

Systematic studies in *Lepidosperma* (Cyperaceae: Schoeneae) with particular reference to *L. laterale*

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Abstract. *Lepidosperma laterale* exhibits much morphological variation across its geographical range. This study included *L. laterale*, and morphologically similar species, as well as several comparator species. Phenetic analyses based on 27 morphological and 25 vegetative anatomical characteristics were undertaken in an attempt to resolve taxonomic issues within the study group. Evidence for broadening the delimitation of *L. laterale* is strong as OTUs of this variable species formed a group with indistinct clusters in all analyses. The mixed, diffuse clusters obtained of OTUs of specimens identified as *L. gunnii* with specimens of *L. laterale* suggest that the species limits of the former lie within the limits of the latter. Specimens of most other study group taxa formed relatively cohesive, discrete clusters in ordination and cluster analyses. The results provide strong support for recognition of *L. sp.* Whian Whian S.F. (J. Hodgson 331 & D.M. Hodgson) and *L. sp.* Mt Coolum (P.R. Sharpe 5605A) as new species.

Introduction

Lepidosperma Labill. is a primarily Australian genus of ~70 species, with a few species found in New Zealand, New Caledonia and Malesia (Kern 1974). All but two of the ~63 species native to Australia are endemic (Kern 1974; Wilson 1993). The genus is characterised by isobilateral, distichous leaves and short, fleshy or scale-like and persistent perianth members commonly referred to as hypogynous scales (Dahlgren *et al.* 1985; Bruhl 1995; Geotghebeur 1998).

Although Bentham (1878, p. 385) considered the genus ‘one of the most natural among Cyperaceae’ he acknowledged the difficulty of recognising species limits within *Lepidosperma* due to a lack of variation across certain characters, including the positioning of leaves and flowers, and the structure of flowers and fruit. Few characters appear to differentiate species of *Lepidosperma* (Kern 1974; Wilson 1994a, 1994b), yet some species are nevertheless highly variable in morphology (Wilson 1993, 1994a, 1994b; Curtis and Morris 1994). This contrast is no more apparent than in the group of species consisting of *L. laterale* and those considered similar or closely related to it, including *L. elatius* and *L. gunnii* (Wilson 1993, 1994a, 1994b; Curtis and Morris 1994).

Lepidosperma laterale sens. lat. is a widespread species found in a variety of mesic to sclerophyllous habitats in eastern and south-eastern Australia (i.e. Queensland, New South Wales, Victoria, Tasmania and south-eastern

South Australia), New Zealand and New Caledonia (Sharpe 1986; Wilson 1993, 1994a; Curtis and Morris 1994). Throughout much of this geographical range the taxon exhibits much morphological variation both within and between populations (Wilson 1993, 1994a, 1994b; Curtis and Morris 1994).

The need to clarify the limits of *L. laterale* has long been recognised (Willis 1970; Wilson 1993, 1994a, 1994b), but to date no detailed and analytical, systematic study has been attempted. Localised recognition of three varieties of *L. laterale* (the typical variety and *L. laterale* var. *angustum* and *L. laterale* var. *majus*; e.g. in Sharpe 1986) highlighted the need for a better understanding of taxon limits in this complex (Wilson 1993, 1994a; Curtis and Morris 1994).

While selecting specimens for the present analysis, significant differences became apparent between specimens and species descriptions of *L. curtisiae*, *L. elatius* and *L. gunnii* provided by Sharpe (1986) and Wilson (1993, 1994a). These discrepancies indicated that the limits of these three species also warranted investigation. Specimens displaying consistent morphological differences were designated for the analyses as *L. sp.* Hardacres, *L. sp.* Whian Whian S.F. and *L. sp.* Coaldale respectively (Table 1). Specimens from Mt Coolum, which could be assigned to *Lepidosperma* but not to any described species in Sharpe (1986) or Wilson (1993, 1994a), were recognised as *L. sp.* ‘Mt Coolum’.

Table 1. Study group taxa

Citation of authorities follows Brummitt and Powell (1992) except where indicated. Format of citations of undescribed taxa follows Briggs and Leigh (1996): abbreviated to *L. sp.* Hardacres, *L. sp.* Whian Whian S.F., *L. sp.* Coaldale and *L. sp.* Mt Coolum respectively throughout the text

Core group taxa	Comparator taxa
<i>Lepidosperma curtisiae</i> K.L. Wilson & D.I. Morris	<i>L. filiforme</i> Labill.
<i>L. sp.</i> Hardacres (J. Hodgon 357 & J. J. Bruhl)	<i>L. tortuosum</i> F. Muell.
<i>L. ensiforme</i> (Rodway) D.I. Morris	<i>Schoenus ericetorum</i> R.Br.
<i>L. elatius</i> Labill.	<i>S. melanostachys</i> R.Br.
<i>L. sp.</i> Whian Whian S.F. (J. Hodgon 331 & D.M. Hodgon)	
<i>L. globosum</i> Labill.	
<i>L. gunnii</i> Boeck.	
<i>L. sp.</i> Coaldale (J. Hodgon 313 & D.M. Hodgon)	
<i>L. inops</i> Rodway ex F. Muell.	
<i>L. latens</i> K.L. Wilson	
<i>L. laterale</i> R.Br. var. <i>laterale</i>	
<i>L. laterale</i> var. <i>angustum</i> Benth.	
<i>L. laterale</i> var. <i>majus</i> Benth.	
<i>L. oldfieldii</i> Hook. f.	
<i>L. sp.</i> Mt Coolum (P.R. Sharpe 5605A)	
<i>L. viscidum</i> R.Br.	

Current supposed relationships of *L. laterale* and its putative relatives, as outlined in Fig. 1, were deduced from various treatments (Bentham 1878; Sharpe 1986; Wilson 1993, 1994a, 1994b; Wilson and Morris 1993; Curtis and Morris 1994). Nomenclature reflects useage in current treatments of *Lepidosperma* for Queensland (Sharpe 1986), New South Wales (Wilson 1993), Victoria (Wilson 1994a) and Tasmania (Curtis and Morris 1994). Hypothesised relationships between several taxa are based on gross morphological similarities between them, for example *L. laterale* and *L. elatius* (Wilson 1993) or *L. globosum* and *L. laterale* (Bentham 1878).

Relationships within this group, in common with all other relationships depicted in Fig. 1, have not been tested. There is a single, partial reconstruction of phylogeny for a sample of New South Wales *Lepidosperma* species (Gray 1994), but we agree with the author that the value of the analysis is low as it did not include all species of the genus and was only weakly supported by strict consensus.

The aims of this study were to (1) explore the taxonomy of *L. laterale sens. lat.* with non-molecular data sources, (2) test species limits within *L. laterale*, *L. curtisiae*, *L. elatius* and *L. gunnii* based on phenetic analysis and (3) determine the status of specimens of *L. sp.* Mt Coolum based on phenetic analysis.

Materials and methods

Selection of study group taxa

The study group was divided into a core group (of which *Lepidosperma laterale* R.Br. formed the basis) and comparator group (Table 1). Other members of the core group were included to obtain a broader perspective and allow thorough testing of taxonomic issues within and surrounding *L. laterale* (Fig. 1).

Two comparator species of *Lepidosperma* (*L. filiforme* and *L. tortuosum*; Table 1) were selected on the basis of their apparent taxonomic stability and taxonomic separation from the study group (Wilson 1993; Fig. 1). Similarly, two species of *Schoenus* (*S. ericetorum*

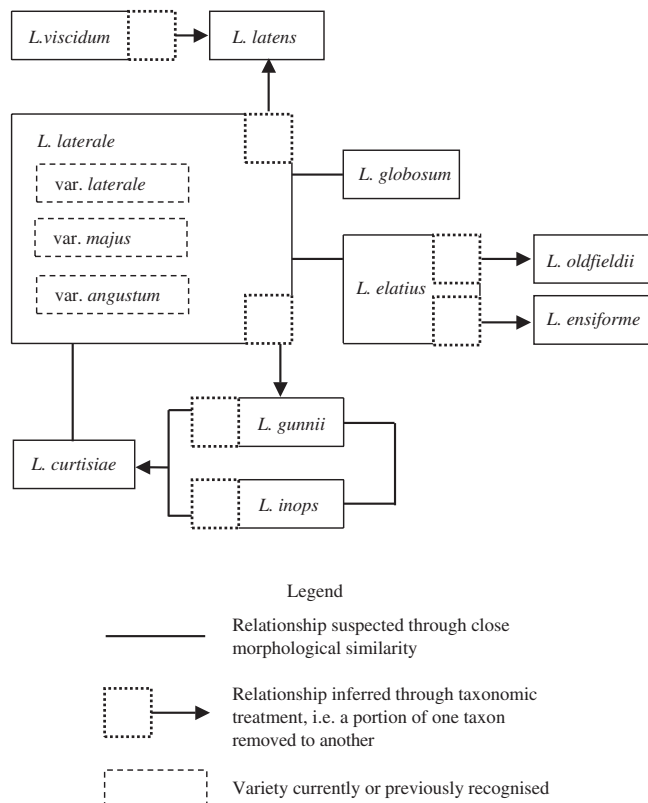


Fig. 1. Putative taxonomic relationships of *Lepidosperma laterale* and associated species.

and *S. melanostachys*; Table 1) were included because of their relatively close relationship to *Lepidosperma* (Bruhl 1995).

Sampling intensity and method

A combination of herbarium specimens and field collection of whole plants (including roots, stems, leaves and inflorescences) was used. Collecting effort was concentrated on the area between Bundaberg and Sydney (from the coast to ~250 km inland), an area identified as containing most of the apparent morphological variation within *L. laterale*. Wherever possible sampling was conducted across ecological boundaries, and to obtain material at comparable developmental stages. Unfortunately, many incomplete herbarium specimens without leaves or plant bases had to be excluded because many of the characters could not be scored.

The 141 specimens used in the phenetic analysis (i.e. the Operational Taxonomic Units or OTUs) are listed in Appendix 1 (see the website of Australian Systematic Botany). The putative species were represented by at least four specimens, with the maximum being 42 for *L. laterale* (including its previously recognised varieties but excluding *L. gunnii*).

Phenetic analysis

The phenetic approach to resolving taxonomic issues is commonly used at and below the species level (Duncan and Baum 1981; Stuessy 1990). At lower taxonomic levels phenetics (i.e. cluster analysis and ordination) is considered more appropriate than cladistics because it does not assume a linear model of evolution (i.e. ancestor–descendant relationship) that may not be appropriate where reticulate relationships may be common (particularly in plants, owing to hybridisation and allopolyploidy; Stuessy 1990; Judd *et al.* 2000). Ordination is particularly useful in this context as it does not attempt to impose a hierarchical pattern on the data where no such pattern exists (Crisp and Weston 1993). Both ordination and cluster analyses were used to seek congruence and provide greater confidence in the results.

Selection of characters

Characters were selected (Table 2) on the basis of examination of the variation observed among specimens of *L. laterale* and assessment of prior work on *Lepidosperma* and Cyperaceae (cf. Metcalfe 1971; Bruhl *et al.* 1992; Wilson 1993, 1994a; Gray 1994; Bruhl 1995).

The issue of time v. return for effort was also taken into account and in some cases a character was rejected on the basis of being overly time-consuming to assess properly. One such character was the number of silica bodies per epidermal cell, which was indicated as a source of variation among species of *Lepidosperma* by Metcalfe (1971), but which, in practice, proved to be both time-consuming and difficult to assess.

Character-state data collection

Morphological characters (Table 2) were measured to an accuracy of 0.5 mm with a ruler and eyepiece graticule. Anatomical characters (Table 2) were observed in transverse sections and epidermal scrapes from herbarium specimens or specimens fixed in formalin:propionic acid:70% ethanol = 5:5:90 (FPA) and stored in liquid preservative (70% ethanol:glycerol = 99:1). Material from herbarium specimens was rehydrated before sectioning by gently boiling in water, with a few drops of liquid household detergent, until soft. Material from specimens stored in liquid preservative required no such treatment before sectioning.

Sections were hand-cut with one half of a double-edged razorblade. Epidermal scrapes were prepared by cutting sections of culm or leaf longitudinally and then scraping away all internal tissue with a scalpel to leave only the epidermis intact. Cross-sections and epidermal scrapes

were stained with Toluidine Blue (cf. Prakash 1986) and mounted in 50% glycerol before examination under a Leitz HM-LUX compound microscope.

Datasets

Morphological and anatomical character-state data from all OTUs were prepared as a spreadsheet in Microsoft Excel 7.0 (Appendix 1). Several comparisons between character states and specimen attributes were made during the course of data collection to ensure consistency in interpretation and application of character states.

Subsets (Table 3; Appendices 2–4) of data matrix 1 (Appendix 1) were subsequently analysed to further clarify the pattern of similarity among OTUs of various taxa.

Data matrix 1 contained 141 OTUs and 43 characters (26 morphological and 17 anatomical) and 104 character states (following removal of invariant states) including 20 quantitative and 24 qualitative characters comprising nine binary, 10 three-state, three four-state, one 12-state and one 14-state characters (Table 3; Appendix 1).

Data matrix 2 (Table 3; Appendix 2, see website of Australian Systematic Botany) was used to examine more closely the phenetic relationships among OTUs representing *L. laterale* var. *laterale*, *L. laterale* var. *angustum*, *L. laterale* var. *majus*, *L. gunnii*, *L. sp.* Coaldale and *L. sp.* Hardacres as these putative taxa exhibited the most diffuse clusters in analyses of data matrix 1. The data matrix comprised 40 characters (23 morphological and 17 anatomical) with 86 attributes (following removal of invariant states) including 17 quantitative and 23 qualitative characters comprising 11 binary, seven three-state, two four-state, one 9-state and one 13-state characters.

Data matrix 3 (Table 3; Appendix 3, see website of Australian Systematic Botany) included OTUs representing all study group taxa except those in data matrix 2, i.e. excluding *L. laterale* var. *laterale*, *L. laterale* var. *angustum*, *L. laterale* var. *majus*, *L. gunnii*, *L. sp.* Coaldale and *L. sp.* Hardacres. The data matrix comprised 43 characters (26 morphological and 17 anatomical) with 94 attributes (following removal of invariant states) including 20 quantitative and 24 qualitative characters comprising 16 binary, three three-state, three four-state and two 10-state characters.

Data matrix 4 (Table 3; Appendix 4, see website of Australian Systematic Botany) included OTUs representing *L. elatius*, *L. sp.* aff. *elatius*, *L. ensiforme* and *L. oldfieldii*. The data matrix comprised 42 characters (25 morphological and 17 anatomical) with 79 attributes (following removal of invariant states) including 20 quantitative and 22 qualitative characters comprising 11 binary, six three-state, four four-state and one seven-state characters.

Data matrices containing only morphological or anatomical character-state data were subjected to phenetic analysis using the methods described below as part of a trial phenetic analysis conducted once data collection was complete. These results are not presented (but see Table 3) as much clearer and discernible groupings, in both ordination and cluster analyses, were obtained when morphological and anatomical data were combined (i.e. Appendices 1–4).

Data analysis

Ordination and cluster analyses were performed with PATN v. 3.6 (Belbin 1993). For each data matrix, characters or character states containing only invariant or missing values were removed before analysis (Appendices 1–4). Data relating to leaf-to-culm length ratio (Table 2; Appendix 1) were transformed by $\log(x + 1)$ but no discernible difference was found between ordinations or clustering analyses using transformed or untransformed data so all analyses presented include the untransformed data for this character (Appendices 1–4). Gower distance

Table 2. Morphological and anatomical characters and states used in phenetic analyses

Characters 1, 3, 4 and all anatomical characters were assessed within the mid-third of culm or leaf length. Characters 10–14 and 16–21 were assessed within the mid-third of the inflorescence length. All numeric characters were the mean of five measurements (Appendix 1). Novel characters not previously used in studies of *Lepidosperma* are italicised. Other morphological and anatomical characters are from Metcalfe (1971), Bruhl (1990, 1995), Bruhl *et al.* (1992) and Wilson (1993) unless otherwise stated. Hewson (1988) and Harden (1993) were used as glossaries for terms given in the table. *Anatomical character observed in transverse section (all other anatomical characters were observed in longitudinal section)

Character

Morphology

1. Culm: maximum width (mm)
2. Culm: maximum length to base of involucre bract sheath (mm)
3. Culm margins: smooth (1), scabrous (2), viscid (3)
4. Leaf: maximum width (mm)
5. Leaf: maximum length (mm)
6. Leaf length-to-culm length ratio
7. Leaf bases (whether breaking down into fibres): fibrous (1), not fibrous (2)
8. Inflorescence shape in outline: circular (1), ovate (2), linear (3), oblong (4)
9. *Inflorescence: maximum length of main axis (mm)*
10. *Inflorescence: length of node plus internode unit along main axis (mm)*
11. *Inflorescence: number of lateral branches per node*
12. *Inflorescence: maximum lateral branch length (mm)*
13. *Lateral inflorescence branch: number of spikelets*
14. Spikelet: length excluding pedicel (mm)
15. Rachis: flexuose (1), straight (2)
16. Fertile floral bracts: number per spikelet
17. Fertile floral bract: length (mm)
18. Fertile floral bracts shape in dorsiventral view: circular (1), ovate (2), oblong (3), elliptical (4), obovate (5)
19. Fertile floral bract apex shape: subulate (1), retuse (2), truncate (3), rounded (4), obtuse (5), acute (6), acuminate (7)
20. Fertile floral bract margin indumentum type: glabrous (1), papillose (2), scabrous (3), ciliate (4), pilose (5)
21. Sterile floral bracts: number per spikelet
22. Shape of perianth members: subulate (1), retuse (2), truncate (3), rounded (4), obtuse (5), acute (6), acuminate (7)
23. Style branch: number. (Invariant, 3 in all taxa studied)
24. Fruit in lateral view: round (1), ovate (2), oblong (3), elliptical (4), obovate (5)
25. Fruit in transverse section: circular (1), elliptical (2), trigonous (3)
26. Fruit: maximum length (mm)
27. Fruit: maximum diameter (mm)

Anatomy

28. *Culm cross-sectional shape (Metcalfe 1971): triangular (1), circular (2), truncate circular (3), square with rounded corners (4), subhemispherical (5), oblong (6), fusiform (7), thickly crescentiform (8), thinly crescentiform (9), broadly elliptical (10), broadly elliptical and winged (11), broadly elliptical with one rounded margin (12), broadly elliptical with deeply furrowed outline (13), narrowly elliptical (14)
29. *Culm stomata: position relative to epidermal cells: sunken (1), flush (2), raised (3). (Invariant, flush in all taxa studied)
30. Culm stomatal rows within each intercostal zone: 1 (1), 2 (2), > 2 (3)
31. Culm stomata, outline shape in surface view at 40×: elliptical (1), circular (2). (Invariant, elliptical in all taxa studied)
32. *Culm vascular bundles: number
33. *Culm 'maximum cells-distant count' (indicative of C₃ or C₄ photosynthetic pathway; Hattersley and Watson 1975): 1 = C₄ (1), > 1 = C₃ (2). (Invariant, > 1 = C₃ in all taxa studied)
34. *Culm sclerenchyma, whether in direct contact with vascular bundles: in direct contact (1), not in direct contact (2)
35. *Culm multicellular trichomes: present singly (1), present in groups (2), absent (3)*
36. *Culm multicellular trichome shape: domed and smooth (1), domed with prickle hairs (2)*
37. Culm intercostal cell shape: regular and rectangular (1), irregular (2). (Invariant, irregular in all taxa studied)
38. Culm: rows of intercostal cells per epidermal zone (Metcalfe 1971)
39. Culm relative width of epidermal zones: wider costally (1), of equal width (2), wider intercostally (3)
40. *Leaf cross-sectional shape (Metcalfe 1971): truncated circular (1), oblong (2), fusiform (3), winged fusiform (4), thickly crescentiform (5), thinly crescentiform (6), broadly elliptical (7), broadly elliptical and winged (8), broadly elliptical with one rounded margin (9), broad elliptical and constricted (10), narrowly elliptical (11), narrowly elliptical with deeply furrowed outline (12)
41. *Leaf stomata, position relative to epidermal cells: sunken (1), flush (2), raised (3). (Invariant, flush in all taxa studied)
42. Leaf stomatal rows within each intercostal zone: 1 (1), 2 (2), > 2 (3)
43. Leaf stomata, outline shape in surface view at 40×: elliptical (1), circular (2). (Invariant, elliptical in all taxa studied)
44. *Leaf vascular bundles: number
45. *Leaf 'maximum cells-distant count' (indicative of C₃ or C₄ photosynthetic pathway; Hattersley and Watson 1975): 1 = C₄ (1), > 1 = C₃ (2). (Invariant, > 1 = C₃ in all taxa studied)
46. *Leaf 'midrib' if present, whether anatomically symmetrical: absent (1), symmetrical (2), not symmetrical (3)
47. *Leaf sclerenchyma, whether in direct contact with vascular bundles: in direct contact (1), not in direct contact (2)
48. *Leaf multicellular trichomes: present singly (1), present in groups (2), absent (3)*
49. *Leaf multicellular trichome shape: domed and smooth (1), domed with prickle hairs (2)*
50. Leaf intercostal cell shape: regular and rectangular (1), irregular (2). (Invariant, irregular in all taxa studied)
51. Leaf: rows of intercostal cells per epidermal zone (Metcalfe 1971)
52. Leaf relative width of epidermal zones: wider costally (1), of equal width (2), wider intercostally (3)

Table 3. Data matrices used in phenetic analyses

Data sources: A = anatomy; M = morphology

Data matrix	Taxa included	Data sources	No. of OTUs
1	All study group taxa	M, A	141
1a	as for 1	M	141
1b	as for 1	A	141
2	<i>Lepidosperma laterale</i> (all varieties) <i>L. gunnii</i> <i>L. sp. Coaldale</i> <i>L. sp. Hardacres</i>	M, A	67
2a	as for 2	M	70
2b	as for 2	A	70
3	All study group taxa except: <i>L. laterale</i> (all varieties) <i>L. gunnii</i> <i>L. sp. Coaldale</i> <i>L. sp. Hardacres</i>	M, A	85
3a	as for 3	M	85
3b	as for 3	A	85
4	<i>L. elatius</i> <i>L. sp. aff. elatius</i> <i>L. ensiforme</i> <i>L. oldfieldii</i> <i>Schoenus ericetorum</i> <i>S. melanostachys</i>	M, A	34
4a	as for 4	M	34
4b	as for 4	A	34

coefficient (which includes range standardisation of data) was applied to all data matrices (Table 3) as it is considered most able to deal with mixed binary, multi-state and quantitative data (Stuessy 1990; Crisp and Weston 1993).

Ordination analyses were performed by the semi-strong-hybrid multidimensional scaling (SSH) technique with all default settings, and default settings with 20 random starts and 100 iterations. No decrease in ordination stress values was achieved by employing 100 iterations over 20 iterations (the default setting). No difference in ordination analyses of any data matrix was produced when all default settings were used compared with default settings with 20 random starts, so only those in which all default settings were used are presented. Two-dimensional plots of ordinations were constructed with Microsoft Excel 7.0. Ordinations were assessed by examining stress values and correlations between character states and ordination vectors (performed with the Scatter Plots, SCAT, module available under the Ordination Evaluation Menu in PATN; Belbin 1993).

Two agglomerative, polythetic approaches to clustering analysis (available under the Classification Menu, FUSE module in PATN; Belbin 1993) were used on each data matrix: Ward's sum of squares (WSS) and unweighted pair-group method with arithmetic mean (UPGMA, with $\beta = -0.25$) fusion strategies. All attributes (not characters) were equally weighted before analysis. Cluster analyses using WSS and UPGMA fusion strategies produced very similar results, except those for data matrix 1. In contrast to the UPGMA analysis of data matrix 1, WSS produced a pattern of clustering not consistent with the ordination. As UPGMA clusters OTUs on the basis of mean distances of all possible pairwise combinations it is preferred over WSS (Quicke 1993; Weston and Crisp 1994) and only the results of UPGMA analyses are presented.

Results and discussion

Ordination analyses

The results of all ordinations and clustering analyses are summarised in Table 4. Discrete groupings were found in two ordinations (Figs 2, 7) for OTUs representing *Lepidosperma ensiforme*, *L. elatius*, *L. latens*, *L. oldfieldii*, *L. sp. 'Mt Coolum'*, *L. viscidum*, *L. tortuosum*, *Schoenus ericetorum* and *S. melanostachys*. Discrete groupings were not retrieved from data matrix 1 for *L. curtisiae*, *L. filiforme*, *L. globosum* and *L. inops* (Fig. 2). OTUs of these four species grouped tightly and discretely in an ordination of data matrix 3 (Table 3, Fig. 7). A discrete group of OTUs representing *L. sp. Whian Whian S.F.* (except for one distant outlier, the result of missing data, in the ordination of data matrix 1; Fig. 2) was also recovered and was distinct from those of the morphologically similar *L. elatius* and *L. ensiforme* (Figs 2, 7). Some outliers occurred despite the process of cross-checking data and comparison of specimens and character states.

Operational taxonomic units representing what was originally considered *L. ensiforme* from Victoria (based on the description of this species given by Curtis and Morris 1994) grouped with those of *L. sp. Whian Whian S.F.* in the ordination of data matrix 1 (Fig. 2) rather than with those of *L. ensiforme* from Tasmania as had been expected. Following re-examination of the specimens of

Table 4. Results of ordination and cluster analyses

✓ = OTUs formed a single, discrete group; ✕ = OTUs did not form a single discrete group; – = taxon omitted from analysis

Taxon data matrix	Ordination				Phenogram			
	1	2	3	4	1	2	3	4
Core group								
<i>Lepidosperma curtisiae</i>	✓	–	✓	–	✓	–	✓	–
<i>L. sp. Hardacres</i>	✕	✕	–	–	✓	✓	–	–
<i>L. ensiforme</i>	✓	–	✓	✓	✓	–	✓	✓
<i>L. elatius</i>	✓	–	✓	✓	✓	–	✓	✓
<i>L. sp. Whian Whian S.F.</i>	✕	–	✓	✓	✓	–	✓	✓
<i>L. globosum</i>	✕	–	✓	–	✓	–	✓	–
<i>L. gunnii</i>	✕	✕	–	–	✕	✕	–	–
<i>L. sp. Coaldale</i>	✕	✕	–	–	✓	✓	–	–
<i>L. inops</i>	✕	–	✓	–	✓	–	✓	–
<i>L. latens</i>	✓	–	✓	–	✓	–	✓	–
<i>L. laterale</i> var. <i>laterale</i>	✕	✕	–	–	✕	✕	–	–
<i>L. laterale</i> var. <i>angustum</i>	✕	✕	–	–	✕	✕	–	–
<i>L. laterale</i> var. <i>majus</i>	✕	✕	–	–	✕	✕	–	–
<i>L. oldfieldii</i>	✓	–	✓	✓	✓	–	✓	✓
<i>L. sp. Mt Coolum</i>	✓	–	✓	–	✓	–	✓	–
<i>L. viscidum</i>	✓	–	✓	–	✓	–	✓	–
Comparator group								
<i>L. filiforme</i>	✓	–	✓	–	✓	–	✓	–
<i>L. tortuosum</i>	✓	–	✓	–	✓	–	✓	–
<i>Schoenus ericetorum</i>	✓	–	✓	✓	✓	–	✓	✓
<i>S. melanostachys</i>	✓	–	✓	✓	✓	–	✓	✓

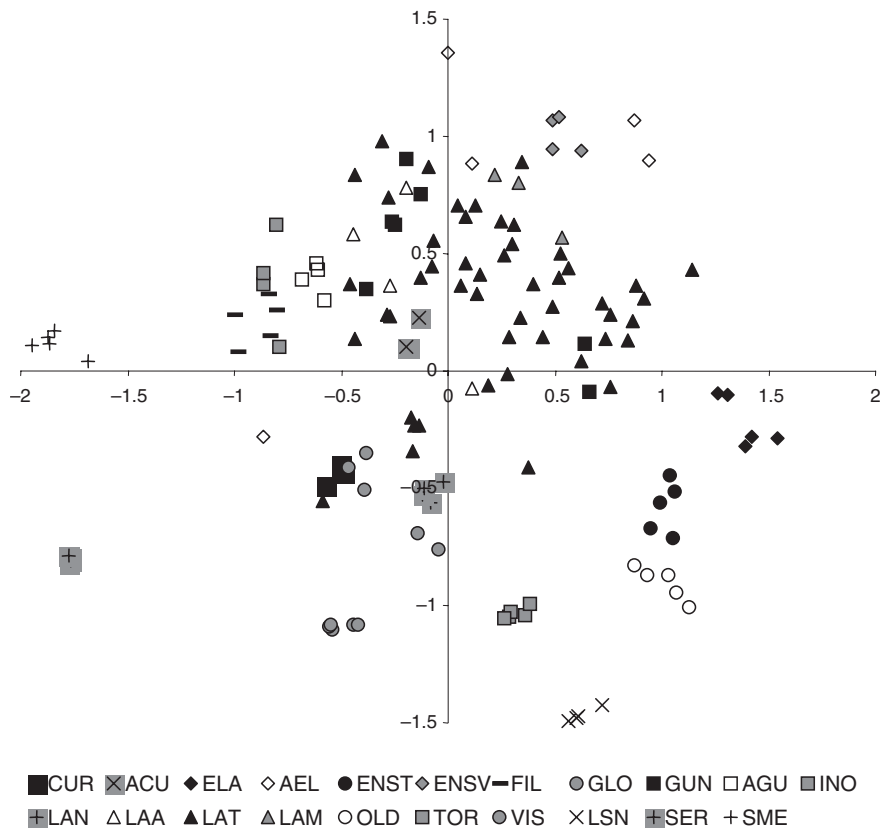


Fig. 2. Ordination plot of data matrix 1 (all study group taxa: Table 3; Appendix 1) using weighted character states, Gower association measure and semi-strong-hybrid multidimensional scaling. Stress value for the ordination = 0.239. OTU codes: CUR, *Lepidosperma curtisiae*; ACU, *L. sp.* Hardacres; ELA, *L. elatius*; AEL, *L. sp.* Whian Whian S.F. from Queensland and New South Wales; ENST, *L. ensiforme* from Tasmania; ENSV, *L. ensiforme* from Victoria; FIL, *L. filiforme*; GLO, *L. globosum*; GUN, *L. gunnii*; AGU, *L. sp.* Coaldale; INO, *L. inops*; LAN, *L. latens*; LAA, *L. laterale* var. *angustum*; LAT, *L. laterale* var. *laterale*; LAM, *L. laterale* var. *majus*; OLD, *L. oldfieldii*; TOR, *L. tortuosum*; VIS, *L. viscidum*; LSN, *L. sp.* Mt Coolum; SER, *Schoenus ericetorum*; SME, *S. melanostachys*.

L. ensiforme from Victoria, these OTUs were redesignated as *L. sp.* Whian Whian S.F. in subsequent analyses (Figs 7, 9).

While most groups were more or less discrete from each other in ordinations of data matrices 1, 3 and 4 (Table 3; Figs 2, 7, 9), some groups were rather loosely clustered (e.g. *L. sp.* aff. *elatius* in Figs 2, 7, 9). This probably reflects variation over geographic range among specimens. For example, within OTUs of *L. elatius* the two specimens from Tasmania formed a group slightly separated from a group comprising the remaining three Victorian specimens (Figs 2, 7, 9). Similar explanations can be offered for the spread of specimens of *L. viscidum*, *L. tortuosum*, *L. filiforme*, *L. curtisiae*, *L. sp.* aff. *elatius*, and *S. ericetorum* (Figs 2, 7, 9). Missing data (i.e. not able to be scored) may also be partly responsible for loosely defined groups in these ordinations.

Some species were not as clearly separated as expected, for example, *L. inops* and *L. filiforme*, and *L. curtisiae* and

L. globosum, in the ordination of data matrix 1 (Fig. 2). Clear morphological and anatomical differences among these species were not reflected in their spatial separation in the ordination (Fig. 2). A few missing values may also provide an explanation for these unexpected results.

No discrete groupings were obtained for OTUs representing *L. laterale* var. *laterale*, *L. laterale* var. *angustum*, *L. laterale* var. *majus*, *L. gunnii*, *L. sp.* Coaldale or *L. sp.* Hardacres in the ordination for data matrices 1 or 2 (Figs 2, 4). Another ordination plot (Fig. 5), using the same coordinates, was constructed to look for any broad geographical grouping of specimens of *L. laterale* var. *laterale*, *L. laterale* var. *angustum*, *L. laterale* var. *majus*, *L. gunnii*, *L. sp.* Coaldale and *L. sp.* Hardacres, but again no clear groupings or pattern could be discerned.

In contrast to the ordination of data matrix 1 (Fig. 2), there were no species with very distant outliers in the ordination

of data matrix 3 (Fig. 7; e.g. the groupings of *L. sp. Whian Whian S.F.* in Figs 2, 7). Additionally, the spatial separation between groups increased (compare the placement of *L. inops* and *L. filiforme* and *L. curtisiae* and *L. globosum* between Figs 2, 7). Although discrete from others, some of the groups (e.g. *L. elatius*, *L. sp. aff. elatius*, *L. filiforme* and *L. globosum*) were not particularly tightly clustered. This may again be a result of geographical variation and/or missing data.

While all character states contribute to the pattern observed in an ordination, correlations above 0.7 between character states and ordination vectors are considered most diagnostic of the taxa involved (Crisp 1991). Correlations above 0.7 were obtained for only 10 of 104 character states used in the analysis of data matrix 1, which indicates that the majority of characters included did not strongly contribute to the observed pattern. It also probably accounts for the poor spatial separation of some species such as *L. inops* and *L. filiforme*, and *L. curtisiae* and *L. globosum*, and the loosely defined groupings obtained for species such as *L. inops*, *L. elatius* and *L. sp. Whian Whian S.F.* (Fig. 2). The largely weak correlations are probably due to a high level of homoplasy in dataset 1.

Subsets of data matrix 1 (Table 3; Appendices 2–4) were analysed to explore more closely the support for the observed pattern in the ordination analysis of data matrix 1 (Fig. 2) and to obtain clearer definition of patterns of OTU grouping.

The number of characters contributing strongly (i.e. with correlations above 0.7) to the ordination pattern of data matrix 2 (Fig. 4) was 27 of the possible 86. This provides a higher level of confidence in the ordination plot of data matrix 2 (Fig. 4), compared with data matrix 1 (Fig. 2), reflecting the likely phenetic patterns of the taxa involved. That a great number of both morphological and anatomical characters were highly correlated with the pattern lends support to the combination of both data sources in all analyses performed (Appendices 1–4). It also underlines the contribution that anatomical characters can make to systematic studies in *Lepidosperma*, which has limited obvious morphological variation.

Twenty-two of the 94 characters contributed strongly (i.e. with correlations above 0.7) to the ordination pattern of data matrix 3 (Fig. 7) providing a higher level of confidence in the ordination plot of data matrix 3 (Fig. 7) than in that of data matrix 1 (Fig. 2). Over half of all characters (46 out of 79) contributed strongly (i.e. with correlations above 0.7) to the ordination pattern for data matrix 4 (Fig. 9) and this again indicates strong support for the ordination.

Clustering analyses

Cluster analysis of all data matrices (Table 4; Figs 3, 6, 8, 10) largely reflected the results of the ordinations (Table 4;

Figs 2, 4, 5, 7, 9). As expected, the major dissimilarity among OTUs occurs in phenograms where both species of *Schoenus* are present (Figs 3, 8, 10) between a branch representing the species of *Schoenus* (although both are clearly separated from each other) and all others. In the phenogram of data matrix 1 (Fig. 3) the next major dissimilarity is a branch containing clusters of OTUs representing *L. elatius*, *L. ensiforme*, *L. oldfieldii*, *L. sp. Mt Coolum* and *L. tortuosum*. This indicates the similarity among *L. elatius*, *L. ensiforme* and *L. oldfieldii* (the last two previously treated as varieties of the former in Tasmania; see Curtis and Morris 1994; Fig. 1) and how dissimilar *L. sp. Mt Coolum* and *L. tortuosum* are to all other species of *Lepidosperma* in this study.

The next major branch in the phenogram of data matrix 1 (Fig. 3) comprises a mixture of clusters of *L. curtisiae*, *L. sp. Hardacres*, *L. filiforme*, *L. globosum*, *L. gunnii*, *L. sp. Coaldale*, *L. inops*, *L. latens*, *L. laterale* var. *laterale*, *L. laterale* var. *angustum* and *L. viscidum*. In contrast to the other taxa of this branch, *L. sp. Hardacres* did not form a discrete group in the ordination of data matrix 1 (Fig. 2). The mix of taxa in this branch is not an expected result as some of them are very different morphologically from each other. For example, *L. filiforme* is the only species of *Lepidosperma* included in the study with culms that are circular in cross-section, and a leaf-to-culm-length ratio that is much higher than others included in this branch (Appendix 1). This result can probably be explained by the correlations obtained for the ordination where very few characters contributed strongly to the pattern obtained. Those characters that did contribute would not have delimited *L. filiforme* from others within the same major branch of the phenogram (Fig. 3). The conflict between expected and observed results provided the incentive and rationale for analyses of subsets of data matrix 1 (Appendices 2–4) to better resolve phenetic patterns among the OTUs.

The next branch in the phenogram of data matrix 1 (Fig. 3) is composed solely of a cluster of all *L. sp. Whian Whian S.F.* OTUs (including OTUs representing *L. ensiforme* from Victoria; see above).

The least amount of dissimilarity for major branches within the phenogram (Fig. 3) occurs among three branches composed of a mixture of specimens of *L. gunnii*, *L. laterale* var. *laterale*, *L. laterale* var. *angustum* and *L. laterale* var. *majus*. This is very similar to the ordination pattern (Fig. 2) where OTUs of *L. gunnii* were mixed with the varieties of *L. laterale*. These three branches do not match clusters in the ordination (Fig. 2) and as they do not correlate with any pattern of geographic distribution (Fig. 5), support for the pattern of clustering of these three groups is thus weak.

The phenogram of data matrix 2 (Fig. 6) shows six major branches. Five are composed of mixtures of OTUs of

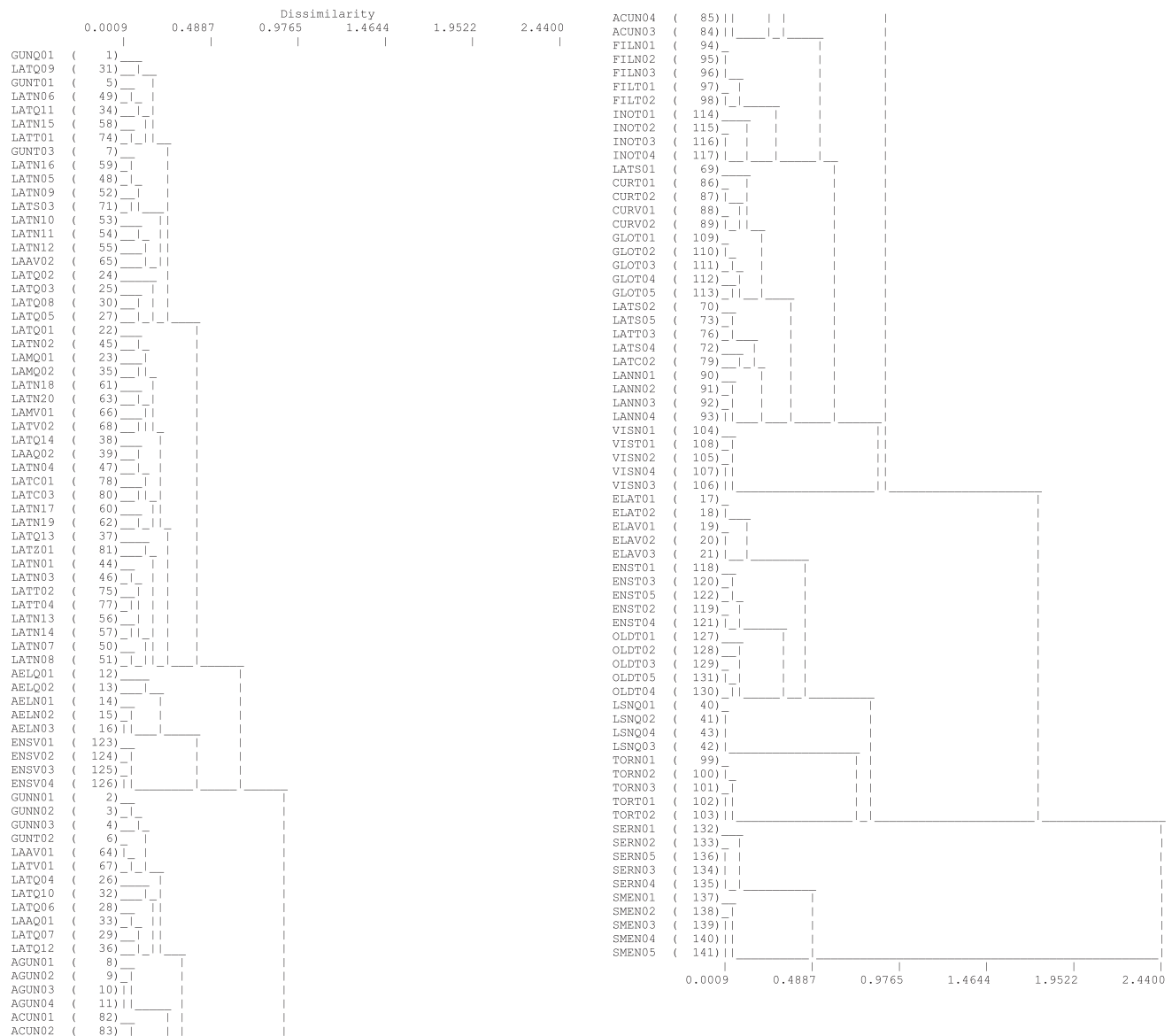


Fig. 3. Phenogram of data matrix 1 (Table 3; Appendix 1) using weighted character states, Gower association measure and UPGMA ($\beta = -0.25$) fusion strategy. OTU codes, first three letters: CUR, *Lepidosperma curtisiae*; ACU, *L. sp. Hardacres*; ELA, *L. elatius*; AEL, *L. sp. Whian Whian S.F.*; ENS, *L. ensiforme*; FIL, *L. filiforme*; GLO, *L. globosum*; GUN, *L. gunnii*; AGU, *L. sp. Coaldale*; INO, *L. inops*; LAN, *L. latens*; LAA, *L. laterale var. angustum*; LAT, *L. laterale var. laterale*; LAM, *L. laterale var. majus*; OLD, *L. oldfieldii*; TOR, *L. tortuosum*; VIS, *L. viscidum*; LSN, *L. sp. Mt Coolum*; SER, *Schoenus ericetorum*; SME, *S. melanostachys*. Fourth letter: Q, Queensland; N, New South Wales; V, Victoria; T, Tasmania; S, South Australia; C, New Caledonia; Z, New Zealand.

L. laterale var. laterale with or without OTUs of *L. laterale var. angustum*, *L. laterale var. majus* and *L. gunnii* while the other contains OTUs of *L. sp. Coaldale* and *L. sp. Hardacres*. This pattern is not apparent in the ordinations of data matrices 1 or 2 (Figs 2, 4, 5). Given the mixed branches of OTUs of *L. laterale* in Fig. 6, there is no clear clustering of *L. laterale* into varieties.

The major branches of the phenogram for data matrix 3 (Fig. 8) conformed to the groupings of OTUs obtained in

the ordination (Fig. 7). For taxa common to both analyses this reflected results of ordination and cluster analyses for data matrix 1 (Table 4; Figs 2, 3). Certain pairs of species (e.g. *L. globosum* and *L. curtisiae*) clustered close to each other as in the phenogram for data matrix 1 (Fig. 3). This result was unexpected and could indicate that *L. globosum* and *L. curtisiae* are closer phenetically than first envisaged or that further characters are required to achieve a clearer separation.

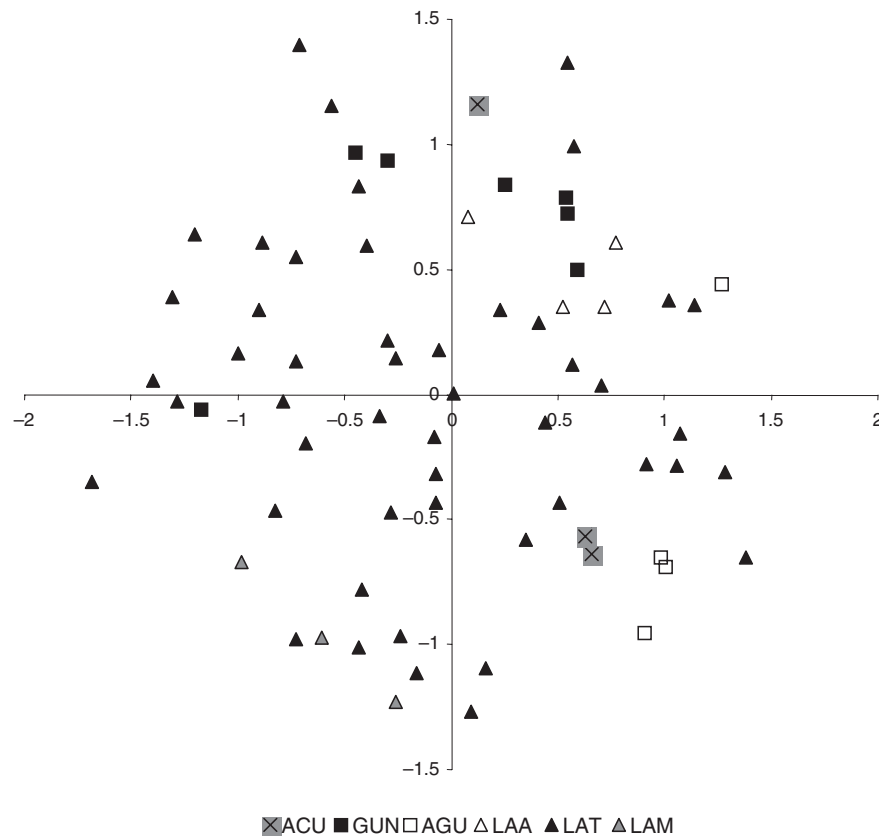


Fig. 4. Ordination plot of data matrix 2 (Table 3; Appendix 2) using weighted character states, Gower association measure and semi-strong-hybrid multidimensional scaling. Ordination stress value = 0.303. OTU codes: ACU, *Lepidosperma* sp. Hardacres; GUN, *L. gummii*; AGU, *L. sp.* Coaldale; LAA, *Lepidosperma laterale* var. *angustum*; LAT, *L. laterale* var. *laterale*; LAM, *L. laterale* var. *majus*.

Major branches of the cluster analysis for data matrix 4 (Fig. 10) mirror (for those taxa in common) parts of the phenograms (Figs 3, 8) and ordinations (Figs 2, 7) obtained for data matrices 1 and 3. The members of subgroups of *L. sp.* Whian Whian S.F. are not exactly the same in the ordination (Fig. 9) and phenogram (Fig. 10), which suggests that only one group should be recognised for these nine OTUs.

Evaluation of characters

Of the 43 characters employed in the phenetic analyses, 34 (21 morphological and 13 anatomical) appear to be strongly diagnostic (Table 5) in delimiting entities in ordinations of data matrices 1, 3 and 4 (Figs 2, 7, 9).

The value of most morphological characters used in this study (Table 2) is well established as they have been repeatedly used to delimit species of *Lepidosperma* (Labillardière 1805; Brown 1810; Boeckeler 1874; Bentham 1878; Rodway 1903; Wilson and Morris 1993; Wilson 1993, 1994a, 1994b; Curtis and Morris 1994; Gray 1994). However, anatomical characters, while well-established in

studies of Cyperaceae (Pfeiffer 1927; Chermezon 1929; Peisl 1957; Metcalfe 1971; Bruhl 1995), have been under-utilised within studies of *Lepidosperma*, with Gray (1994) being an exception. The high proportion of anatomical characters of diagnostic value (Table 5) in this study has demonstrated their value to future systematic studies in *Lepidosperma* and related genera. Novel characters employed in this study (Table 2) also appear diagnostically important and should prove informative in future systematic studies of *Lepidosperma*, and possibly other genera of Cyperaceae.

Species recognition

The approach taken here to species recognition relies on the testing of species limits through an objective assessment (i.e. the phenetic analyses) of characteristics (Table 2) of the study group taxa (Table 1). However, we believe it is not sufficient to recognise species on the basis of statistical analyses alone. To be of practical use, species recognition should also be based on clear

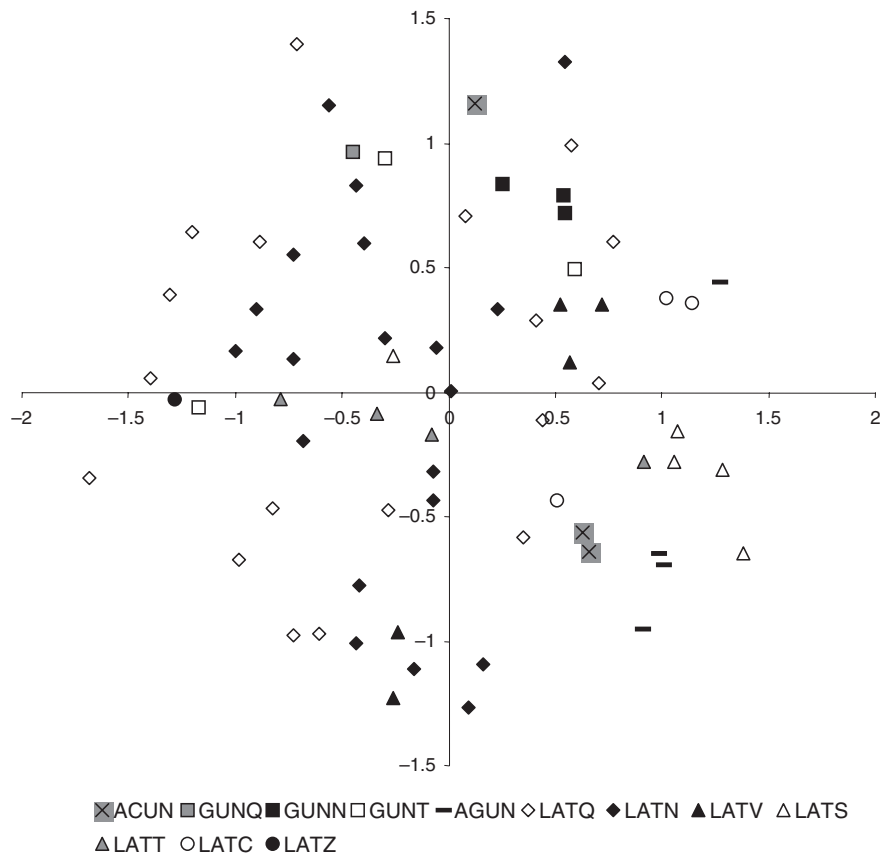


Fig. 5. Ordination plot of data matrix 2 (Table 3; Appendix 2) using weighted character states, Gower association measure and semi-strong-hybrid multidimensional scaling. OTUs of *Lepidosperma* sp. Hardacres, *L. gunnii*, *L. laterale* var. *angustum*, *L. laterale* var. *laterale* and *L. laterale* var. *majus* and have been segregated into state or country of origin. OTU codes, first three letters: ACU, *Lepidosperma* sp. Hardacres; GUN, *L. gunnii*; AGU, *L. sp.* Coaldale; LAT, *L. laterale* all varieties. Fourth letter: Q, Queensland; N, New South Wales; V, Victoria; S, South Australia; T, Tasmania; C, New Caledonia; Z, New Zealand.

and diagnosable discontinuities among specimens of the taxa concerned. In practice, this entails finding greater separation between than within OTU-clusters. These discontinuities were sought for taxa to complement any species boundaries recognised from the phenetic analyses to provide maximum confidence in any species thus recognised.

Recognition of entities from phenetic analyses (Figs 2–10) was used as the starting point for recognising species limits within the study group. In this we followed Doyen and Slobodchikoff (1974), who considered species as populations of phenetically similar individuals placed in the same taxonomic category. While this approach essentially falls within the Morphological Species Concept, we also construe this to be a proxy for the Phylogenetic Species Concept ‘in which the smallest diagnosable unit is recognised as a species’ (see Luckow 1995, p. 589).

The first step is to examine groupings of OTUs and determine whether they are ‘phenetically different’ (Doyen and Slobodchikoff 1974). We would define ‘phenetically different’ groupings of OTUs on the basis of agreement between ordination and cluster analyses that a particular group is clearly separated from all others. Applying this approach to the current study results in the groupings of OTUs representing *L. curtisiae*, *L. ensiforme*, *L. elatius*, *L. sp.* aff. *elatius*, *L. filiforme*, *L. globosum*, *L. inops*, *L. latens*, *L. oldfieldii*, *L. tortuosum*, *L. viscidum*, *L. sp.* ‘Mt Coolum’, *Schoenus ericetorum* and *S. melanostachys* (Table 4) being recognised as phenetically distinct, and therefore confirming or warranting species status. The recognition of these entities as species is supported by diagnosable differences among them. In contrast, OTUs representing *L. laterale* var. *laterale*, *L. laterale* var. *angustum*, *L. laterale* var. *majus*, *L. sp.* Hardacres, *L. gunnii* and *L. sp.* Coaldale

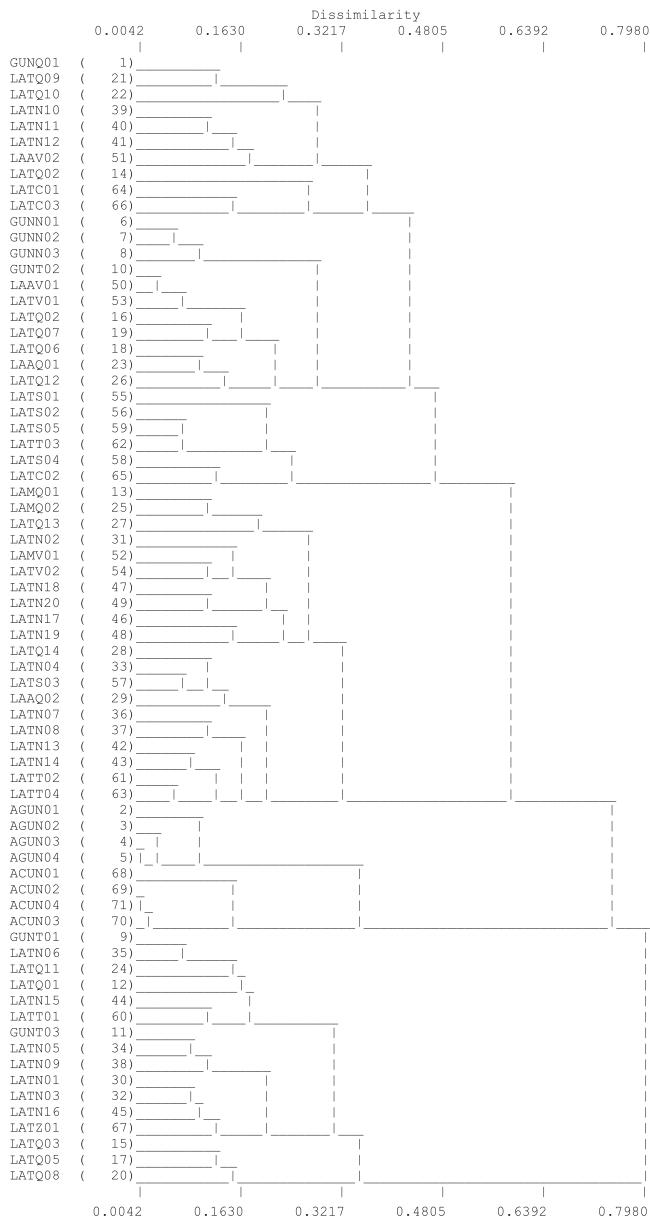


Fig. 6. Phenogram of data matrix 2 (Table 3; Appendix 2) using weighted character states, Gower association measure and UPGMA ($\beta = -0.25$) fusion strategy. OTU codes, first three letters: ACU, *Lepidosperma* sp. Hardacres; GUN, *L. gunnii*; AGU, *L. sp.* Coaldale; LAT, *L. laterale* all varieties. Fourth letter: Q, Queensland; N, New South Wales; V, Victoria; T, Tasmania; S, South Australia; C, New Caledonia; Z, New Zealand.

are not phenetically different from each other (Table 4). Unlike the other taxa considered phenetically similar, the clusters of *L. sp.* Hardacres and *L. sp.* Coaldale formed in the phenograms of data matrices 1 and 3 (Table 4; Figs 3, 6) are not reflected in the respective ordinations (Table 4; Figs 2, 4, 5).

Lepidosperma laterale sens. lat., itself, remains the most weakly supported species of those studied. Based on our field observations the ‘varieties’ of *L. laterale* occur sympatrically and in similar ecological habitats. Our tentative conclusion is that the OTUs representing *L. laterale* var. *laterale*, *L. laterale* var. *angustum* and *L. laterale* var. *majus*, *L. sp.* Hardacres, *L. gunnii* and *L. sp.* Coaldale constitute a single variable species without subspecific taxa. This is also supported by close examination of over 400 herbarium specimens by JH, and the characters and phenetic analyses used in this study. However, the obvious morphological variation seen in *L. laterale sens. lat.* indicates the need for further study, in particular studies applying appropriate molecular techniques.

Assignment of taxonomic rank

The phenetic approach to classification assigns rank to all OTUs (individuals or groups of OTUs) on the basis of similarity, and is in general an arbitrary process (Abbott *et al.* 1985; Stuessy 1990; Cranston *et al.* 1991). The ranking process depends on several factors, historical trends and perspectives about classification within the study group, numbers and nature of characters employed, and subjective application of concepts of taxonomic rank. Regardless of whether phenetic and/or cladistic analysis is the analytical tool, assignment of rank remains essentially subjective (Stuessy 1990; Judd *et al.* 2000).

Assignment of taxonomic rank to members of the study group was based on species being the fundamental taxonomic rank. The placement of well defined species *Lepidosperma curtisiae*, *L. elatius*, *L. ensiforme*, *L. filiforme*, *L. globosum*, *L. gunnii*, *L. inops*, *L. latens*, *L. oldfieldii*, *L. tortuosum*, *L. viscidum*, *Schoenus ericetorum* and *S. melanostachys* in relation to each other in the ordination and clustering analyses (Figs 2, 3, 7–10) was therefore used as a guide in assigning taxonomic rank to those entities that are here recognised for the first time as species (i.e. *L. sp.* Whian Whian S.F. and *L. sp.* ‘Mt Coolum’). Given the relatively large extent of separation between previously recognised species such as *L. elatius*, *L. ensiforme* and *L. oldfieldii*, the relative isolation of *L. sp.* Whian Whian S.F. and *L. sp.* Mt Coolum (Figs 2, 3, 7–10) provides strong evidence for their recognition at the rank of species.

Based on current knowledge, *L. sp.* Whian Whian S.F. occurs from southern Queensland, through New South Wales into Victoria and Tasmania. Judging by descriptions (Sharpe 1986; Wilson 1993; Gray 1994), comparison with the protologue (Labillardière 1805) and examination of type specimens of *L. elatius* (KLW) it would appear that the name *L. sp.* Whian Whian S.F. should be applied to specimens previously known as *L. elatius* in Queensland

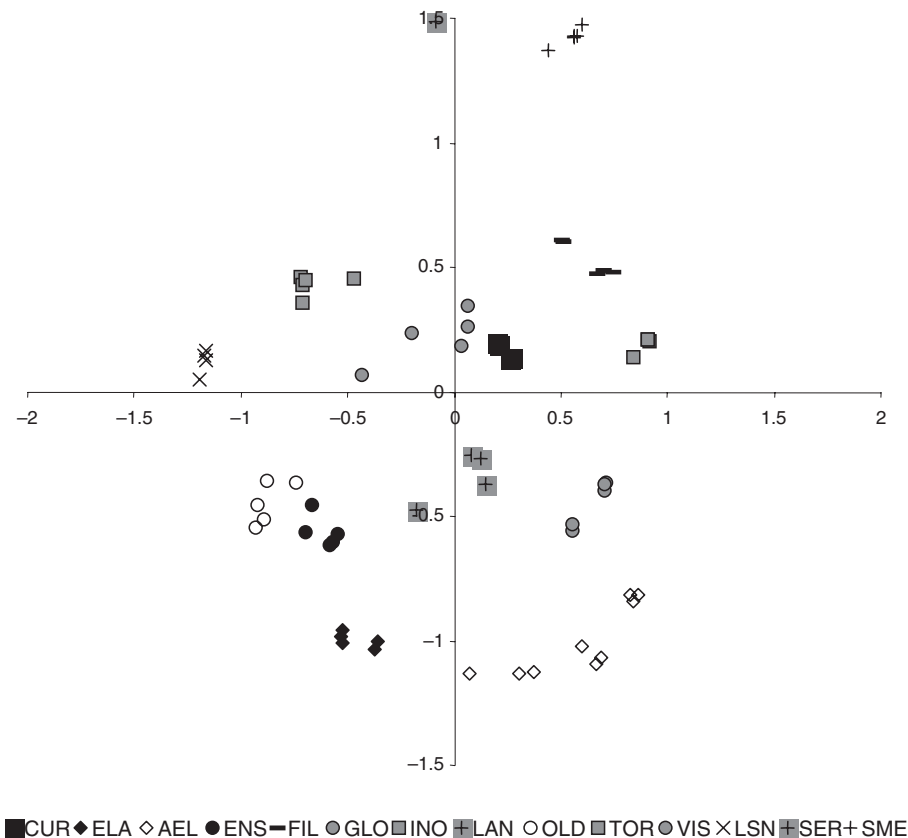


Fig. 7. Ordination plot of data matrix 3 (Table 3; Appendix 3) using weighted character states, Gower association measure and semi-strong-hybrid multidimensional scaling. Ordination stress value = 0.194. OTU codes: CUR, *Lepidosperma curtisiae*; ELA, *L. elatius*; AEL, *L. sp. Whian Whian S.F.*; ENS, *L. ensiforme*; FIL, *L. filiforme*; GLO, *L. globosum*; INO, *L. inops*; LAN, *L. latens*; OLD, *L. oldfieldii*; TOR, *L. tortuosum*; VIS, *L. viscidum*; LSN, *L. sp. Mt Coolum*; SER, *Schoenus ericetorum*; SME, *S. melanostachys*.

and at least the northern half of New South Wales. Based on specimens examined, we consider typical *L. elatius* to be restricted to Tasmania, Victoria and south-eastern New South Wales although further field investigation is required to determine how far it extends into south-eastern New South Wales. *Lepidosperma sp. aff. elatius* also occurs in Victoria and includes material previously ascribed to *L. elatius var. ensiforme* (from Victoria only; Willis 1970) that was subsequently synonymised under *L. elatius* (Wilson 1994a). The circumscription of *L. sp. Whian Whian S.F.* should include material previously referred to *L. elatius var. planoconvexum* as confirmed by examination of the type material of the latter. Specimen records indicate that the ranges and habitat preferences of *L. sp. Whian Whian S.F.* and *L. elatius* probably overlap in eastern Victoria but this needs confirmation through further field studies.

Evidence from the analyses (Figs 2–6) for treating *L. laterale*, *L. gunnii* *L. sp. Hardacres* and *L. sp. Coaldale* as a

single variable species is strong. Even though OTUs of *L. sp. Hardacres* and *L. sp. Coaldale* each form discrete clusters in the phenograms of data matrices 1 and 2 (Figs 3, 6) these groups are embedded within a heterogeneous assemblage of OTUs of *L. laterale* and *L. gunnii*.

There is no compelling evidence for a novel division of *L. laterale* into subspecific entities (Figs 2–6). Support is therefore strong for the treatments of Wilson (1993, 1994a) and Curtis and Morris (1994), who synonymised all varieties under *L. laterale* in New South Wales, Victoria and Tasmania respectively. *Lepidosperma laterale* is not known as a variable species in New Zealand, and no varieties are recognised (Moore and Edgar 1970). Although based on a small sample, it would appear that material of *L. laterale* from New Zealand and New Caledonia falls within the range of variation found in material from eastern Australia.

The lack of a phylogeny covering all study group taxa made interpreting relationships among them pointless. A comprehensive cladistic analysis of *Lepidosperma*, which

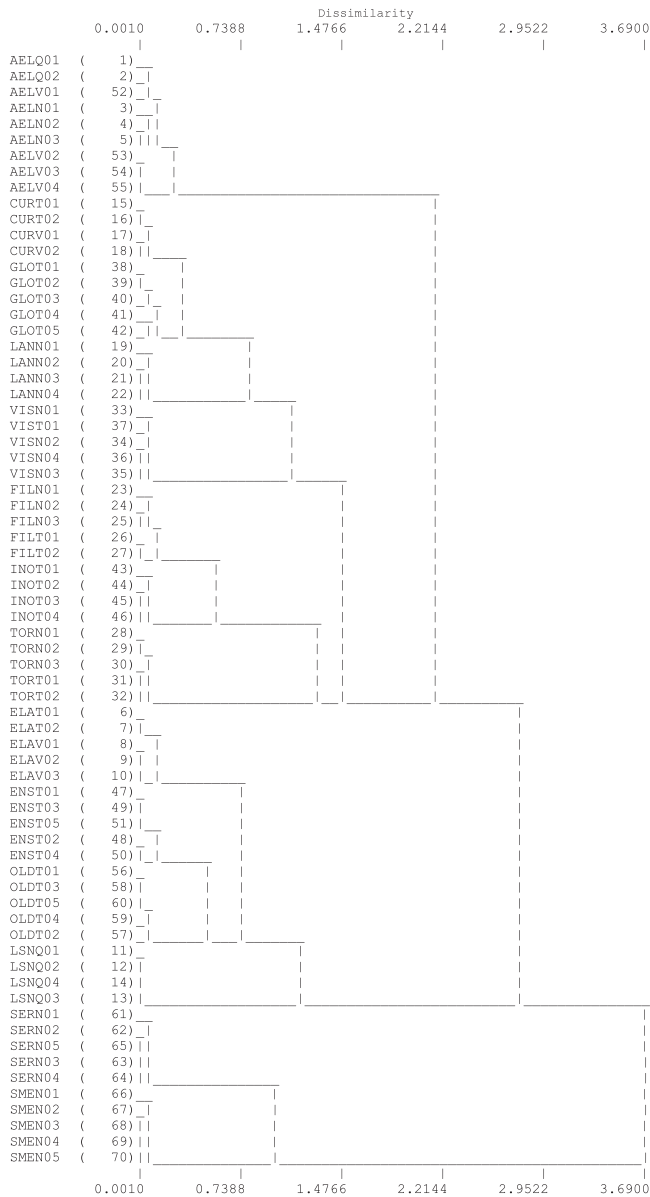


Fig. 8. Phenogram of data matrix 3 (Table 3; Appendix 3) using weighted character states, Gower association measure and UPGMA ($\beta = -0.25$) fusion strategy. OTU codes, first three letters: CUR, *Lepidosperma curtisiae*; ELA, *L. elatus*; AEL, *L. sp. Whian Whian S.F.*; ENS, *L. ensiforme*; FIL, *L. filiforme*; GLO, *L. globosum*; INO, *L. inops*; LAN, *L. latens*; OLD, *L. oldfieldii*; TOR, *L. tortuosum*; VIS, *L. viscidum*; LSN, *L. sp. Mt Coolum*; SER, *Schoenus ericetorum*; SME, *S. melanostachys*. Fourth letter: Q, Queensland; N, New South Wales; V, Victoria; T, Tasmania.

was beyond the scope of this project, is the next logical step in further testing species limits and expanding on our work and that of Gray (1994). Molecular data (i.e. ISSRs and DNA sequencing) are needed to test and extend the findings of this study (we have already collected material for taxa mentioned here for that study).

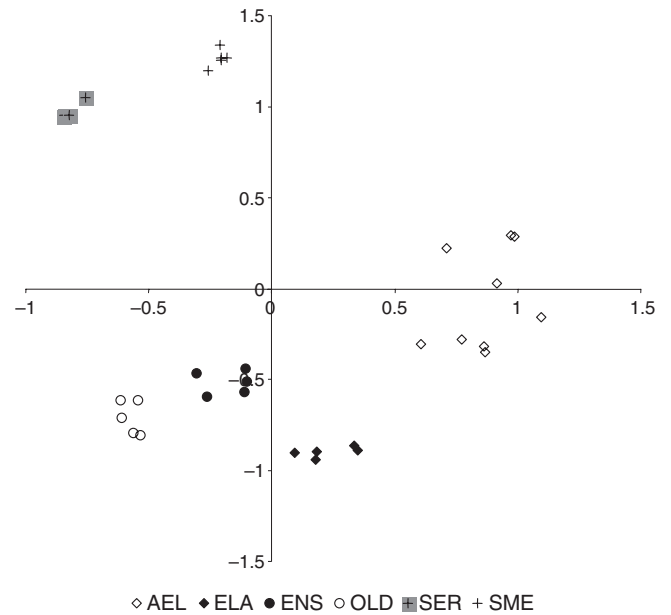


Fig. 9. Ordination plot of data matrix 4 (Table 3; Appendix 4) using weighted character states, Gower association measure and semi-strong-hybrid multidimensional scaling. Ordination stress value = 0.089. OTU codes: ELA, *Lepidosperma elatus*; AEL, *L. sp. Whian Whian S.F.*; ENS, *L. ensiforme*; OLD, *L. oldfieldii*; SER, *Schoenus ericetorum*; SME, *S. melanostachys*.

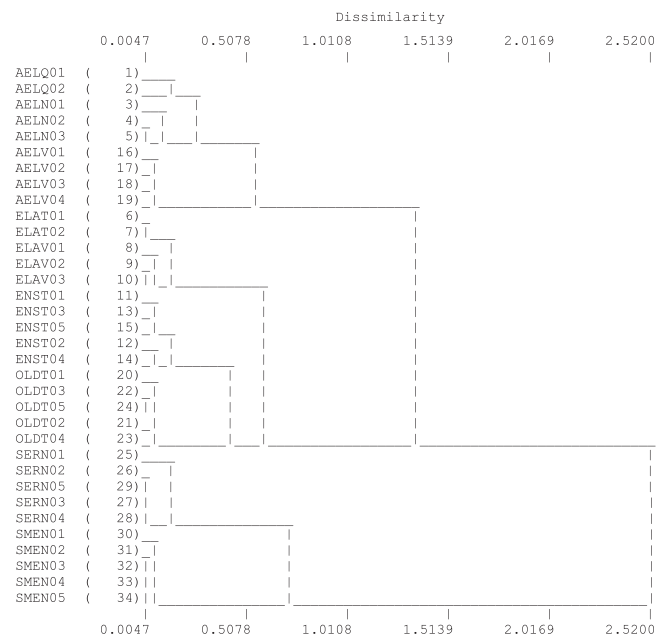


Fig. 10. Phenogram of data matrix 4 (Table 3; Appendix 4) using weighted character states, Gower association measure and UPGMA ($\beta = -0.25$) fusion strategy. OTU codes, first three letters: ELA, *Lepidosperma elatus*; AEL, *L. sp. Whian Whian S.F.*; ENS, *L. ensiforme*; OLD, *L. oldfieldii*; SER, *Schoenus ericetorum*; SME, *S. melanostachys*. Fourth letter: Q, Queensland; N, New South Wales; V, Victoria; T, Tasmania.

Table 5. Characters considered strongly diagnostic for study group taxa based on correlations with ordination vectors in all ordinations

Characters are not ranked in order of importance. Novel characters not previously used in studies of *Lepidosperma* are italicised. Character numbers refer to those in Table 2

Character
Morphology
1. Culm: maximum width
2. Culm: maximum length to base of involucral bract sheath
3. Culm margins: whether scabrous
4. Leaf: maximum width
5. Leaf: maximum length
6. Leaf length-to-culm length ratio
7. Leaf bases (whether breaking down into fibres)
8. Inflorescence shape in outline
9. Inflorescence: maximum length of main axis
10. <i>Inflorescence: length of node plus internode unit along main axis</i>
11. <i>Inflorescence: number of lateral branches per internode</i>
12. <i>Inflorescence: maximum lateral branch length</i>
13. <i>Lateral inflorescence branch: number of spikelets</i>
14. Spikelet: length excluding pedicel
18. Fertile floral bracts shape in dorsiventral view
19. Fertile floral bract apex shape
20. Fertile floral bract margin indumentum type
21. Sterile floral bracts: number per spikelet
22. Perianth members shape of apex
24. Fruit shape in lateral view
25. Fruit shape in transverse section
Anatomy
28. Culm cross-sectional shape
30. Culm stomatal rows within each intercostal zone
32. Culm vascular bundles: number
34. Culm sclerenchyma, whether in direct contact with vascular bundles
35. <i>Culm multicellular trichomes: whether present</i>
38. Culm: rows of intercostal cells per epidermal zone
39. Culm relative width of epidermal zones
40. Leaf cross-sectional shape
42. Leaf stomatal rows within each intercostal zone
44. Leaf vascular bundles: number
47. Leaf sclerenchyma, whether in direct contact with vascular bundles
51. Leaf: rows of intercostal cells per epidermal zone
52. Leaf relative width of epidermal zones

Conclusion

The taxonomic treatments of Labillardière (1805), Brown (1810), von Mueller (1875), Rodway (1903), Wilson and Morris (1993), Wilson (1993, 1994b) and Curtis and Morris (1994) in recognising *Lepidosperma curtisiae*, *L. ensiforme*, *L. filiforme*, *L. globosum*, *L. inops*, *L. latens*, *L. oldfieldii*, *L. tortuosum*, *L. viscidum*, *Scheonus ericetorum* and *S. melanostachys* at the specific rank are strongly supported by ordination and cluster analyses (Figs 2, 3, 7–10). Similarly, recognition of *L. sp. Whian Whian S.F.* and *L. sp.*

Mt Coolum as new, undescribed species of *Lepidosperma* is also strongly supported (Figs 2, 3, 7–10).

In contrast, the treatments of Bentham (1878) and Boeckeler (1874) in recognising *L. laterale* var. *angustum*, *L. laterale* var. *majus* and *L. gunnii* are not supported (Figs 2–6) and these taxa appear to belong to the same, variable taxon. Although we would now include *L. sp. Hardacres* and *L. sp. Coaldale* in *L. laterale*, further study is required to investigate the circumscription of these putative entities and the limits of *L. laterale sens. lat.*

Description of *L. sp. Whian Whian S.F.* and *L. sp. 'Mt Coolum'*, and the circumscription of *L. laterale* will be the subjects of a separate paper by the authors.

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Appendix 1. Data matrix 1 (full data matrix) used in phenetic analyses (for data matrix see the website of Australian Systematic Botany)

Each column represents a character state. Characters and character states with all invariant and/or missing values have been removed from the matrix. –9999 = missing value. OTU codes, first three letters: GUN, *Lepidosperma gunnii*; AGU, *L. sp.* Coaldale; ELA, *L. elatius*; AEL, *L. sp.* Whian Whian S.F.; LAT, *L. laterale* var. *laterale*; LAM, *L. laterale* var. *majus*; LAA, *L. laterale* var. *angustum*; LSN, *L. sp.* Mt Coolum; CUR, *L. curtisiae*; ACU, *L. sp.* Hardacres; LAN, *L. latens*; FIL, *L. filiforme*; TOR, *L. tortuosum*; VIS, *L. viscidum*; GLO, *L. globosum*; INO, *L. inops*; ENS, *L. ensiforme*; OLD, *L. oldfieldii*; SER, *Schoenus ericetorum*; SME, *S. melanostachys*. Fourth letter: Q, Queensland; N, New South Wales; V, Victoria; T, Tasmania; S, South Australia; C, New Caledonia; Z, New Zealand. Herbarium location for each specimen is given in parentheses following collector information.

Appendix 2. Data matrix 2 used in phenetic analyses

The matrix is constructed by deleting all OTUs (rows) from data matrix 1, except those representing *Lepidosperma laterale* var. *laterale*, *L. laterale* var. *angustum*, *L. laterale* var. *majus*, *L. gunnii*, *L. sp.* Coaldale and *L. sp.* Hardacres. Characters and character states with all invariant and/or missing values are then removed.

Appendix 3. Data matrix 3 used in phenetic analyses

The matrix is constructed by deleting all OTUs (rows) from data matrix 1 representing *Lepidosperma laterale* var. *laterale*, *L. laterale* var. *angustum*, *L. laterale* var. *majus*, *L. gunnii*, *L. sp.* Coaldale and *L. sp.* Hardacres. Characters and character states with all invariant and/or missing values are then removed and the OTU code ENSV is changed to AELV (see text for explanation).

Appendix 4. Data matrix 4 used in phenetic analyses

The matrix is constructed by deleting all OTUs (rows) from data matrix 1, except those representing *Lepidosperma elatius*, *L. sp.* aff. *elatius*, *L. ensiforme*, *L. oldfieldii*, *Schoenus ericetorum* and *S. melanostachys*, from data matrix 1. Characters and character states with all invariant and/or missing values are then removed and the OTU code ENSV is changed to AELV (see text for explanation).