	Character state														
	1	0	2	0	3	0	3	0	3	0					
<i>Archeria</i>	01101-	0	0--000	0	0(01)0	00	0	0	0000(01)	0	0	1	0		
<i>Epacris</i>	00001-	(01)	0--000	0	0(01)0	00	0	0	0000	0	0(01)	1	0		
<i>Richea</i> A	00101-	-	---000	0	0	0	0	00	0	0	0000	0	0	0(01)-	
<i>Sprengelia</i>	00001-	0	0--100	0	1	0	0	00	0	0	0000	0	1	0(01)0	
<i>Brachyloma</i> A	00011-	0	001100	0	0	0	0	10	1	0	1100	0	0	0	0
<i>Brachyloma</i> B	20020-	0	110000	0	0	0	0	10	1	0	1100	1	0	0	0
<i>Brachyloma</i> C	010110	0	000000	0	0	0(12)	10	1	0	1100	0	0	0	0	0
<i>Conostephium</i>	00001-	0	300011	(12)	1	1	0	10	1	1	1100	0	0	0	0
<i>Cyathodes</i> A	00001-	0	310000	0	0	0(12)	11	1	0	1100	(013)	0	0	0	0
<i>Cyathodes</i> B	000100	0	310000	0	0	0(12)	11	(01)	0	1100	1	0	0	0	0
' <i>Pseudactinium</i> '	00001-	0	302101	3	0	0	1	11	1	0	1100	0	0	0	0
<i>Melichrus</i>	00001-	0	322101	3	0	0	0	11	1	0	1100	1	0	0	0
<i>Leucopogon</i> A	001100	0	310020	0	0	0	0	10	1	0	1100	1	0	0	0
<i>L. kingianus</i>	00001-	0	310011	6	0	1	0	11	1	0	1100	1	0	0	0
<i>Leucopogon</i> C	000100	0	310001	1	0	0	0	10	1	0	1100	1	0	0	0
<i>Leucopogon</i> D	000100	0	310001	7	0	1	0	10	1	0	1100	1	0	0	0
<i>Leucopogon</i> E	011100	0	310000	0	0	1(12)	11	1	0	1100	1	0	0	0	0
<i>Styphelia</i>	000111	1	310001	5	0	1	0	10	1	0	1100	1	0	0	0
<i>Coleanthera</i>	000111	1	310001	4	1	1	0	10	1	0	1100	1	1	0	0
<i>Astroloma</i> A	000111	0	310101	4	0	1	0	10	1	0	1100	1	0	0	1
<i>A. xerophyllum</i>	000111	0	310001	4	0	1	0	10	1	0	1100	1	0	0	0
<i>A. stomarrhena</i>	000111	1	310001	2	0	1	0	10	1	0	1100	1	0	1	0
<i>A. pinifolium</i>	00001-	0	310101	-	0	1	0	10	1	0	1100	1	0	0	0
<i>A. constephioides</i>	00011-	0	312101	3	0	1	0	10	1	0	1101	1	0	0	0
<i>A. baxteri</i>	00011-	1	302101	2	0	1	0	10	1	0	1100	3	0	0	0
<i>Needhamiella</i>	00110-	0	410000	0	0	0	1	11	1	0	1100	2	0	0	0
<i>Oligarrhena</i>	10110-	0	3--001	0	0	0	1	11	0	1	1110	0	0	0	0
<i>Monotoca</i> A	00010-	0	3--001	0	0	0	1	10	0(01)	1100	(01)	0	0	0	0
<i>Monotoca</i> B	10010-	0	3--001	0	0	0	1	11	0	0	1100	0	0	0	0
<i>M. elliptica</i>	20120-	0	3--001	0	0	0	1	10	0	0	1100	0	0	0	0
<i>Lissanthe</i>	011100	0	310000	0	0	1	0	11	1	0	1100	1	0	0	0
<i>Acrotriche</i>	000100	(02)	310000	0	0	0(12)	10	1	0	1100	3	0	0	0	0
<i>Cyathopsis</i>	001100	1	310000	0	0	1	2	10	1	1	1100	1	0	0	0
<i>Pentachondra</i>	001100	0	310000	0	0	0	0	20	1	0	1100	1	0	0	0
<i>Decatoca</i>	001100	0	210200	0	0	1	2	20	1	0	1100	1	0	0	0
<i>Trochocarpa</i>	001100	0	210200	0	0	1	2	20	1	0	1100	0	0	0	0
<i>Astroloma ciliatum</i>	000111	0	310101	4	0	1	0	10	0	0	1100	1	0	0	0

clades was inferred by bootstrap (Felsenstein 1985). Output trees from PAUP were also transferred into MacClade (Maddison and Maddison 1992) and manipulated to test other topologies and to explore character-state evolution. Character polarities were determined by outgroup analysis (Maddison *et al.* 1984).

## Results and Discussion

To the extent that the several currently accepted genera with two or more species (i.e. *Acrotriche*, *Coleanthera*, *Conostephium*, *Pentachondra*) are highly homogeneous in the data base, the integrity of these taxa is supported.

A heuristic search with 500 replicates of random taxon addition found 1759 equally parsimonious trees of 112 steps (re-scaled consistency index 0.45, retention index 0.75); strict and majority rule consensus trees are shown in Figs 1 and 2, respectively. Styphelieae form a

**Table 3. Further autapomorphies for terminal taxa (not used in analysis)**

Taxon	Autopomorphy
<i>Acrotriche</i>	pyrene splitting under pressure
<i>Astroloma</i> A	pollen vestibulate; corolla tube with five tufts of hair below middle
<i>A. baxteri</i>	lobes papillose or with tufts of hair at the apices
<i>A. pinifolium</i>	inapperturate pollen, anthers apically attached
<i>A. xerophyllum</i>	non-vestibular pollen
<i>Cyathopsis</i>	anthers apically attached
<i>Leucopogon</i> C	style broadly tapering to ovary
<i>Leucopogon</i> D	corolla hairs twisted
<i>L. kingianus</i>	style hairy toward base
<i>Melichrus</i>	corolla tube rotate or urceolate
'Pseudoactinia'	ovary trilocular
<i>Styphelia</i>	pollen warty or verrucate-baculate

clade (Fig. 1), within which can be distinguished a major sub-clade, termed the *Astroloma* clade, comprising, *inter alia*, *Styphelia*, *Astroloma*, *Melichrus* and much of *Leucopogon* s.l. There are also several smaller clades, including the *Monotoca*, *Melichrus* and *Styphelia* clades (Fig. 1). Despite the limited resolution of relationships in this analysis, several features of the consensus trees have significance for the taxonomy of the tribe.

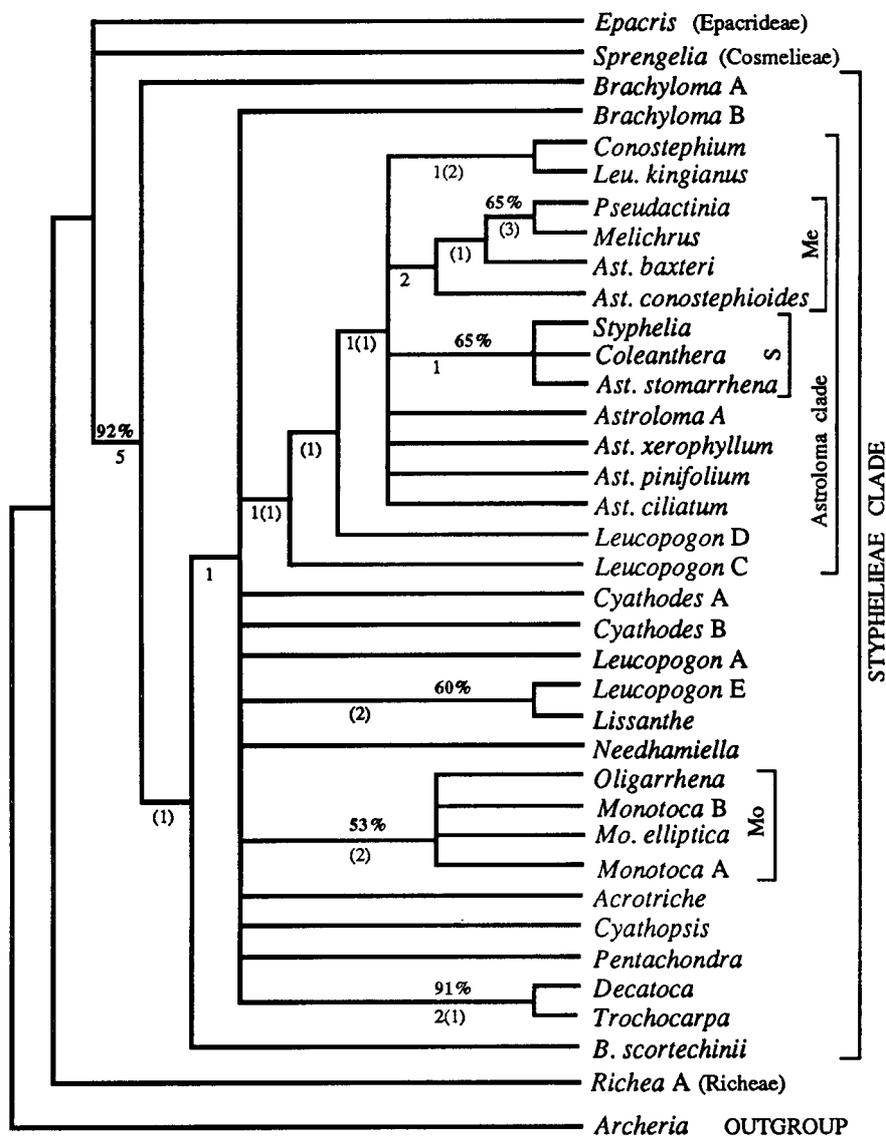
Given the limited resolution in the heuristic analysis, it is not surprising that bootstrap and decay analyses quickly exhausted the available computer memory. In order to obtain some assessment of the support for the clades recognised, a bootstrap analysis was performed with the steepest descent option selected and saving a single tree for each of 2000 replicates. The frequency with which clades appeared in the trees obtained, and the character support for clades is given in Fig. 1; changes of state are shown in Fig. 2. The association of *Decatoca* and *Trochocarpa* received strong support, being found in 91% of replicates; it is defined by three unambiguous changes including two unique synapomorphies (8/2, 11/2). There was some support for the link between *Melichrus* and 'Pseudactinia' (63%; three unambiguous changes) and *Leucopogon* E and *Lissanthe* (62%; two changes). The *Monotoca* clade was only weakly supported (51%; two changes). The remaining clades, including the *Astroloma*, *Styphelia* and *Melichrus* clades and the basal placement of *Brachyloma* A and *B. scortechinii*, received values below 50%, indicating little support for the topology.

On the basis of the intermediate type of pyrene, Bentham (1869) implied that the relationships of *Acrotriche* were with *Trochocarpa* and *Leucopogon*, but there is no support for this in the data base.

#### Reassessment of Generic Concepts

Much broader concepts of *Styphelia* than that generally accepted today have been used by Mueller (1867, 1889), Drude (1889), Sleumer (1963, 1964) and Viot (1975): *Acrotriche*, *Astroloma*, *Conostephium*, *Coleanthera*, *Cyathodes*, *Cyathopsis*, *Leucopogon*, *Lissanthe* p.p., *Melichrus* and *Monotoca* have all been included at some time. The inclusion of *Cyathodes*, *Cyathopsis* and *Leucopogon*, for example, within *Styphelia*, while separating *Conostephium*, *Coleanthera* and *Trochocarpa* (Sleumer 1964) does not accord with the results of this analysis. Initially two groups of *Styphelia* s. str. were recognised, based on the sections of Bentham (1869), but these proved to be homogeneous in the data base and were combined for the analyses. The genus is characterised by its monad, warty or verrucate-baculate pollen with 8–10 pores (14/5) (Table 3).

*Acrotriche* is characterised by a number of autapomorphies: restriction of corolla lobe hairs to an apical tuft (26/3), anthers exerted and/or reflexed on short filaments, and an intermediate fruit type (pyrene splitting under pressure). The genus also has corolla hairs spreading across the throat, and the flowers in a number of species are cauliflorous.



**Fig. 1.** Strict consensus of 1759 equally parsimonious trees. Me, *Melichrus* clade; Mo, *Monotoca* clade; S, *Styphelia* clade; Mo., *Monotoca*; Leu., *Leucopogon*. Bootstrap values shown above the branch for clades occurring in more than 50% of replicates; number of synapomorphies below, with those showing homoplasies within the tribe in parentheses.

*Cyathopsis* is defined by tetramerous flowers (21/1), anthers attached at the apex, long filaments and fully exerted anthers (7/1) as in *Styphelia*, but with the corolla lobes erect to spreading, not revolute as in that genus.

*Melichrus* is characterised by the autapomorphy corolla-tube hairs glandular (9/2). A related taxon comprising two new species from Western Australia and designated 'Pseudactinia' (Powell, unpublished data) is defined by its trilocular ovary (17/1), and is also distinguished from *Melichrus* by its thin-walled non-glandular corolla-tube hairs (9/0), glabrous corolla lobes (26/0) and distinctive filament insertion. The clade comprising these two genera is defined by three unambiguous changes, two of which are reversals (4/0, 16/0) and two (4/0, 19/1) are

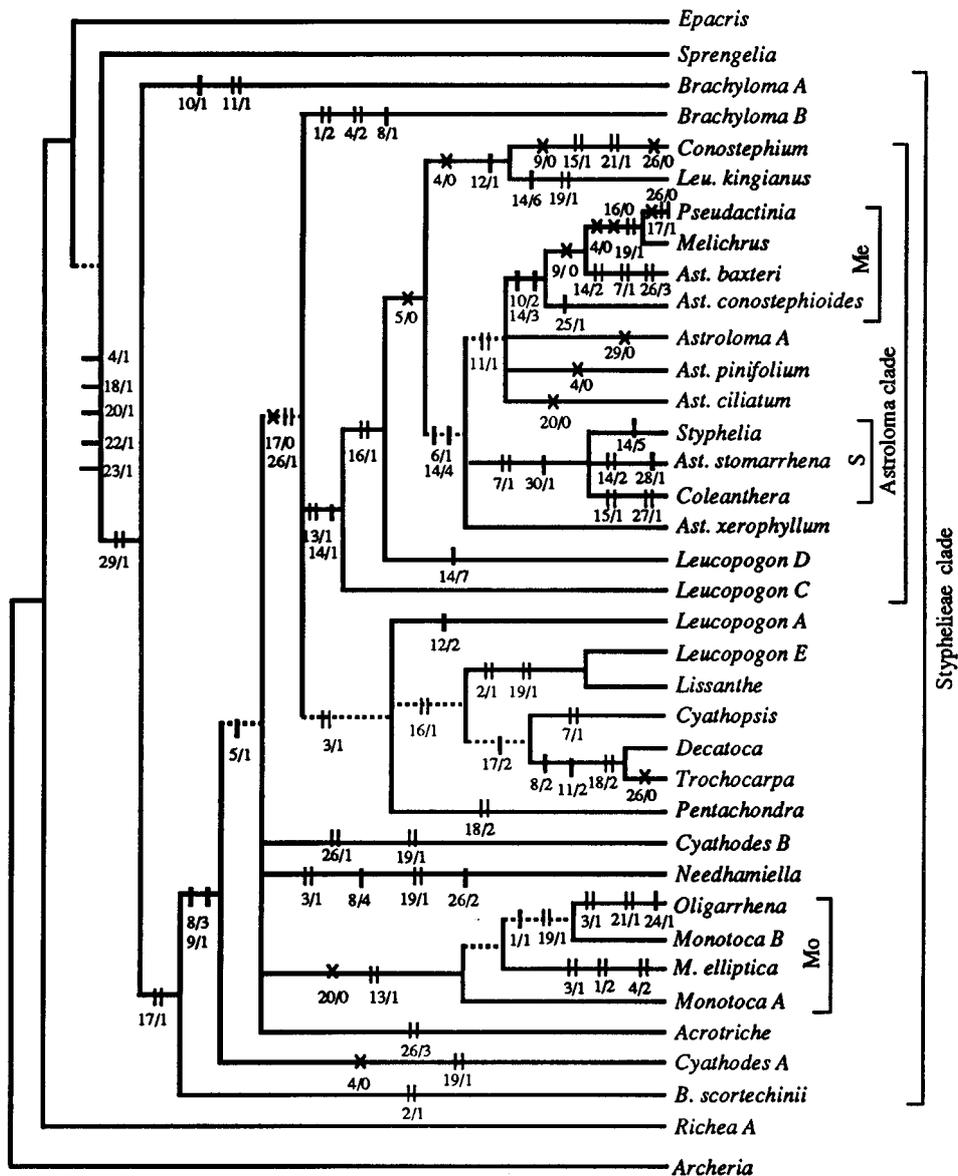


Fig. 2. Majority rule consensus tree with changes of state shown as follows: single bar, synapomorphy unique with Styphelieae clade; double bar, parallelism; cross, reversal. Labels as in Fig. 1; dotted branches collapse in the strict consensus.

highly homoplastic. The clade appeared in all the most parsimonious trees found, but received only moderate support in the bootstrap analysis (63%). In view of this weakness in character and bootstrap support, it seems preferable to recognise two distinct genera.

*Needhamiella* is distinguished by its induplicate-valvate aestivation (8/4) and by the restriction of hairs to the mid-line of the corolla lobe (26/2), both unique features in the tribe.

*Astroloma* as currently formulated is paraphyletic, and should be redefined to include only those species within *Astroloma* A, which is defined by vestibular pollen, fleshy corolla lobe apices, a reversal to capitate stigmas (29/0) and corolla tubes with five tufts of hair below the middle (Table 3).

*Astroloma stomarrhena*, *Coleanthera* and *Styphelia* form a sub-clade that is defined by the unique synapomorphy revolute corolla lobes (30/1) and also characterised by long erect stamens and exserted anthers (7/1). These three terminal taxa could be combined in a single genus. *Styphelia* is distinguished from the other two by its pollen apertures (14/5). *Coleanthera* possesses anthers that cohere around the style (27/1), a unique feature in the tribe, and also lacks a nectary (15/1). *Astroloma stomarrhena* has filaments that are hairy (28/1), which is again unique in the tribe, and its 6-colporate pollen (14/2) differs from that found in most *Styphelia*. This group warrants further detailed study before taxonomic changes are made.

The two species in section *Pentataphrus* Benth. (*Astroloma baxteri* and *A. conostephioides*) each share a closer relationship with *Melichrus* and 'Pseudactinia' than with *Astroloma* s. str., but the section appears paraphyletic (Fig. 1). Three other species are placed in isolated positions outside *Astroloma* s. str. Each of these five species is distinguished by autapomorphies: *A. xerophyllum* by non-vestibular pollen; *A. pinifolium* by inaperturate pollen and the filament attached to the anther at the apex, and a reversal to multibracteate flowers (4/0); *A. ciliatum* by absence of corolla-tube hairs (20/0); *A. conostephioides* by large coloured bracts and bracteoles (25/1); *A. baxteri* by six-colporate pollen (14/2), acuminate anthers on exserted filaments (7/1), corolla lobes with thick fleshy tissue towards the apex and sparse hairs restricted to it (26/3). Each appears to warrant recognition as a monotypic genus. The establishment of so many monotypic genera may seem rather extreme splitting, but the only valid alternative would involve the inclusion of *Coleanthera*, *Styphelia*, *Conostephium*, *Leucopogon kingianus*, *Melichrus*, 'Pseudactinia' and *Astroloma* s.l. in *Styphelia*. Such a generic concept does not appear to sit comfortably with the range of other currently accepted genera within the tribe, either in size or information content in the morphological data base; nor does it coincide with any of the broader concepts of *Styphelia* (e.g. Mueller 1889; Sleumer 1964). Formalisation of any changes will be left until the completion of a revision of *Astroloma* s.l. which is currently underway (A. Wilson, pers. comm.).

*Brachyloma* presently includes a very diverse set of taxa. In Fig. 1, *Brachyloma* A and *B. scortechinii*, which together constitute section *Lobopogon* Benth., occupy separate basal positions within the tribe. Both possess the series of synapomorphies defining Styphelieae (4/1, 18/1, 20/1, 22/1, 23/1). Each is distinguished by apomorphies: *Brachyloma* A possesses the unique hair pads near the base of the corolla lobes (10/1) and flattened filaments (11/1) that are quite distinct from the much broader ones found in *Astroloma*; in *B. scortechinii*, the flowers are pedicellate above the bracteoles (2/1). *Brachyloma* B (section *Lissanthoides* Benth.) is included along with most members of the tribe within the major polychotomy defined by non-keeled floral bracteoles (5/1), corolla lobes that are valvate in the bud, at least in the upper part (8/3) and ornamented corolla hairs (9/1). Hence, *Brachyloma* s. str. should be restricted to the species within *Brachyloma* A, and two new segregate genera are required to accommodate the other species.

*Cyathodes* consists of two groups, *Cyathodes* A and B, that share no close relationship. There was a tendency for them to be separated by the *Monotoca* clade (Fig. 2). *Cyathodes* A is characterised by a reversal to many unkeeled bracteoles (4/0) and a strongly keeled pair of bracts at the base of the inflorescence. There are no synapomorphies in this data base defining *Cyathodes* B (only homoplasies in 19/1 and 26/1), but recent work on leaf waxes supports this division of the genus: *Cyathodes* A has 'ribbon' wax on the abaxial leaf surface, whereas *Cyathodes* B has amorphous or plate forms of wax (Weiller *et al.* 1994). *Cyathodes empetrifolia*, which lacks corolla tube hairs, was initially separated from *Cyathodes* B but recombined for the final analysis. The two terminal taxa within *Cyathodes* show no close relationship and should be recognised as separate genera.

*Leucopogon* is clearly polyphyletic, consisting of five quite distinct entities. *Leucopogon* s. str. should be restricted to the 63 named species (58 from section *Perojoa* Benth. and five from section *Heteranthus* Benth.) and some 50 unnamed species belonging to *Leucopogon* A. A sterile tip to the anther (12/2) is a unique synapomorphy defining this genus.

*Leucopogon* C and D are placed basally in the *Astroloma* clade. *Leucopogon* C, comprising eight species from section *Pleuranthus* Benth., one from section *Perojoa*, and

another nine newly described species, is characterised by four-colporate pollen (14/1), a cone-like gynoecium and narrow-cylindrical fruit. *Leucopogon* D, totals some 80 species, including the remainder of section *Pleuranthus*, and is characterised by multiporate pollen (14/7) and twisted corolla hairs.

*Leucopogon* E, consisting of four species in section *Heteranthus*, can be united with *Lissanthe*. The two genera were clustered in all trees and in 62% of bootstrap replicates, and share flowers that are pedicellate above the bracteoles (2/1) and parallelodromous venation (19/1). This change will be formalised elsewhere. Two species originally assigned to *Lissanthe* section III (Brown 1810) were later transferred to *Brachyloma* (Bentham 1869; *B. daphnoides*, *B. ciliatum*). These are placed within *Brachyloma* B in this analysis, quite distant from *Lissanthe*.

*Leucopogon kingianus* and *Conostephium* were associated in all of the most parsimonious trees, sharing the unique synapomorphy anthers that are shortly bifurcate (12/1). This arrangement, however, is poorly supported: it occurred in only 34.5% of bootstrap replicates, and the taxa are distinguished by the strictly parallelodromous venation (19/1), annular porate pollen (14/6) and the unusual style bearing hairs towards its base in *Leucopogon kingianus*, and by the reduced locule number (21/1), unique corolla form with the anthers enclosed within a cone, very short glabrous corolla lobes (26/0), unornamented hairs (9/0) and absence of the nectary (15/1) in *Conostephium*. Large bracteoles and the strongly keeled pair of bracts at the base of the inflorescence are other distinguishing features of *Leucopogon kingianus*. In view of these pronounced differences, the erection of the monotypic genus, *Croninia* (Powell 1993), to accommodate this distinctive species seems appropriate.

*Monotoca* is shown to be paraphyletic, *Oligarrhena* occupying a derived position in the same clade (Fig. 1). The *Monotoca* clade, although only weakly supported in the bootstrap analysis (52%), is defined by monad pollen (13/1) and a glabrous corolla tube (20/0). Only the reduction in number of stamens (24/1) is unique to *Oligarrhena*, the reduced number of corolla lobes (21/1) also occurring in *M. empetrifolia* (*Monotoca* A). *Monotoca* A is distinguished by unilocular ovaries, *Monotoca* B has lost the inflorescence rudiment, while *M. elliptica* has caducous inflorescence bracts (1/2) and a reduced number of floral bracts (4/2). Two species from *Monotoca* A, *M. empetrifolia* and *M. rotundifolia*, the former with tetramerous flowers and the latter lacking the rudiment, were initially segregated but recombined in the final analysis. In view of the small size of the segregates and their weak separation, a single more broadly defined genus, *Monotoca* s.l., incorporating *Oligarrhena* seems most appropriate.

The monotypic *Decatoca* from eastern New Guinea differs from *Trochocarpa* only in the corolla lobes being imbricate rather than valvate at anthesis (Sleumer 1964). Since the lobes in *Trochocarpa* are sometimes slightly imbricate distally in the bud, there seems little justification for maintaining the generic distinction. *Trochocarpa* is represented in this analysis only by species within subgenus *Trochocarpa* Sleumer (Table 1), suitable material of the two New Guinean species of subgenus *Pseudocyathodes* being unavailable. Since the flowers are multibracteate, solitary or in clusters and the habit ranges from prostrate to erect in *Pseudocyathodes*, their inclusion may influence the distinction between *Pentachondra* and *Trochocarpa*. The separation of these genera, which Mueller (1889) combined, appears to be based solely on the number of locules within the ovary. The fact that *Decatoca*, *Trochocarpa* and *Pentachondra* are the only genera in Epacridaceae to be devoid of structured epicuticular wax (Weiller *et al.* 1994) may be further evidence of an affinity between them. It is concluded here, however, that *Pentachondra* should be maintained pending further testing of its relationships on an expanded data base.

#### Suprageneric Relationships

*Leucopogon* A shows no close affinity to any other genus, although there is a weak tendency for it to be linked to the *Lissanthe* and *Trochocarpa* groups (Fig. 2). The relationship of *Melichrus* to *Astroloma* and *Leucopogon*, suggested by Bentham (1869), is consistent with this analysis to the extent that several segregates of these last two genera are also placed within the *Astroloma* clade, but there is no evidence that such links are

significantly closer than those between other members of the clade. Further, the clade itself and virtually all its internal topology was unsupported in the bootstrap analysis (Fig. 1), so the implied affinities must be treated as tentative.

There is no evidence of a close relationship between either segregates of *Cyathodes* and *Styphelia*, as proposed by Mueller (1867) and Sleumer (1963), or to *Leucopogon* (Allan 1961). Neither is there support for an affinity between *Needhamiella* and any of the segregates of *Leucopogon*, as suggested by Bentham (1869), although the position of the *Needhamiella* within Styphelieae (Powell *et al.* 1996) is certainly confirmed (cf. Watson 1967).

Styphelieae constitute a strongly supported monophyletic group defined by five synapomorphies and identified in 98% of bootstrap replicates (Figs 1, 2; see also Powell *et al.* 1996). The intergeneric pattern of relationships that has been resolved within the tribe on this data base is, however, only poorly supported. Hence the basal position of *Brachyloma* A and *B. scortechinii*, and the major affinity group implied by the *Astroloma* clade must be regarded as highly speculative. A molecular data base is presently being assembled in order to test these tentative phylogenetic hypotheses, and also the revised generic concepts that are proposed here.

### Acknowledgments

We are particularly indebted to Drs B. G. Briggs and L. A. S. Johnson for their detailed comments on drafts of this work. We also thank the many colleagues with whom we have discussed this project: Drs B. Conn, M. Crisp, W. Judd, K. Kron, P. Stevens and P. Weston, and Mr A. Doust. We gratefully acknowledge funding support for parts of this work from the Australian Biological Resources Study and Australian Research Council grant No. A19330712.

### References

- Allan, H. H. (1961). 'Flora of New Zealand.' Vol. 1. (Government Printer: Wellington.)
- Anderberg, A. A. (1993). Cladistic interrelationships and major clades of the Ericales. *Plant Systematics and Evolution* **184**, 207–231.
- Bentham, G. (1869). 'Flora Australiensis.' Vol. 4. (Reeve and Co.: London.)
- Brown, R. (1810). 'Prodromus Florae Novae Hollandiae et Insulae Van Diemen.' Vol. 1. (Taylor: London.)
- Copeland, H. F. (1954). Observations on certain Epacridaceae. *American Journal of Botany* **41**, 215–221.
- Crayn, D. M., Kron, K. A., Gadek, P. A., and Quinn, C. J. (1996). Delimitation of Epacridaceae: preliminary molecular evidence. *Annals of Botany* **77**, 317–321.
- Drude, O. (1889). Epacridaceae. In 'Die natürlichen Pflanzenfamilien'. Vol. 4, 1st edn (Eds A. Engler and K. Prantl.) pp. 66–79. (Engelmann: Leipzig.)
- Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791.
- Franks, J. W., and Watson, L. (1963). The pollen morphology of some critical Ericales. *Pollen et Spores* **5**, 51–68.
- Judd, W. S., and Kron, K. A. (1993). Circumscription of Ericaceae (Ericales) as determined by preliminary cladistic analyses based on morphological, anatomical, and embryological features. *Brittonia* **45**, 99–114.
- Kron, K. A. (1996). Phylogenetic relationships in the Ericales: evolution of Epacridaceae and Ericaceae based on nuclear ribosomal 18S sequence data. *Annals of Botany* **77**, 293–303.
- Kron, K. A., and Chase, M. W. (1993). Systematics of the Ericaceae, Empetraceae, Epacridaceae and related taxa based upon *rbcL* sequence data. *Annals of the Missouri Botanical Garden* **80**, 735–741.
- McGlone, M. S. (1978). Pollen structure of the New Zealand members of the Styphelieae (Epacridaceae). *New Zealand Journal of Botany* **16**, 91–101.
- Maddison, W. P., Donaghue, M. J., and Maddison, D. R. (1984). Outgroup analysis and parsimony. *Systematic Zoology* **33**, 83–103.
- Maddison, W. P., and Maddison, D. R. (1992). 'MacClade: an Analysis of Phylogeny and Character Evolution.' Version 3. (Sinauer: Sunderland, MA.)
- Mueller, F. von (1867). 'Fragmenta Phytographiae Australiae.' Vol. 6. (Government Printer: Melbourne.)

- Mueller, F. von (1889). 'Second Systematic Census of Australian Plants. Part I. Vasculares.' (McCarron Bird: Melbourne.)
- Powell, J. M. (1993). *Croninia kingiana* (Epacridaceae), a change in status for *Leucopogon kingianus*. *Nuytsia* **9**, 123–130.
- Powell, J. M., Crayn, D. M., Gadek, P. A., Quinn, C. J., Morrison, D. A., and Chapman, A. R. (1996). A re-assessment of relationships within Epacridaceae. *Annals of Botany* **77**, 305–315.
- Rao, C. V. (1961). Pollen types in the Epacridaceae. *Journal of the Indian Botanical Society* **40**, 409–423.
- Sleumer, H. (1963). *Florae Malesianae Praecursores 37: Materials towards the knowledge of the Epacridaceae mainly in Asia, Malaysia and the Pacific*. *Blumea* **12**, 145–171.
- Sleumer, H. (1964). Epacridaceae. In 'Flora Malesiana'. Series 1, Vol. 6. (Ed. C. G. G. J. van Steenis.) pp. 422–444. (Noordhoff: Groningen.)
- Smith-White, S. (1948). A survey of chromosome numbers in the Epacridaceae. *Proceedings of the Linnean Society of New South Wales* **73**, 37–56.
- Smith-White, S. (1955). Chromosome numbers and pollen types in the Epacridaceae. *Australian Journal of Botany* **3**, 48–67.
- Smith-White, S. (1959). Pollen development patterns in the Epacridaceae. *Proceedings of the Linnean Society of New South Wales* **84**, 8–35.
- Swofford, D. L. (1993). 'PAUP: Phylogenetic Analysis using Parsimony.' Version 3.1.1. (Illinois Natural History Survey: Champaign, Illinois.)
- Virost, R. (1975). Epacridaceae. In 'Flora de la Nouvelle-Caledonie et Dependances'. Vol. 6. (Ed. N. Hallé.) pp. 1–161. (Museum National d'Histoire Naturelle: Paris.)
- Watson, L. (1967). Taxonomic implications of a comparative anatomical study of Epacridaceae. *New Phytologist* **66**, 495–504.
- Weiller, C. M., Crowden, R. K., and Powell, J. M. (1994). Morphology and taxonomic significance of leaf epicuticular waxes in the Epacridaceae. *Australian Systematic Botany* **7**, 125–152.
- Williamson, H. B. (1924). Description of a new Victorian plant. *Victorian Naturalist* **40**, 231–234.