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Authors: Wilson, Peter G., Heslewood, Margaret M., and Tarran, Myall A.

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The publisher regrets to inform readers that, owing to the incorrect pagination of an earlier paper, the paper by Wilson *et al.* published in issue 4 included incorrect final page numbers. This paper was published with pp. 181–197 instead of pp. 279–295. As such, the suggested citation for this paper is as follows:

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These errors have been corrected in the version that is online.

We apologise for the errors and any confusion this may have caused.

Wilson PG *et al.* (2022) *Australian Systematic Botany*, **35**(4), 341. doi:10.1071/SB21032_CO

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RESEARCH PAPER
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Australian Systematic Botany

Three new tribes in Myrtaceae and reassessment of Kanieae

Peter G. Wilson[A,*], Margaret M. Heslewood[A] and Myall A. Tarran[B,C]

For full list of author affiliations and declarations see end of paper

***Correspondence to:**
Peter G. Wilson
National Herbarium of New South Wales, Australian Institute of Botanical Science, Royal Botanic Gardens and Domain Trust, Sydney, NSW 2000, Australia
Email:
peter.wilson@botanicgardens.nsw.gov.au

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ABSTRACT

The current tribal classification of Myrtaceae was based on analysis of the plastid *mat*K coding region within the *trn*K intron. The phylogenetic position of the genera *Cloezia* and *Xanthomyrtus* was poorly supported, and the original sequence for *Kania*, the type genus of the tribe Kanieae, was rather poor. To clarify relationships, we sequenced plastid *psb*A–*trn*H and an extended portion of the *trn*K intron, including the spacer regions flanking *mat*K, and nuclear ribosomal ITS and ETS regions for representative species across the tribes, including denser sampling of the three genera of interest. Analyses of these extended datasets show a strong relationship between *Kania* and the tribe Metrosidereae but not with other genera presently assigned to the Kanieae. The relationship between *Kania* and the tribe Metrosidereae is strongly correlated with morphological features recently documented in *Metrosideros* fossils. Consequently, a new tribe, Tristaniopsideae PeterG.Wilson, is described to accommodate most genera presently assigned to Kanieae. Furthermore, the morphological divergence and genetic distance shown by *Cloezia* and *Xanthomyrtus* are here considered as justifying their recognition as the tribes Cloezieae Peter G.Wilson and Xanthomyrteae Peter G.Wilson. Recognition of these tribes brings to four the number of tribes absent from present-day mainland Australia. Prior to this study, Metrosidereae was the only tribe in subfamily Myrtoideae that was absent from mainland Australia.

Keywords: *Cloezia*, *Kania*, molecular phylogenetics, Myrtaceae, taxonomy, tribes, *Tristaniopsis*, *Xanthomyrtus*.

Introduction

Kanieae Engler was named as a monogeneric tribe erected to accommodate the genus *Kania* Schltr., which had been published earlier by Schlechter (1914). When Schlechter described the genus, he was uncertain of its affinities and, after considering placement in Clusiaceae, Myrtaceae and Saxifragaceae, finally described it as an aberrant genus in Saxifragaceae. Engler's placement of Kanieae within its own subfamily, Kanioideae, within Saxifragaceae, was similarly a reflection of its anomalous position in that family. Morphological investigations (Erdtman and Metcalfe 1963; Weberling 1966) strongly suggested that *Kania* had Myrtaceous affinities. Van Steenis (1969) noted that vegetative characters, leaf venation type, presence of an intramarginal vein and presence of oil glands clearly indicated that the genus was a member of the family Myrtaceae. However, he took a conservative view of the generic position of Schlechter's *Kania eugenioides* Schltr. and transferred the species to the genus *Metrosideros* Banks ex Gaertn., listing a further six names as synonyms. Wilson (1982) accepted Kania as a genus distinct from *Metrosideros* and made new combinations for two Philippine species that had originally been described in the genera *Cloezia* Brongn. & Gris and *Tristania* R.Br., and Scott (1983) increased the number of accepted species when he published a further two new species from West Papua. Subsequently, Scott (1990) transferred a further West Papuan species from *Myrtella* F.Muell. to *Kania*, making a total of six named taxa. However, it is likely that several of the synonyms listed by van Steenis should also be recognised as distinct species (G. P. Guymer, pers. comm.) to bring the total to ~10.

When van Steenis (1969) reduced *Kania* to synonymy under *Metrosideros*, he downplayed the value of two distinctive floral features, namely, the elongated anther connectives and the placentas in the basal angles of the loculi, remote from the base of

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the style. Regarding the latter, van Steenis noted the similarity of this arrangement to that found in the Australian monotypic genus *Lysicarpus* F.Muell. A third taxon, the New Caledonian genus *Cloezia*, is also known to have basal placentas remote from the base of the terminal style. The significance of this morphological arrangement in all three genera was first pointed out by Dawson (1972*a*) in his assessment of *Cloezia* (as *Mooria* Montrouz.) in relation to *Metrosideros*. However, he concluded that *Cloezia* and *Metrosideros* were not closely related because the placentas in *Metrosideros* and allied genera are always adjacent to the style base, even in the South American genus, *Tepualia* Griseb., which has a basal placenta (see, for example, the description and illustrations in Dawson 1972*b*). On the basis of the similarity in placentation, Dawson (1972*a*) suggested that the affinities of *Cloezia* might lie with *Lysicarpus* and *Kania*. Briggs and Johnson (1979) adopted this view and included these three genera in their informal 'Kania alliance'. However, as noted by Wilson (2011), the ovules of *Kania* species are scattered on the placentas, whereas those of *Lysicarpus* and *Cloezia* are arranged in a more-or-less circular series.

Tristanieae Peter G.Wilson (Wilson *et al.* 2005) originally comprised three genera, namely, *Tristania*, *Thaleropia* Peter G.Wilson and *Xanthomyrtus* Diels, although the last of these showed significant variation in fruit and seed characters and molecular support for its inclusion in the tribe was modest. Recent phylogenetic analyses by Biffin *et al.* (2010), Thornhill *et al.* (2015), and Maurin *et al.* (2021) recovered a clade that includes these genera but also includes *Cloezia*. The analysis of Wilson *et al.* (2005) had not confidently placed *Cloezia* and they considered it to be *incertae sedis*. Wilson (2011), on the basis of the ovule arrangement, tentatively included *Cloezia* in Kanieae *sens. lat.*

Early evidence from pollen (Pike 1956) found that the pollen of *Metrosideros parviflora* C.T.White (a synonym of *Kania eugenioides sens. lat.*) did not conform to that of other *Metrosideros* species. Pike summarised the differences in pollen morphology as follows: 'the grains are smaller and the colpi are absent on the polar surfaces' (p. 40). Erdtman (in Erdtman and Metcalfe 1963) examined pollen from a type specimen of *Kania eugenioides* and found much the same, but recorded the colpi as 'narrow, tenuimarginate, about 2.5–3 μm long, with tapering ends' (p. 249). Gadek and Martin (1981) examined *Kania* pollen by light microscopy only; they confirmed the differences between *Kania* and *Metrosideros* but did not detect colpi. Thornhill *et al.* (2012*a*, 2012*b*) also confirmed the size difference between the genera but the improved resolution of the scanning electron microscope showed more detail such that *Kania* pollen could now be described as 'parasyncolpate with arcuate colpi' (Thornhill *et al.* 2012*a*, p. 262); however, in general form, *Kania* pollen was not dissimilar to pollen of species of *Lysicarpus* and *Tristaniopsis* Brongn. & Gris, differing only by being obscurely parasyncolpate with a less ornamented exine. In contrast with this, Thornhill *et al.* (2012*b*), in agreement with all previous workers (Pike 1956; McIntyre 1963; Gadek and Martin 1981), noted that all *Metrosideros* species examined had much larger pollen (~11–17 μm long and wide, compared with ~7 × 11 μm), and almost all taxa they examined had well developed apocolpial islands.

Pollen morphology of *Cloezia* is neutral on the question of relationships. Thornhill *et al.* (2012*a*) found little difference in pollen morphology between *Cloezia* and the genera of Kanieae *sens. lat.* and that there was little difference in pollen morphology between *Cloezia* and *Xanthomyrtus*, because both have parasyncolpate pollen that is similar in size and exine pattern. In strong contrast with these taxa, the genera of core Tristanieae (*Tristania* and *Thaleropia*) share highly derived pollen that is the smallest found in the family so far (~7 μm in diameter) and is triporate and acolpate with a psilate exine (Pike 1956; Gadek and Martin 1981; Patel *et al.* 1984 for *Tristania*; Thornhill *et al.* 2012*a* for both genera).

Comparative wood anatomy has provided some insights into relationships of these taxa. An apparently informative feature of wood anatomy in some tribes of Myrtaceae is the presence of elongated vessel-ray pitting, which Ingle and Dadswell (1947) found could be used to distinguish *Syzygium* P.Browne ex Gaertn. and its allies (tribe Syzygieae) from *Eugenia* L. *sens. strict.* (tribe Myrteae), confirming that these taxa were not congeneric. Metcalfe (in Erdtman and Metcalfe 1963) noted similar pitting in wood from a type specimen of *Kania eugenioides*, an observation confirmed by a more recent image in an atlas of woods (Ilic 1991). Similar vessel-ray pitting has been observed in the tribe Metrosidereae. Ingle and Dadswell (1953) described the wood of *Tepualia* as having vessel-ray pits that appear simple and rounded to elongated, and Meylan and Butterfield (1978), who studied the woods of three New Zealand species of *Metrosideros*, described the vessel-ray pits as 'commonly axially elongated and large and form prominent cross fields' (pp. 94, 96, 98). So, wood anatomy does show more similarity between *Kania* and *Metrosideros* than between *Kania* and many other genera. In contrast to this, the vessel-ray pitting in *Cloezia* is fine and alternate, similar to intervessel pitting (P. Gasson, pers. comm.), very like that recorded for *Xanthomyrtus* by Ingle and Dadswell (1953; confirmed by P. Gasson).

The phylogenetic analysis of Wilson *et al.* (2005), based on sequences of the plastid *mat*K gene, was accompanied by a revised classification of Myrtaceae. In this classification, the tribe Kanieae included *Kania*, the type of the tribe, and seven other genera, including *Barongia* Peter G.Wilson & B.Hyland, *Basisperma* C.T.White, *Lysicarpus*, *Mitrantia* Peter G.Wilson & B.Hyland, *Ristantia* Peter G.Wilson & J.T.Waterh., *Sphaerantia* Peter G.Wilson & B.Hyland, and *Tristaniopsis*. The main morphological characters given for the tribe included 'stamens frequently in bundles' and 'style base not adjacent to placentas' (Wilson *et al.* 2005, p. 15), but these features are not unique to this tribe. Wilson (2011) tentatively included *Cloezia* in Kanieae but analyses by Biffin *et al.*

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(2010), Thornhill and Crisp (2012), Thornhill *et al.* (2015) and Maurin *et al.* (2021) indicated that this genus is instead weakly associated with the tribe Tristanieae.

More recently, Tarran *et al.* (2016) discussed myrtaceous leaf fossils from an Early Oligocene site in north-western Tasmania. These authors identified several characters on the cuticles of fossil leaves that were found in association with fossil *Metrosideros* fruits and were potentially of diagnostic value within *Kania* and associated genera. They were (1) peristomatal rings, (2) distinctive granulate-papillose cuticular texture, (3) striate water stomata and lid cells, and (4) varying degrees of stomatal clumping. The authors noted, from a comparative study of 175 species of extant taxa, that this combination of features was shared with very few of them. An earlier suggestion by Pole (1992) that these fossils might represent a species of *Xanthomyrtus* was rejected on the basis of differences in the nature of the stomatal clumping that he recorded, plus other cuticular characters that were not found in *Xanthomyrtus* but were present in *Kania* and, to a lesser extent, in some *Metrosideros* species.

Some, but not all, of these lines of evidence suggest that *Kania* is more closely related to *Metrosideros* than it is to the other genera that were grouped with it by Wilson *et al.* (2005) in the tribe Kanieae. Equally, these data provide no support for a possible relationship with *Lysicarpus* and *Cloezia*, as suggested by Dawson (1972*a*). The aim of the present paper is to establish the affinities of *Cloezia* and *Xanthomyrtus*, which have both been poorly resolved in previous studies, and to re-examine the relationships of *Kania*, and other genera presently assigned to the tribe Kanieae, by expanding the phylogenetic analysis of this and related tribes of capsular Myrtaceae. To this end, our primary goal was to generate new sequences of *Kania* to replace the very poor DNA sequence utilised by Wilson *et al.* (2005) and, additionally, to broaden the number of regions sequenced for each taxon. The phylogeny will be augmented with more detailed observations on epidermal and floral characters.

Materials and methods

Molecular sampling

We compiled a 61-taxon molecular dataset including limited representation of both subfamilies and all tribes in family Myrtaceae. Where possible, we utilised existing sequences available on GenBank to augment our own data, so that for some taxa, sequences are from different accessions for some loci (all details given in Table 1). For *Kania*, we sampled three new accessions of *K. eugenioides sens. lat.*, with DNA extracted from leaf or seeds. To cover the groups historically associated with *Kania*, we sampled eight species in six genera from the remainder of Kanieae and four species of *Metrosideros sens. lat.* (Metrosidereae). To represent other tribes of Myrtaceae subfamily Myrtoideae, we included one to six samples from each of the remaining tribes *sensu* Wilson *et al.* (2005), but with Tristanieae *sens.strict.* (*Tristania* + *Thaleropia*), we added two species of *Cloezia* and three of *Xanthomyrtus*, often considered genera of uncertain affinity, in line with the apparent phylogenetic position of these two genera in recent analyses (Biffin *et al.* 2010; Thornhill and Crisp 2012; Thornhill *et al.* 2015). We rooted the trees using *Heteropyxis* Harv. and *Psiloxylon* Thouars ex Tul. (subfamily Heteropyxidoideae Reveal) as outgroups, on the basis of previous research showing them to represent the sister lineage in the family (Wilson *et al.* 2001, 2005; Thornhill *et al.* 2015); more distant outgroups proved difficult to align at some loci. Details of all taxa included in the molecular analyses and associated GenBank numbers are provided in Table 1.

Molecular data

New extractions of total genomic DNA were made mostly from frozen silica-dried leaf material, but some were from fresh material, and a few from leaf or seed taken from herbarium specimens. Tissue was disrupted dry with tungsten beads by using the Qiagen Tissue Lyser (Qiagen, Hilden, Germany), and extractions used the Qiagen DNeasy Plant DNA Mini kit following the manufacturer's protocol.

Where possible, sequences were compiled for a total of six regions, including two from the nuclear-encoded internal transcribed spacer (ITS) and external transcribed spacer (ETS) regions of the rRNA gene, plus four plastid regions, including three contiguous components of the *trn*K intron, the *mat*K-coding region (*mat*K) and its 5′ and 3′ spacers (preM and postM respectively), and the *psb*A–*trn*H intergenic spacer (*psb*A–*trn*H). Details of primers used for PCR amplification and sequencing as well as details of PCR reactions were those outlined in Wilson and Heslewood (2016).

Sequence alignment and analysis

Sequence chromatograms were edited in Sequence Navigator (ver 1.0, Applied Biosystems) or GeneStudio Professional (ver. 2.2.0.0, GeneStudio, Inc., see https://genestudio.software.informer.com/) and consensus sequences generated were then aligned manually in PAUP* (ver. 4.0a build 169 for 32-bit Windows, see http://phylosolutions.com/paup-test; Swofford 2003). In aligning sequences, gaps were positioned to maximise conformity to known indel types such as simple and inverted duplications of adjacent sequences (Levinson and Gutman 1987; Golenberg *et al.* 1993). Overlapping indels of different lengths, and insertions of the same length but bearing different relationships to surrounding sequence, were treated as having independent origins, whereas indels of the same length and position and showing minor differences in nucleotide sequence were scored as the same state (Simmons and Ochoterena 2000). Potentially informative indels were scored as additional

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Table 1. Taxa, vouchers and accession numbers.

Taxon	Tribe	Collector (voucher)	Locality	*ITS*	*ETS*	*psb*A	*trn*K
Subfamily Myrtoideae							
Agonis flexuosa	Leptospermeae	Gadek 129 (UNSW23029)	Australia: WA	KM064814*	**OM730292**	–	AF184711.3
Angophora hispida	Eucalypteae	G. Parker *s.n.* (UNSW22897/RBG 811196)	Cult. RBGS (Wild source: Australia: NSW)	KT630896*	KT631415*	KT632066*	**AF368196.3**
Archirhodomyrtus beckleri	Myrteae	P. G. Wilson *s.n.* (UNSW23517)	Australia: NSW	**OM218672**	**OM730293**	**OM752313**	**AF368197.2**
Arillastrum gummiferum	Eucalypteae	P. Weston 1635 (NSW238936)	New Caledonia	AF190355*	DQ352479*	AF190372*	**AF368198.3**
Babingtonia cherticola	Chamelaucieae	P. G. Wilson 1514 (NSW448578)	Australia: WA	**OM218673**	**OM730294**	**OM752314**	**OM752354**
Backhousia citriodora	Backhousieae	Conti 110 (WIS)	Unknown source	KM064852*	KM064763*	KC134151*	**AY525129.2**
Backhousia myrtifolia	Backhousieae	P. G. Wilson *s.n.* (UNSW22391)	Cult. RBGS (Wild source: Australia: NSW)	KC134143*	–	KC134156*	AF368200.2
Baeckea frutescens	Chamelaucieae	P. G. Wilson *et al.* SAN152555 (NSW901256)	Malaysia: Sabah	MN715377*	**OM730295**	MH069879*	**OM752355**
Barongia lophandra	Tristaniopsidae	G. Sankowsky *s.n.* (UNSW24027)	Cult. (Wild source: Australia: Queensland)	**OM218674**	**OM730296**	**OM752315**	**AY525130.2**
Callistemon polandii	Melaleuceae	Jacobs 5362 & Clarkson (NSW388559)	Australia: Queensland	–	**OM730297**	–	AF184705.3
Calothamnus quadrifidus	Melaleuceae			KM064815*	–	HQ170471*	KM065325*
Choricarpia subargentea	Backhousieae	P. G. Wilson UNSW22896 (UNSWDB10849)	Cult. RBGS (Wild source: Australia: Queensland)	**OM218675**	**OM730298**	**OM752316**	**AF368202.3**
Cloezia artensis	Cloezieae	K. L. Wilson 7122 (NSW205857)	New Caledonia	**OM218676**	**OM730299**	**OM752317**	**OM752356**
Cloezia floribunda	Cloezieae	J. W. Dawson, 31.5.1997 (WELTU19376)	New Caledonia	AF172767	AY606255	–	**AY521533.2**
Corymbia gummifera	Eucalypteae			AF390463	KT631456	KT632098	KT632662
Eucalyptopsis papuana	Eucalypteae	F. Udovicic 191 (MELU)	Cult. (Wild source: Papua New Guinea)	AF190354	DQ352538	AF190371	**AF368205.3**
Homoranthus darwinioides	Chamelaucieae	P. Johnson *s.n.* (UNSW23267)	Australia: NSW	HM160108	**OM730300**	–	AF489399.2
Kania eugenioides 1	Kanieae	Lovave 48 (NSW486578)	Papua New Guinea	**OM218677**	**OM730301**	**OM752318**	–
Kania eugenioides 2	Kanieae	Conn 5611 (NSW870234)	Papua New Guinea	–	**OM730302**	**OM752319**	**OM752357**
Kania eugenioides 3	Kanieae	Takeuchi 7068 (NSW779227)	Papua New Guinea	**OM218678**	**OM730303**	**OM752320**	**OM752358**

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Table 1. (*Continued*)

Taxon	Tribe	Collector (voucher)	Locality	*ITS*	*ETS*	*psb*A	*trn*K
Kjellbergiodendron celebicum	Lophostemoneae	Yuzammi 399099 (NSW739086)	Cult. Bogor BG (Wild source: Indonesia: Sulawesi)	HM160110/ HM160109	**OM730304**	**OM752321**	**AF368209.2**
Kunzea pulchella	Leptospermeae	P. G. Wilson 1379 (NSW414061)	Australia: WA	EU833177*	**OM730305**	JX417092*	**AF184726.2**
Lenwebbia prominens	Myrteae	P. G. Wilson 1347 (NSW406575)	Australia: NSW	**OM218679**	**OM730306**	**OM752322**	**AY521538.2**
Leptospermum anfractum	Leptospermeae	Wannan 5420 (NSW835234)	Australia: Queensland	–	**OM730307**	**OM752323**	**OM752359**
Leptospermum grandifolium	Leptospermeae	P. G. Wilson 1894 (NSW990491)	Australia: NSW	**OM218680**	**OM730308**	**OM752324**	**OM752360**
Lindsayomyrtus racemoides	Lindsayomyrteae	K. D. Hill 2039 (NSW200341)	Cult. RBGS (Wild source: Australia: Queensland)	HM160111/ HM160112	KU945983	**OM752325**	AF184706.3
Lophostemon confertus	Lophostemoneae	M. O'Brien *s.n.* (UNSW23606)	Cult. (Wild source Australia: NSW)	AF390444*	**OM730309**	AF190368*	**AF184707.3**
Lysicarpus angustifolius	Tristaniopsidae	Conti *s.n.* (WIS)	Australia: Queensland	**OM218681**	**OM730310**	**OM752326**	**AF368210.3**
Melaleuca viridiflora	Melaleuceae	P. D. Hind 616 (RBG 10144)	Australia: Queensland	MH731215*	**OM730311**	MK011961*	**AF184708.2**
Metrosideros angustifolia	Metrosidereae	Linder 7855 (Z)	South Africa: Western Cape	KM064788*	KM064668*	**OM752327**	**OM752361**
Metrosideros carminea	Metrosidereae	D. Orlovich *s.n.* (UNSW23266)	Cult. (Wild source: New Zealand)	KM064795*	KM064696*	**OM752328**	**AY521541.2**
Metrosideros macropus	Metrosidereae	Sytsma *s.n.* (WIS)	USA: Hawaii	AF172745*	AF328052*	**OM752329**	**AF368212.3**
Mitrantia bilocularis	Tristaniopsidae	G. Sankowsky *s.n.* (UNSW24028)	Cult. (Wild source: Australia: Queensland)	**OM218682**	**OM730312**	**OM752330**	**AY521543.2**
Myrtastrum rufopunctatum	Myrteae	N. Snow 9188 *et al.* (BISH733420)	New Caledonia	HQ225439	**OM730313**	**OM752331**	**OM752362**
Myrtella beccarii	Myrteae	S. A. James SAJ0945 (PCMB11265)	Papua New Guinea	**OM218683**	**OM730314**	**OM752332**	**OM752363**
Neofabricia mjoebergii	Leptospermeae	P. G. Wilson 1354 (NSW410027)	Australia: Queensland	–	**OM730315**	**OM752333**	**AF184737.2**
Neomyrtus pedunculata	Myrteae	D. Glenny 8174 (CHR631167)	New Zealand	KM064787*	–	–	**KU945998.2**
Osbornia octodonta	Osbornieae	M. O'Brien and P. A. Gadek (UNSW23593)	Australia: Queensland	**OM218684**	**OM730316**	**OM752334**	**AF368213.3**
Ristantia gouldii	Tristaniopsidae	P. G. Wilson 1350 (NSW410053)	Cult. (Wild source: Australia: Queensland)	**OM218685**	**OM730317**	–	**AF368219.2**
Ristantia pachysperma	Tristaniopsidae	P. G. Wilson 1360 (NSW410034)	Australia: Queensland	–	**OM730318**	**OM752335**	**OM752364**
Sphaerantia chartacea	Tristaniopsidae	P. G. Wilson 1348 (NSW410056)	Cult. (Wild source: Australia, Queensland)	HM160115/ HM160116	**OM730319**	**OM752336**	**AY521547.2**
Syncarpia hillii	Syncarpieae	P. G. Wilson 1577 (NSW892014)	Cult. RBGS (Wild source: Australia: Queensland)	KT631410*	KT632062*	KT632620*	AY525139

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Table 1. (*Continued*)

Taxon	Tribe	Collector (voucher)	Locality	*ITS*	*ETS*	*psb*A	*trn*K
Syzygium alatum	Syzygieae	S. A. James SAJ1225 (PCMB11992)	Papua New Guinea	**OM218686**	**OM730320**	**OM752337**	**OM752365**
Syzygium australe	Syzygieae	P. G. Wilson *s.n.* (UNSW21775)	Cult. RBGS (Wild source: Australia: NSW)	A-Y187177.2*	AY187111*	**OM752338**	**AF368221.2**
Syzygium cymosum	Syzygieae	K. L. Wilson 10742 (NSW891692)	France: Reunion Is	**OM218687**	**OM730321**	**OM752339**	**OM752366**
Tepualia stipularis	Metrosidereae	Sytsma *s.n.* (WIS)	Unknown source	AM234071*	AM489969*	AM489884*	**AF368222.3**
Tetrapora verrucosa	Chamelaucieae	P. G. Wilson 1638 (NSW612780)	Australia: WA	**OM218688**	**OM730322**	**OM752340**	**OM752367**
Thaleropia queenslandica	Tristanieae	B. Hyland *s.n.* (UNSW23045)	Cult. (Wild source: Australia: Queensland)	AY264945	AY264946	**OM752341**	**AF368223.2**
Tristania neriifolia	Tristanieae	P. G. Wilson *s.n.* (UNSW23243)	Cult. RBGS (Wild source: Australia: NSW)	EF026608	**OM730323**	**OM752342**	**AF368224.3**
Tristaniopsis laurina	Tristaniopsidae	P. G. Wilson *s.n.* (UNSW22390)	Cult. RBGS (Wild source: Australia: NSW)	EF041514	KU945985	**OM752343**	AF184710.3
Tristaniopsis macrosperma	Tristaniopsidae	Conn 5261 (NSW805404)	Papua New Guinea	**OM218689**	**OM730324**	–	**OM752368**
Uromyrtus neomyrtoides	Myrteae	Wulff & Wilson (NSW846522)	New Caledonia	**OM218690**	**OM730325**	**OM752344**	**OM752369**
Welchiodendron longivalve	Lophostemoneae	G. Sankowsky *s.n.* (NSW504439)	Cult. (Wild source: Australia: Queensland)	**OM218691**	**OM730326**	**OM752345**	**AY525143.2**
Whiteodendron moultonianum	Lophostemoneae	Stephen Teo S75422 (NSW739081)	Malaysia: Sarawak	**OM218692**	**OM730327**	**OM752346**	**AF368225.3**
Xanthomyrtus flavida	Xanthomyrteae	P. G. Wilson *et al.* SAN152562 (NSW857308)	Malaysia: Sabah	**OM218693**	**OM730328**	**OM752347**	**OM752370**
Xanthomyrtus kanalaensis	Xanthomyrteae	J. Benson *s.n.* (UNSW22387)	New Caledonia	**OM218694**	**OM730329**	**OM752348**	**OM752371**
Xanthomyrtus papuana	Xanthomyrteae	M. Heads 6601 (AK235115)	Papua New Guinea	**OM218695**	**OM730330**	**OM752349**	**AF368226.3**
Xanthostemon aurantiacus	Xanthostemoneae	J. W. Dawson, 19.5.1997 (WELTU19383)	New Caledonia	**OM218696**	**OM730331**	**OM752350**	**AY525144.2**
Xanthostemon cf. *petiolatus*	Xanthostemoneae	Conn 5613 (NSW870236)	Papua New Guinea	**OM218697**	**OM730332**	**OM752351**	**OM752372**
Subfamily Heteropyxidoideae							
Heteropyxis natalensis	Heteropyxideae	Adam *s.n.* (ZBG 3931)	Cult. RBGS (ex Harare BG, Zimbabwe)	KM064805*	**OM730333**	**OM752352**	AF368208.2
Psiloxylon mauritianum	Psiloxyleae	Briggs 7233 (NSW4189783)	Cult. RBGS (Wild source: France: Reunion Is.)	EF026606	**OM730334**	**OM752353**	**AF368215.3**

Voucher details correspond to material sequenced by these authors; bold indicates new or updated sequence generated for this study; asterisks (*) indicate sequences sourced from GenBank from a different voucher. Herbarium abbreviation codes follow Index Herbariorum (RBGS, Royal Botanic Gardens, Sydney, for cultivated plants).

presence or absence characters and appended to the database. Gaps were treated as missing data in the phylogenetic analyses. Coding sequences of the *mat*K gene were translated in MacClade (ver. 4.08a, see https://mesquiteproject.github.io/MacClade//macclade; Maddison and Maddison 2000) to check for internal stop codons.

Preliminary analyses using maximum parsimony or Bayesian inference were run using either individual loci, or the concatenated plastid or nuclear loci, each run with or without appended indels. Heuristic searches were conducted in PAUP* using tree bisection reconnection branch-swapping on best trees to recover the most-parsimonious (MP) trees. One thousand replicates of random taxon-addition searching were conducted in which multistate characters were treated as polymorphisms, so as to detect multiple islands of trees. Where preliminary analyses of single plastid loci exhausted computer memory, restricted heuristic searching was conducted, saving only 100 trees per replicate. Relative support for the clades identified by parsimony analysis was estimated using the jackknife rather than bootstrap resampling in PAUP*, following the recommendations of Simmons and Freudenstein (2011). For jackknife analyses, 10 000 replicates of faststep searching were conducted in which each replicate used random-taxon addition, no branch swapping, and the percentage of characters deleted was set at 33%. Jackknife (jk) values >50% were interpreted as weak support for clades, >75–89% as moderate support, 90–99% as strong support and 100% jackknife was considered robust. Sequence statistics for each locus are presented in Table 2.

The MP phylogenies generated were compared with those obtained using the Markov-chain Monte Carlo (MCMC) method implemented in MrBayes (ver. 3.2.7a, see https://github.com/NBISweden/MrBayes/; Ronquist *et al.* 2012) in the CIPRES Science Gateway (ver. 3.3, see https://www.phylo.org; Miller *et al.* 2010). The most appropriate nucleotide substitution models to apply in likelihood-based analyses were determined using the Akaike information criterion (AIC) in MrModelltest (ver. 2.3, J. A. Nylander, see https://github.com/nylander/MrModeltest2/releases/tag/v2.3), with data partitioned into the six regions indicated above, with each partition assigned a unique substitution model. Under the AIC, five regions fit general time-reversible likelihood (GTR) substitution models (nst = 6), with gamma distribution of rate variation among sites (GTR + Γ model; preM, *mat*K, postM), or also with a proportion of invariant sites (GTR + Γ + I model; ITS, *psb*A–*trn*H). The ETS region fit a Hasegawa–Kishino–Yano substitution model (nst = 2, HKY + Γ + I model). Where Bayesian analyses also included indels, these were binary encoded as an extra partition, and we applied a default two-state Markov model with gamma distribution of rates and coding set to variable (because there were no invariant sites). Statefreqpr was set to fixed (empirical) for this partition to reflect only having two states.

Bayesian posterior probabilities (PP) were estimated using two independent runs of 10 million generations by using four chains with tree sampling every 1000 generations. All parameters were set to be unlinked and with rates variable between partitions, with all other priors for the analysis set flat (i.e. as Dirichlet priors). Runs were assessed as sufficient when displaying convergence of effective sample size (ESS) for all statistics in Tracer (ver. 1.7.1, see https://github.com/beast-dev/tracer/releases/tag/v1.7.1, accessed 5 March 2020), the standard deviation of split frequencies was clearly <0.01 and the PSRF for all parameters neared 1.000. Trees generated before the four Markov chains reaching stationarity (the burn-in ~25%) were

Table 2. Sequence statistics for molecular data.

Genome	Aligned length included in analyses (bp)	CI	PI	PU	Locus		Aligned length (bp)	Indels	AIC model
Plastid	3470	0.695	700	513	*trn*K intron	5′ *mat*K spacer	856	9	GTR + Γ
						*mat*K gene	1571	5	GTR + Γ
						3′ *mat*K spacer	324	4	GTR + Γ
					*psb*A–*trn*H spacer		821	23	GTR + Γ + I
								Subtotal 41	
Nuclear	1538	0.424	552	235	ITS		896	29	GTR + Γ + I
					ETS		582	44	HKY + Γ + I
								Subtotal 73	
								Total 114	

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discarded. The remaining trees were used to construct a 50% majority-rule consensus tree, with nodes assigned posterior probabilities (PP) of 0.95–1.00 considered as supported.

TreeGraph 2 (ver. 2.15.0–887 β, see http://treegraph.bioinfweb.info/; Stöver and Müller 2010) was used to construct the figures of the phylogenetic trees. The PP (upper) and jk (lower) support values were imported onto the Bayesian consensus trees for each analysis and various annotations made to clades. Clades with strong support (1.00 PP, ≥90% jk) are indicated by heavier lines. Supplementary figures mapping jackknife (jk) values of >50% onto the strict consensus of the most parsimonious trees are also supplied for referencing conflicting areas.

Morphological sampling

Cuticles were mounted on glass slides for standard light microscopy (LM) or on aluminium stubs for analysis by scanning electron microscope (SEM) following the protocols described in Tarran *et al.* (2016).

Fruits of *Kania* sp. and *Tristaniopsis collina* Peter G.Wilson & J.T.Waterh. were cleared in a solution of 5% potassium hydroxide (KOH) over a medium heat. The fruits were left in the solution until the flesh became translucent and soft enough to be teased away if necessary. The remaining parts were thoroughly rinsed to remove any traces of the KOH, then bleached in a solution of commercial grade bleach until the vascular skeletons became white to translucent. The skeletonised fruits were then placed in a solution of 10% Safranin O, and left to stain, then the bleaching, rinsing and staining were repeated until the lignified vascular structures were darkly stained. Excess stain was rinsed off, the fruits were then stored in deionised water and photographed using a Nikon D5000 digital SLR with a macro lens over a bright light box. Full details of specimens used in these studies are given in Table 3.

Results

Molecular phylogeny

Aligned sequence lengths, variable characters, number of scored informative indels and models applied to each partition for Bayesian analyses are presented in Table 2. Although 21 taxa were missing some data (1–10 taxa lacking sequence at individual loci), our dataset was largely complete. There is some level of saturation of substitutions in the two nuclear regions in this dataset, reducing their utility at resolving deeper levels of relationships across the family, with homoplasy likely confounding the phylogenetic signal. In this family, these nuclear loci will be most useful for within-tribe analyses. Including indels, the nuclear dataset had 51% variable characters, 36% of which were informative under parsimony (compared with 35% variable characters, 20% informative under parsimony for the plastid data). Regardless of differences in the arrangements of some poorly supported branches uniting tribes in separate analyses, all analyses retrieved the same robustly supported major clades.

Inclusion of scored indels in both Bayesian and parsimony analyses resulted in improvements in branch supports. Therefore, indels were included in all analyses presented here. Mostly comprising small sections of sequence that could not be unambiguously aligned, a total of 156 bp, including a 93-bp highly variable portion of the *psb*A–*trn*H alignment, were excluded from analyses, leaving a 5008-bp alignment to be used in analyses, inclusive of 114 appended indels. Separate analyses of plastid (3470 bp including 41 indels) and nuclear (1538 bp including 73 indels) data retrieved clades corresponding to most currently recognised tribes, with the major difference being in the composition of the Kanieae clade of Wilson *et al.* (2005), but there were differences in supported relationships within and among some tribes in these analyses, and between the two types of analysis. For this reason, we have not combined the

Table 3. Voucher details for specimens examined for morphological characters.

	Species	Collector (herbarium)	Locality	
Cuticles	*Barongia lophandra*	*B.Gray 618* (NSW)	Australia: Queensland	Fig. 5*b*
	Kania eugenioides	*Womersley NGF37324* (NSW)	Papua New Guinea	Fig. 3*a*, *b*, 5*a*
	Kania urdanetensis	*Elmer 13694* (NSW)	Phillipines: Mindanao	Fig. 5*c*
	Lophostemon confertus	*Murray 82* (NSW529797)	Australia: NSW	Fig. 4*b*
	Metrosideros (*Carpolepis*) *laurifolia*	*J.Munzinger 594* (NSW)	New Caledonia	Fig. 4*a*
	Metrosideros robusta	*Knightbridge PK42, May 2001* (NSW)	New Zealand	Fig. 5*d*
	Tristaniopsis laurina	*L.A.S.Johnson s.n.* (NSW531466)	Australia: NSW	Fig. 5*e*
	Xanthomyrtus montivaga	*Womersley NGF24859* (NSW)	Papua New Guinea	Fig. 3*c*, *d*, 5*f*
Fruit	*Kania* sp.	*Henty NGF42536* (NSW977918)	Papua New Guinea	Fig. 6*a*
	Tristaniopsis collina	*Tarran s.n., 16 Nov 2014* (ADU)	Australia: Queensland	Fig. 6*b*, *c*

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datasets, but present the results for analyses of the separate genomic regions.

Heuristic searching of the combined plastid dataset yielded 24 equally most parsimonious (MP) trees of 2247 steps in a single island. The MP strict consensus tree (Supplementary Fig. S1) resolved most of the major lineages of the subfamily Myrtoideae congruent with Wilson *et al.* (2005), and although relationships between many tribes were resolved, most lacked support. The Bayesian analysis of these data showed the same tribal structure but with less resolution between clades. Jackknife supports >50% from the MP analysis are indicated on the Bayesian majority-rule consensus tree (Fig. 1) and the MP strict consensus tree (Supplementary Fig. S1).

Sampling of some groups was limited but the analyses provided continued support for most previously recognised tribes. The core Myrtaceae (subfamily Myrtoideae), tribes Backhousieae, Chamelaucieae, Leptospermeae, Myrteae, Syzygieae and Xanthostemoneae all received robust support (100% jk, 1.00 PP); Eucalypteae, Lophostemoneae and Metrosidereae all have strong support (99% jk, 1.00 PP). By contrast, the tribe Kanieae is not resolved as monophyletic. The type genus, *Kania*, is moderately supported as sister to Metrosidereae (81% jk, 1.00 PP), but is not at all closely associated with genera formerly placed with it in the tribe Kanieae. Those other genera, the *Tristaniopsis* group, are weakly monophyletic (68% jk, 1.00 PP), but there is robust internal support (100% jk, 1.00 PP) for the monophyly of a subclade comprising *Ristantia*, *Mitrantia* and *Sphaerantia*. The current tribe Tristanieae is rendered paraphyletic by the placement of *Cloezia*, and the clade is only weakly supported (52% jk, 1.00 PP). Rather, a weak clade (52% jk, 0.99 PP) places *Cloezia* (100% jk, 1.00 PP) sister to *Xanthomyrtus* (97% jk, 1.0 PP), that clade being sister to a robust Tristanieae *sens. strict.*, comprising Tristania + Thaleropia (100% jk, 1.00 PP).

Relationships between some tribes and tribal groupings also receive support in these analyses. As in previous analyses, Xanthostemoneae and Lophostemoneae are resolved as sister (96% jk, 1.00 PP) and form the first diverging lineage in the subfamily, with modest support (68% jk, 0.99 PP); Chamelaucieae and Leptospermeae (99% jk, 1.00 PP) form a strong clade; Melaleuceae (84% jk, 1.00 PP) and Osbornieae are still resolved as sister taxa but with modest support (70% jk, 1.00 PP). Relationships of two other genera that have been unclear previously, *Syncarpia* Ten. and *Lindsayomyrtus* B.Hyland & Steenis, remain unresolved.

Heuristic searching of the combined nuclear dataset yielded 36 equally most parsimonious (MP) trees of 2912 steps in a single island. The Bayesian analysis of these data showed a largely similarly resolved structure but with some areas of conflict (Fig. 2). Jackknife supports >50% from the MP analysis are indicated on the Bayesian majority-rule consensus tree (Fig. 2) and the MP strict consensus tree (Supplementary Fig. S2). Again Myrtoideae and most of the existing tribes were retrieved, although supports were somewhat lower with this dataset; Syzygieae and Xanthostemoneae received robust support (100% jk, 1.00 PP), as did clades of *Xanthomyrtus* and *Cloezia*; Backhousieae, Eucalypteae, Leptospermeae, Metrosidereae all have strong support (>90% jk, 1.00 PP). Moderate support for *Kania* + Metrosidereae (84% jk, 1.00 PP) is again found with the nuclear data. The remainder of the present Kanieae, the *Tristaniopsis* group, is again found to form an unrelated and modestly supported clade (72% jk, 1.00 PP). This group is resolved as a supported sister to a weak Lophostemoneae + Xanthstemoneae (<50% jk, 1.00 PP). Lophostemoneae + Xanthstemoneae is no longer the first diverging lineage in the nuclear analyses, with Myrteae shown as the unsupported first lineage to diverge (<50% jk, 0.86 PP) outside a polytomy containing all remaining tribes. There is very little resolution of the backbone of the tree. A feature of the Leptospermeae clade is that *Leptospermum* J.R.Forst & G.Forst. is shown to be paraphyletic, a situation first demonstrated by O'Brien *et al.* (2000). In the plastid analysis, *L. grandifolium* Sm., a representative of *Leptospermum sens. strict.*, is sister to other members of the tribe (Fig. 1, 69% jk, 1.00 PP) with *L. anfractum* A.R.Bean nested among the remaining genera as sister to *Neofabricia* Joy Thomps. Here, in the nuclear analysis, *Leptospermum* is still found to be paraphyletic, but the topology is rather different, with *L. anfractum* sister to other members of the tribe (98% jk, 1.00 PP) and *L. grandifolium* sister to *Kunzea* Rchb.

A notable difference between the two nuclear analyses is the placement of *Cloezia*. In the nuclear MP analysis (Supplementary Fig. S2), it is placed in a clade with Chamelaucieae, Leptospermeae and Eucalypteae, rather than as a sister to *Xanthomyrtus* where it is placed in all other analyses, albeit on a long branch. Although there is strong support from the plastid Bayesian analyses for the sister arrangement with *Xanthomyrtus* (0.99 PP), the clade is unsupported by the nuclear data (0.83 PP), and there is no jackknife support in either MP analysis for Cloezia's placement. This is evidence that the genus forms a divergent lineage and confirms that its status needs reassessment.

The major differences between the plastid and nuclear analyses lie in largely unsupported resolution of relationships among tribes. Deep branches separating clades tend to be very short and thus are supported by few characters, so it is not unexpected that resolution is poor at this level. As discussed above, there is some conflict in placement of *Cloezia*. Although there is modest support for the placement of *Lindsayomyrtus* sister to Chamelaucieae + Leptospermeae with the plastid data (74% jk, 0.97 PP, Fig. 1, Supplementary Fig. S1), the nuclear MP analysis has it as unsupported sister to *Syncarpia* (<50% jk, Supplementary Fig. S2) and the nuclear Bayesian analysis as unsupported sister to Melaleuceae + Osbornieae (0.75 PP, Fig. 2). Again, this supports the distinctiveness of the genus and confirms that its recognition as a monotypic tribe is warranted.

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Morphological data

Leaf cuticles of *Kania* show stomatal clumping that is uneven and interrupted, as illustrated in *K. eugenioides* (Fig. 3*a*, *b*). However, the two species of *Xanthomyrtus* examined show very distinctive stomatal clumping with distinct bands of dense stomata, as can be seen in *X. montivaga* A.J.Scott (Fig. 3*c*, *d*), where the stomatal distribution is clearly independent of underlying venation patterns. Neither of these stomatal arrangement types is typical in the Myrtaceae and most other species of Myrtaceae demonstrate stomatal distribution types more typical of other dicotyledonous angiosperm leaves. Either the stomata are evenly distributed and unaffected by underlying venation, illustrated in *Metrosideros laurifolia* Brongn. & Gris. (Fig. 4*a*), or else stomata are restricted in areolae, as on the cuticles of *Lophostemon confertus* (R.Br.) Peter G.Wilson & J.T.Waterh. (Fig. 4*b*). In the latter case, the stomata are evenly distributed in the areolae and the gaps occur over leaf veins, which interrupt the underlying spongy mesophyll. The resulting arrangement of stomata does not constitute stomatal clumping.

Water stomata, with associated cuticular striations, occur in both *Kania* and *Tristaniopsis*. Well-developed cuticular striations are found in *Kania* species (Fig. 5*a*, *c*), and also in some other members of the present tribe Kanieae, such as *Barongia lophandra* Peter G.Wilson & B.Hyland (Fig. 5*b*). They can also be found in some species of *Metrosideros*, such as *M. robusta* A.Cunn. (Fig. 5*d*), and *Tristaniopsis*, for example, *T. laurina* (Sm.) Peter G.Wilson & J.T.Waterh. (Fig. 5*e*), but are not quite as well developed. By contrast, both water stomata and cuticular striations are absent from *Xanthomyrtus* species, as observed in *X. montivaga* (Fig. 5*f*) and *X. flavida* (Stapf) Diels.

The cleared fruit of *Kania* sp. (Fig. 6*a*) shows five major veins in the hypanthium, leading to each of the five sepals, with weaker secondary branches leading to the sepals. There also appears to be a well developed band of vascular tissue encircling the hypanthial rim. By contrast, the cleared fruit of *Tristaniopsis collina* (Fig. 6*b*, *c*) does not possess five strongly developed major veins in the hypanthium. Several veins of similar size and staining quality are seen running up to the sepals, but also leading to the petals and staminal bundles, which in *Tristaniopsis* species are located opposite each petal. There is no strong correlation between vein size and perianth and there is no band of vascular tissue encircling the hypanthial rim.

Discussion

The present study confirms most of the previous tribal groupings (Wilson *et al.* 2005; Biffin *et al.* 2010; Thornhill *et al.* 2015). However, note that the so-called BKMMST clade (Backhousieae, Kanieae, Metrosidereae, Myrteae, Syzygieae, Tristanieae) of Biffin *et al.* (2010) was not recovered by our analyses. The chief difference is that we did not find evidence of a robust connection between the Myrteae and the other genera in that grouping. Rather, in our analyses, the Myrteae was associated with an unsupported group comprising many of the remaining tribes (<50% jk, 0.64 PP, plastid), or was unsupported as the earliest diverging lineage in the subfamily (<50% jk, 0.86 PP, nuclear). Thornhill *et al.* (2015) also failed to find support for the BKMMST clade, with the Myrteae having no (0.78 PP) support as sister to the others.

A recent large-scale study across the order Myrtales (Maurin *et al.* 2021) targeted a comprehensive suite of more conserved low-copy nuclear genes. That analysis also found little support for the so-called BKMMST grouping of tribes, with Syzygieae consistently falling outside a clade comprising the other tribes. That study included a wider sampling of genera assigned to the Kanieae and concurs with our finding that *Kania*, which was represented only by a poor, partial sequence in the single plastid locus analysis of Wilson *et al.* (2005), is now resolved as sister to the Metrosidereae with moderate jackknife support, quite separate from the remainder of tribe Kanieae, the *Tristaniopsis* group.

The phylogenetic positions of *Cloezia* and *Xanthomyrtus* have often been the subject of debate. Wilson (2011) tentatively included *Cloezia* in Kanieae *sens. lat.*, on the basis of its placentation being similar to that found in *Lysicarpus*. However, phylogenetic analyses have shown both *Cloezia* and *Xanthomyrtus* to form a clade with core members of Tristanieae. In both Biffin *et al.* (2010) and Thornhill *et al.* (2015), they were successive sisters to the strongly supported core Tristanieae, but the relationship of *Cloezia* to the other taxa was not strongly supported, with a PP of ≤0.95 in the former study, and PP of only 0.31 in the latter study, which analysed sequence data from exactly the same regions. In the present analyses, the three taxa form a single clade but there is only nominal support from parsimony for the placement of *Xanthomyrtus* in a clade that includes the tribe Tristanieae (≤52% jk, 1.00 PP). Rather, *Xanthomyrtus* is resolved as weakly sister to *Cloezia*, a degree of relationship also recovered by Maurin *et al.* (2021) where PP was only 0.54.

Morphological data do not assist with resolution of these relationships. There is little difference in pollen morphology between *Cloezia* and *Xanthomyrtus*; both have parasyncolpate pollen that is similar in size and exine pattern (Thornhill *et al.* 2012*a*). Wood anatomy is similarly uninformative. The vessel-ray pitting in *Cloezia* is fine and alternate, similar to intervessel pitting (P. Gasson, pers. comm.), and in *Xanthomyrtus* it is described as 'small, half-bordered' by Ingle and Dadswell (1953, p. 384), so there is little distinction there. In the context of the family, both of these characters (pollen morphology and wood anatomy) would be interpreted as plesiomorphic and, therefore, not be reliable

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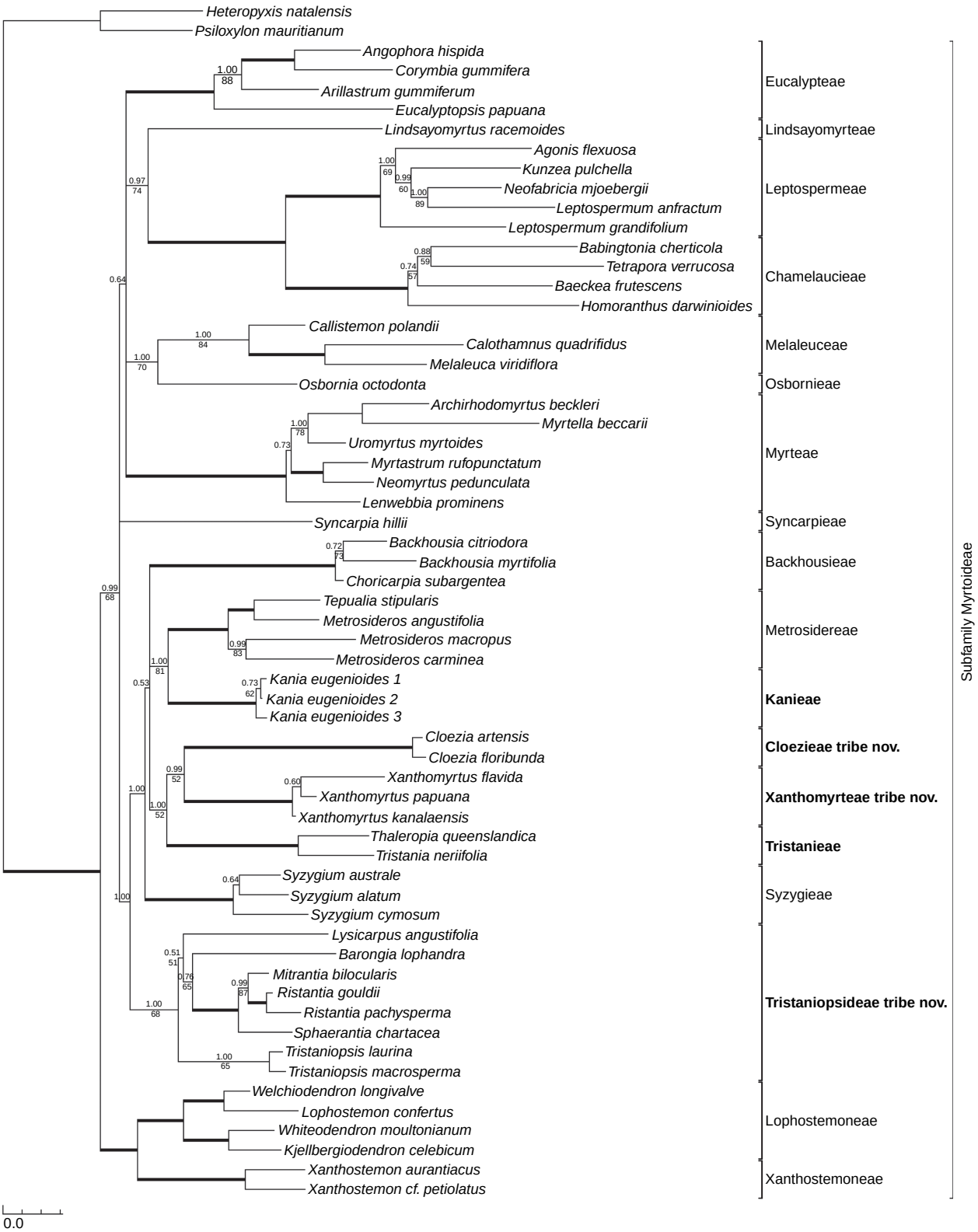


Fig. 1. Bayesian 50% majority-rule consensus tree of combined plastid data. Values shown on tree indicate clade support from Bayesian posterior probabilities (PP, above branches) and jackknife values from maximum parsimony analysis of >50% (jk, below). Thick lines received strong support 1.00 PP and jk ≥ 90%. New or revised tribal assignments are indicated in bold.

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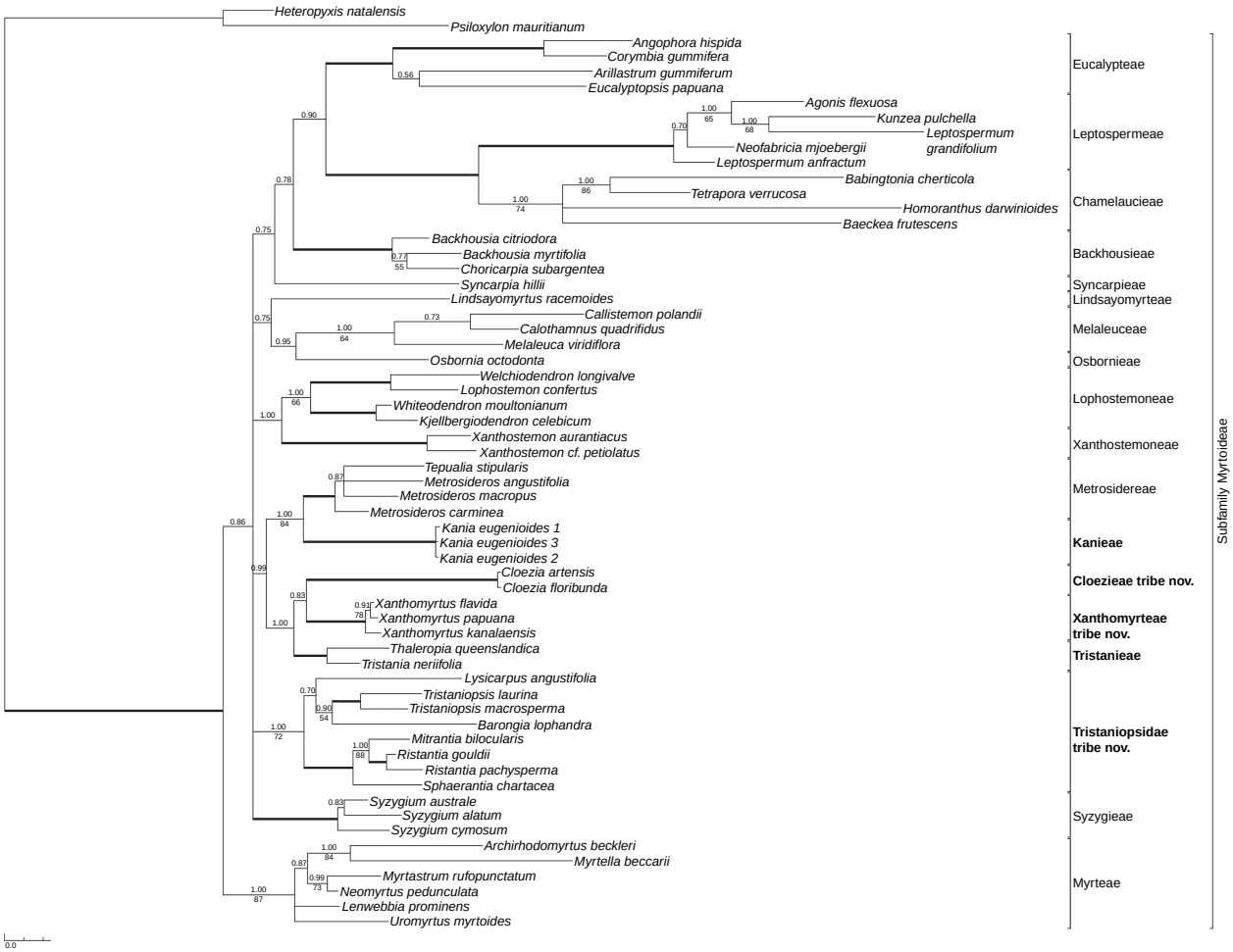


Fig. 2. Bayesian 50% majority rule consensus tree of combined nuclear data. Values shown on tree indicate clade support from Bayesian posterior probabilities (PP, above branches) and jackknife values from maximum parsimony analysis of >50% (jk, below). Thick lines received strong support 1.00 PP and jk ≥ 90%. New or revised tribal assignments are indicated in bold.

indicators of shared evolutionary history. By contrast, the genera of core Tristanieae, *Tristania* and *Thaleropia*, share a highly derived pollen type that is the smallest found in the family so far, and are triporate or acolpate with a psilate exine (Pike 1956, pp. 39, 46; Gadek and Martin 1981, p.179; Patel *et al.* 1984, p, 939 for *Tristania*; Thornhill *et al.* 2012*a*, p. 267 for both genera).

In the case of *Kania*, our results point to a closer relationship with *Metrosideros* than with those genera previously included in Kanieae *sens. lat.* There is some support for this from wood anatomy. Vessel-ray pits are described as 'very large, either circular to horizontally elongated or forming almost scalariform series' (Erdtman and Metcalfe 1963, p. 250) in stems from a type specimen of *Kania eugenioides*, and as 'simple and rounded to elongated' in wood of *Metrosideros* (Ingle and Dadswell 1953, p. 378; Meylan and Butterfield 1978). However, there is less support from pollen morphology because *Metrosideros* pollen is much larger than *Kania* pollen and has distinct apocolpial islands (Pike 1956; McIntyre 1963; Gadek and Martin 1981; Thornhill *et al.* 2012*b*).

Leaf epidermal characters identified by Tarran *et al.* (2016) definitely favour a closer relationship between *Kania* and at least some species of *Metrosideros*, although the latter differs significantly in lacking clumped stomata. The findings relating to floral vascularisation are more significant because the reduction in the number of main vascular traces to only five has not been reported elsewhere in the family. Wilson (1993, 2011) was the first to suggest that this feature was a likely synapomorphy for the tribe Metrosidereae, on the basis of the published observations of Dawson (1970*a*, 1970*b*, 1972*b*, 1972*c*, 1972*d*, 1975) who provided illustrations of transverse sections of flowers or developing fruits in the *Metrosideros* group that consistently showed five main veins in the hypanthium. The cleared flower of *Kania* (Fig. 6*a*) clearly shows five major vascular traces leading to the sepals with strong secondary branches to the petals. This approaches the pattern of vascularisation

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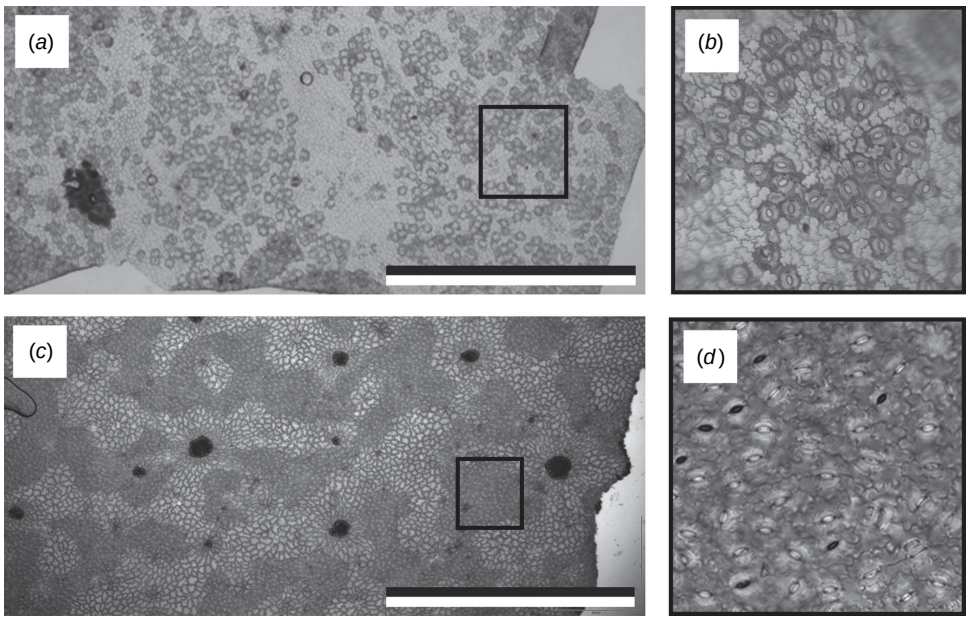


Fig. 3. Examples of variation in stomatal distribution. Light microscopy. (*a*) Cuticle of *Kania eugenioides*, showing 'clumping' of stomata with no clear distribution into vein islets or areolae; scale bar: 200 μm. and (*b*) A close up of the clumped stomata, showing a disorganised distribution in *K. eugenioides*. (*c*) *Xanthomyrtus montivaga*, showing an alternative form of aggregation of stomata into distinct zones, with large non-stomatal areas between zones, with no clear relation to underlying venation; scale bar: 200 μm. (*d*) A close up of the aggregated stomata. There are no spaces between any of the subsidiary cells of stomata in *Xanthomyrtus* species, and stomata are approximately half the size (~5 μm).

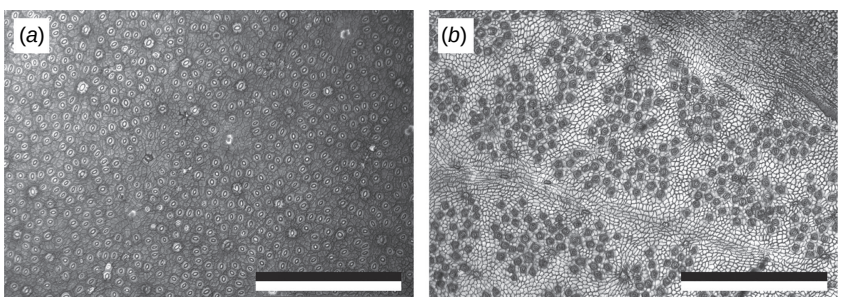


Fig. 4. Examples of the most common forms of stomatal distribution in cuticles from across the Myrtaceae. Light microscopy. (*a*) Cuticle of *Metrosideros* (*Carpolepis*) *laurifolia*, showing an even distribution of stomata, and (*b*) *Lophostemon confertus*, showing separation of stomata by major and minor leaf venation into vein islets or areolae. Scale bars: 500 μm.

observed in Metrosidereae, where the five traces are sometimes heavily thickened in both extant (for example, Dawson 1975, fig. 11) and fossil (Pole *et al*. 2008, fig. 12; Tarran *et al*. 2017, fig. 4) taxa. In *Kania*, there is evidence of a transition to five well developed veins, but the pattern is not as distinctive as it is in many taxa of Metrosidereae. In contrast with this, the vascularisation of the flower of *Tristaniopsis collina* (Fig. 6*b*) does not show a particularly strong association of vascular traces with perianth parts.

Conclusions

Morphological characters, particularly cuticle micromorphology and floral vascularisation, indicate a greater affinity between *Kania* and the tribe Metrosidereae than between it and the genera usually placed in the tribe Kanieae, a relationship also strongly supported by our molecular phylogenetic analysis. *Kania* is independent of the other genera with which it has been grouped in the tribe Kanieae (*sensu* Wilson *et al*. 2005) and shows a robust affinity with the tribe Metrosidereae. However, we also conclude that, because *Kania* differs from Metrosidereae in anther morphology (prominent connective), placentation (placenta remote from base of style), distinctive cuticular characters, and genetic distance, that retention of Kanieae as a separate, monogeneric tribe is justified. A further consequence of our analysis is that a new tribe is required to accommodate most other genera presently assigned to the Kanieae. This new tribe, Tristaniopsideae, is described below.

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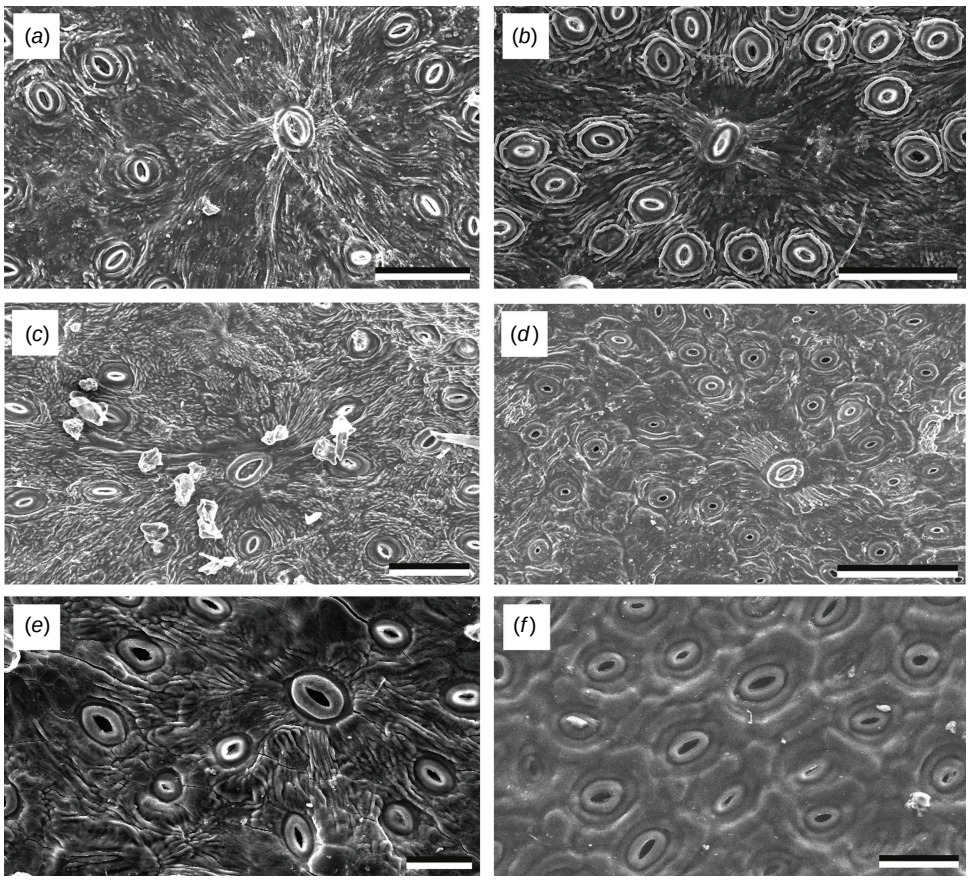


Fig. 5. Cuticles of several species from the tribe Kanieae. (*a*–*f*) SEM images. (*a*) *Kania eugenioides*; scale bar: 50 µm. (*b*) *Barongia lophandra*; scale bar: 50 µm. (*c*) *Kania urdanetensis* (Elmer) Peter G.Wilson; scale bar: 50 µm. (*d*) *Metrosideros robusta*; scale bar: 50 µm. (e) *Tristaniopsis laurina;* scale bar: 20 µm. Note cuticular striations radiating from the water stomata and the papillose texture in *a*–e (but not as well developed in *Metrosideros* and *Tristaniopsis*). (*f*) *Xanthomyrtus montivaga*; scale bar: 20 µm. The cuticles of *Xanthomyrtus* lack water stomata entirely, as well as any associated cuticle striations.

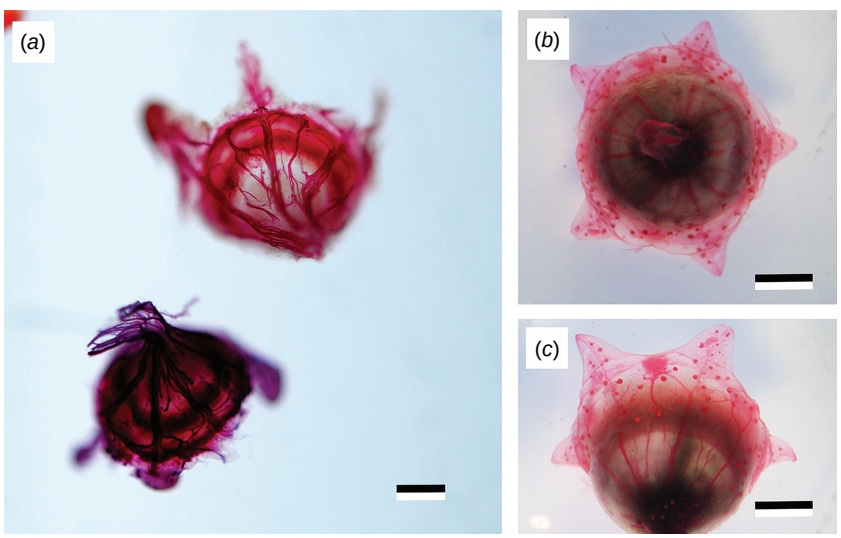


Fig. 6. Vascularisation in skeletonised fruits. (*a*) *Kania* sp., scale bar: 1 mm; and (*b*, *c*) *Tristaniopsis collina*, scale bars: 2 mm.

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The phylogenetic analysis also confirms previous relationships among taxa grouped with Tristanieae. *Xanthomyrtus* had been referred to Tristanieae, but differs from the two core genera, *Tristania* and *Thaleropia*, in having a predominantly four-merous perianth, a compressed-reniform seed with a crustaceous testa, an embryo more like that of *Xanthostemon* F.Muell. and a fleshy fruit. All three genera do have leafy cotyledons that lie face-to-face, but in *Xanthomyrtus* the hypocotyl is bent so that it lies along the edges of the cotyledons (accumbent), as noted by Landrum and Stevenson (1986), whereas in the other two it is straight (Dawson 1974; Wilson 1993). Wilson *et al.* (2005) did not place *Cloezia* in any tribe, whereas Wilson (2011) tentatively included it in Kanieae *sens. lat.*, on the basis of the arrangement of the ovules. However, as already noted, recent phylogenies that have included *Cloezia* have placed it in a grade with *Xanthomyrtus* and core Tristanieae. In our analysis, and that of Maurin *et al.* (2021), *Cloezia* was found to be sister to *Xanthomyrtus* rather than to core Tristanieae and differs significantly from the other genera in having a strongly exserted capsule with basal placentas bearing ovules in a circular series. The Bayesian analyses showed *Cloezia* to be on a strongly supported long branch, an indicator of early divergence and long isolation. Consequently, our preference is to recognise new tribes to accommodate both *Xanthomyrtus* and *Cloezia* to reflect the genetic distance (long branches) and their marked morphological divergence, particularly in placentation and embryo features.

Recognition of these extra tribes, and emending the circumscription of Kanieae, brings to four the number of tribes that do not occur naturally on the Australian mainland today.

Systematic treatment

Tristanieae Peter G.Wilson, *Pl. Syst. Evol.* 251: 15 (2005)

Type: *Tristania* R.Br.

Trees or shrubs; leaves opposite, growth monopodial. Inflorescences thyrsoids or cymes; flowers 5-merous, yellow or orange to red; stamens free or fused into 5 groups opposite petals, usually fewer than 25. Ovary half-inferior, style inserted in the apex of the ovary, style base adjacent to placentas; ovary usually trilocular. Fruit a capsule. Seed linear, embryo straight, cotyledons lying face to face. Pollen grains quite small with a smooth exine.

A small tribe of 2 genera: *Tristania*, *Thaleropia*

Kanieae Engl., in H. G. A. Engler (ed.), *Nat. Pflanzenfam.*, 2nd edn. 2, 18a: 109 (1930)

Kanieae Peter G.Wilson ex Reveal, *Phytoneuron* 2012–37: 217 (2012), isonym.

Type: *Kania* Schlr.

Trees or shrubs; leaves opposite. Inflorescence axillary, cymes or panicles; flowers yellow; stamens free, in a single whorl on the hypanthial rim, evenly spaced or, occasionally, grouped opposite the petals; anthers with elongated connectives. Style terminal on the ovary; ovules scattered on basal placentas that are remote from the style. Fruit a capsule, exserted from the hypanthium; seeds linear; embryo straight; cotyledons lying face-to-face.

A monogeneric tribe of ~10 species that occurs only in Malesia (New Guinea and the Philippines). Fossil evidence (Tarran *et al.* 2016, 2017) indicates that *Kania* may have been present in Australia in the late Eocene to Oligo-Miocene.

Nomenclatural note

Reveal (2012, p. 217) questioned the validity of the tribal name given in Wilson *et al.* (2005) and republished the tribe as 'Kanieae Peter G.Wilson ex Reveal, trib. nov., based on Kanioideae Engl.', with the presumed implication that the simultaneous publication of Kanioideae and Kanieae by Engler (1930) made the latter name superfluous. However, alternative advice (W. Greuter, pers. comm., 2014) is that the name Kanieae was validly published and that the Reveal name is an isonym.

Xanthomyrteae Peter G.Wilson, *trib. nov.*

Type: *Xanthomyrtus* Diels.

Trees or shrubs; branchlets hairy, often conspicuously glandular. Inflorescence of monads or triads. Flowers yellow, mostly 4-merous, sessile; stamens usually numerous, 1(–2)-seriate, free. Ovary inferior, usually 2- or 3-locular; ovules 10–20, arranged around the margin of the axile placenta; stigma small. Fruit a fleshy berry, reddish to blue-black; seeds many, small, with a crustaceous testa. Embryo with broad cotyledons lying face to face; hypocotyl accumbent.

A monogeneric tribe of 23 species, New Caledonia and Malesia (Philippines, Borneo, Sulawesi, Maluku, New Guinea)

Cloezieae Peter G.Wilson, *trib. nov.*

Type: *Cloezia* Brongn. & Gris.

Shrubs or small trees. Inflorescences usually axillary cymes or monads. Flowers 5-merous, yellow or white; stamens in a single whorl, as long as the petals, anthers dorsifixed, versatile, connective sometimes expanded apically; ovary half inferior, 3-locular; ovules few in a ±circular series on the basal placenta; style terminal, remote from the placenta, stigma small. Fruit a woody loculicidal capsule, exserted from the hypanthium; seeds linear; embryo straight, cotyledons lying face to face.

A monogeneric tribe of five species, endemic to New Caledonia.

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Tristaniopsideae Peter G.Wilson, *trib. nov.*

Type: *Tristaniopsis* Brongn. & Gris.

Trees or occasionally shrubs. Inflorescences determinate (panicles, metabotryoids, thyrsoids or cymes). Flowers whitish to yellow. Stamens usually in multiple whorls (not in *Mitrantia*) and grouped opposite petals, sometimes fused into fascicles. Style-bases not adjacent to placentas, ovules often arranged in circular or semi-circular series. Fruit a capsule, frequently exserted from the fruiting hypanthium (except in *Sphaerantia*). Seeds various; hypocotyl straight and cotyledons sometimes foliaceous. Hypanthium vascularisation not reduced to 5 main veins.

A tribe comprising seven genera, *Tristaniopsis*, *Lysicarpus*, *Barongia*, *Sphaerantia*, *Ristantia*, *Mitrantia*, and *Basisperma*. *Tristaniopsis* is a genus of ~50 species, with a distribution extending from Myanmar and Thailand in the north, through Malesia and extending to eastern Australia and New Caledonia. The remaining genera are small, comprising between one and three species, and are narrow endemics in Papua New Guinea (*Basisperma*) and Queensland.

Relationships within the tribe

The phylogenies show some well supported groupings of genera within the new tribe. The three genera *Sphaerantia*, *Ristantia* and *Mitrantia* form a strong subclade (>97% jk, 1.00 PP), agreeing with previous analyses (Wilson *et al.* 2005) and strongly correlated with pollen morphology (Thornhill *et al.* 2012*a*) and shared presence of oil glands in the pith (P. G. Wilson, pers. obs.). Oil glands in the pith are also a feature of *Basisperma* (P. G. Wilson, pers. obs.), which was the basis for the comment in Wilson (1982) that *Basisperma* had no close affinities with the 'Kania Alliance' of Briggs and Johnson (1979). The shared occurrence of oil glands in the pith suggested that the genus was very likely to have affinities with these particular taxa, and this has now been confirmed in genomic analyses (Maurin *et al.* 2021).

Supplementary material

Supplementary material is available online.

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Data availability. New sequence data for this study are available from GenBank https://www.ncbi.nlm.nih.gov/genbank/: OM218672–OM218697 (ITS); OM730292–OM730334 (ETS); OM752313–OM752353 (*trn*K); OM752354–OM752372 (*psb*A–*trn*H). Other data, including molecular alignments and morphological scoring, that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. Peter Wilson is an Associate Editor of *Australian Systematic Botany* but did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Australian Systematic Botany* encourages its editors to publish in the journal and they are kept totally separate from the decision-making processes for their manuscripts. The authors have no further conflicts of interest to declare.

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Author affiliations
[A]National Herbarium of New South Wales, Australian Institute of Botanical Science, Royal Botanic Gardens and Domain Trust, Sydney, NSW 2000, Australia.
[B]School of Biological Sciences, University of Adelaide, Adelaide, SA 5005, Australia.
[C]Environment Institute, The University of Adelaide, North Terrace, Adelaide, SA 5005, Australia.

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