

A chloroplast phylogeny of *Zieria* (Rutaceae) in Australia and New Caledonia shows widespread incongruence with species-level taxonomy

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Abstract. This study presents a molecular phylogeny of *Zieria* Sm., a genus of shrubs and small trees, with 59 species in Australia and one endemic to New Caledonia. The phylogeny is based on four cpDNA markers and 116 samples representing all species of *Zieria* except one, and the monotypic outgroup *Neobyrnesia suberosa*. The New Caledonian species, *Z. chevalieri*, was resolved as sister to a well supported clade of all Australian taxa. There was widespread incongruence between the cpDNA tree and species-level taxonomy, with 14 species shown as polyphyletic or paraphyletic. These included widespread species (e.g. *Z. smithii* and *Z. arborescens*, each falling in at least four well supported clades) and some with narrow geographic ranges (e.g. *Z. alata* and *Z. oreocena*). No species represented by three or more samples was resolved as monophyletic. We suggest that a combination of factors explains this incongruence, including regional cpDNA introgression (chloroplast capture), incomplete lineage sorting and inappropriate taxonomic boundaries. The cpDNA phylogeny provides useful insight into the evolution of *Zieria* but, because of its complexity, does not provide a clear basis for assessing phylogenetic relationships and monophyly of taxa. Better understanding of relationships, taxon limits and evolutionary processes in *Zieria* will require comparisons with nuclear DNA markers and critical assessment of morphological and genetic variation in widespread species.

Additional keywords: biogeography, chloroplast lineage sorting, hybrids, molecular phylogeny, taxonomy.

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Introduction

Zieria Sm. is a predominantly Australian genus of shrubs and small trees, with 59 species and 18 subspecies in Australia and one species endemic to New Caledonia (Fig. 1). In Australia, *Zieria* occurs naturally only in the eastern states, extending as far west as Kangaroo Island in South Australia, as far south as Tasmania, and north to the tropical regions of Queensland (Armstrong 2002; George *et al.* 2013). The greatest diversity of species occurs in New South Wales (34 species) and Queensland (35 species), whereas in Victoria there are nine species, three in Tasmania and a single species in South Australia. The species occupy a range of habitats, including rainforests and rainforest margins, sometimes at high altitudes, vine thickets, wet and dry sclerophyll forest, eucalypt and *Banksia* woodlands (including mallee), heathlands, rock outcrops on dry inland slopes, and exposed coastal headlands.

The genus is traditionally placed in the Australasian tribe Boronieae (*sensu* Engler 1931), and is monophyletic on the basis of morphological (Armstrong 1991) and molecular (Bayly *et al.* 2013) phylogenetic analyses of that group. It is distinguished by a combination of morphological features including opposite leaves, conspicuous and four-merous flowers, free petals, four stamens, free filaments, deeply four-lobed disc and dry dehiscent fruits (Smith 1798; Duretto 1999; Armstrong 2002; George *et al.* 2013). It is most closely related to the monotypic genus *Neobyrnesia* J.A. Armstr. endemic to Arnhem Land, northern Australia (Armstrong and Powell 1980; Bayly *et al.* 2013); *Neobyrnesia* and *Zieria* are allopatric (Fig. 1).

Classification of *Zieria* has undergone extensive revision in recent decades chiefly on the basis of morphology. A comprehensive monograph was provided by Armstrong (2002, based on his earlier PhD thesis, Armstrong 1991), who

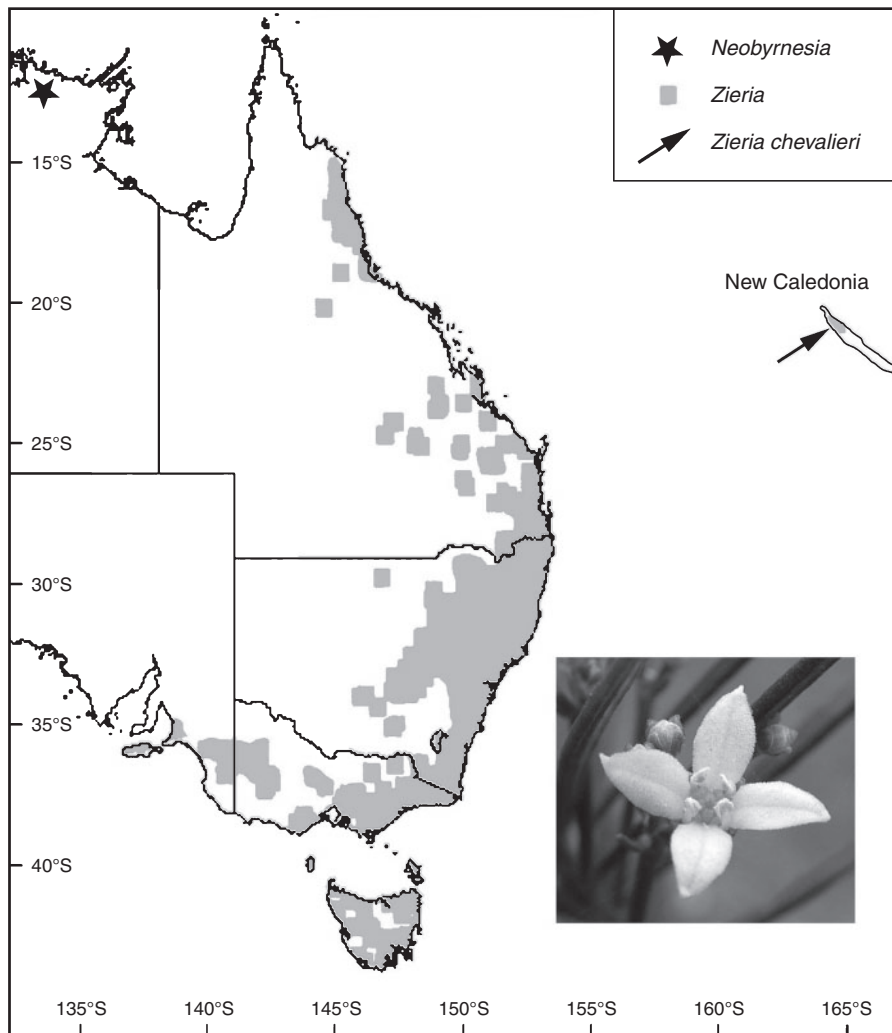


Fig. 1. Map showing the distribution of *Zieria* and *Neobyrnnesia* (outgroup) in Australia and New Caledonia, adapted from Armstrong (2002). Inset shows the flower of *Z. chevalieri*, Mount Kaala, New Caledonia.

recognised 42 species and 16 subspecies, with 28 taxa being newly described. Duretto and Forster (2007) published a subsequent revision of the Queensland taxa, in which 16 new species and one new subspecies were described, one variety was promoted to species rank, and one species previously treated as a subspecies was reinstated. Duretto and Forster (2008) also reviewed the classification of *Z. odorifera*^A, a species endemic to New South Wales, recognising four subspecies, with three newly described. The most recent account of the genus is in *Flora of Australia* (George *et al.* 2013).

Some species of *Zieria* are relatively widespread (e.g. *Z. arborescens*, *Z. aspalathoides*, *Z. cytisoides*, *Z. smithii*); however, the majority are narrow-range endemics. Several taxa are currently known only from single localities, including *Z. actites*, *Z. adenophora*, *Z. arborescens* subsp. *decurrens*, *Z. baeuerlenii*, *Z. boolbunda*, *Z. buxijugum*, *Z. cephalophila*, *Z. chevalieri*, *Z. covenyi*, *Z. floydii*, *Z. formosa*, *Z. hydroscopica*

and *Z. parrisiae* (Armstrong 2002; Duretto and Forster 2007; George *et al.* 2013). Duretto and Forster (2007) discussed the speciation patterns in *Zieria*, including how such narrow endemics, often restricted to rocky areas on mountains, may be related to more widespread species, often present in forests or more mesic vegetation. Narrow endemics may represent taxa differentiated in longstanding refugial habitats, or recent derivatives of more widespread lineages that have locally colonised new habitats (e.g. from forests to rock outcrops).

Of the large number of narrowly endemic taxa in *Zieria*, some are considered threatened under state and federal conservation legislation. These include 13 listed as *Endangered* and eight listed as *Vulnerable* under the national *Environment Protection and Biodiversity Conservation (EPBC) Act* 1999, 13 under the *Queensland Nature Conservation (Wildlife) Regulation* 2006, 17 under the *New South Wales Threatened Species Conservation Act* 1995, one under Victoria's *Flora and Fauna Guarantee Act*

^AAuthorities for *Zieria* species and infraspecific taxa included in the study are given in Appendix 1.

1988, two under South Australia's *National Parks and Wildlife Act 1972*, and two under Tasmania's *Threatened Species Protection Act 1995*.

Some threatened species have been the subject of genetic research, including *Z. baeuerlenii* (Sharma 2001), *Z. granulata* (Sharma and Young 2001), *Z. covenyi* (J. A. Armstrong and I. K. Sharma, unpubl. data, cited by Armstrong 2002) and *Z. prostrata* (Hogbin and Crisp 2003). These studies assessed the levels of genetic variation to provide data to underpin conservation management, and variously reported moderate variation to no variation (e.g. in the clonally reproducing *Z. covenyi*). Most focussed on rare species in isolation and did not consider their broader relationships with other taxa, the exception being that of Hogbin and Crisp (2003), who studied relationships between populations of *Z. prostrata* and geographically close populations of *Z. smithii*.

The phylogeny of *Zieria* produced by Armstrong (2002) was based on a dataset of 48 morphological and 62 chemical characters. The phylogeny showed six major clades, defined by combinations of characters rather than clear synapomorphies, and relationships between and within the clades were poorly resolved or supported. The results were regarded as 'very tentative' by Armstrong, given the high levels of homoplasy, with the consistency index for the analysis being low at 0.25. Since publication of Armstrong's (2002) phylogeny, taxonomic revisions (Duretto and Forster 2007, 2008) have resulted in narrower or significantly altered limits for some taxa (e.g. *Z. montana* and *Z. fraseri*), and 22 newly recognised or reinstated taxa are yet to be included in a phylogenetic analysis. A new, molecular phylogenetic study that includes a greater proportion of currently recognised taxa offers potential to further test relationships and interpret morphological homoplasy demonstrated by Armstrong (2002).

The aim of our current study was to produce a comprehensive molecular phylogeny of *Zieria* in Australia and New Caledonia, based on sequencing four regions of cpDNA. This was done to provide better insight into evolution and classification of the genus, including: the monophyly of taxa, patterns of speciation, e.g. relationships of widespread and narrowly endemic taxa; the distinctiveness of restricted taxa of conservation interest; patterns of variation in widespread species; patterns of habitat diversification; biogeographic history, especially the connection between Australia and New Caledonia.

Materials and methods

Taxon sampling

Ingroup sampling included 116 accessions representing 59 (of 60) *Zieria* species and 16 (of 18) subspecies. *Zieria floydii* J.A. Armstr., *Z. aspalathoides* subsp. *brachyphylla* J.A. Armstr. and *Z. odorifera* subsp. *copelandii* Duretto & P.I. Forst. were the only taxa not sampled. *Neobyrnesia suberosa* was included as the outgroup. Plant material was obtained from field collections, cultivated collections of known provenance, and herbarium specimens. Fresh samples for DNA extraction were dried in silica gel. Details of sampling locations and voucher specimens for all samples are given in Appendix 1. Identification of taxa was straightforward using existing taxonomic concepts (George *et al.* 2013), except for *Z. arborescens*, a variable,

widespread species in which separation of the subspecies is not as clear as identification keys suggest (Duretto and Forster 2007; George *et al.* 2013; R. A. Barrett, pers. obs.). We did not identify accessions of *Z. arborescens* to subspecies, but we note in figures and tables those accessions collected near type localities for the two segregate subspecies (subsp. *glabrifolia* and subsp. *decurrens*).

DNA isolation, polymerase chain reaction (PCR) and sequencing

DNA was extracted from 20–25 mg of dried, ground leaf material using a DNeasy Plant Mini Kit (QIAGEN, Melbourne, Vic., Australia) or ISOLATE Plant DNA Mini Kit (Biolone, Sydney, NSW, Australia), following the manufacturers' instructions, with a final elution volume of 100 μ L. For some herbarium specimens, a modified protocol was used, which included the addition of the following extra reagents during the lysis stage: 8 μ L of proteinase K, 4 μ L RNase A and 30 μ L of β mercaptoethanol, and incubation at 60°C for 1 h.

The following four cpDNA markers were used: the *rpl32-trnL* intergenic spacer, the *trnL-F* region (which included the *trnL* intron and the *trnL-trnF* intergenic spacer), the *trnQ-5'rps16* intergenic spacer and the *trnS-G* region (which included the *trnG* intron and the *trnG-trnS* intergenic spacer). The *rpl32-trnL* region was amplified using the primers *trnL*^(UAG) and *rpl32-F* (Shaw *et al.* 2007). The *trnL-F* region was amplified using the primers c and f of Taberlet *et al.* (1991), and in some cases where amplification was unsuccessful, the region was amplified in two overlapping fragments using the following combinations of internal primers (Taberlet *et al.* 1991): e paired with f; and d paired with c. The *trnQ-5'rps16* region was amplified using the primers *trnQ*^(UUG) and *rps16x1* (Shaw *et al.* 2007). The *trnS-G* region was amplified using the primers of Shaw *et al.* (2005), most commonly *trnG*^(UUC) and *trnS*^(GCU), but in a few cases it was amplified in two overlapping fragments using the internal primers *5'trnG2G*^(UUC) paired with *trnG*^(UUC) and *5'trnG2S*^(GCU) paired with *trnS*^(GCU).

All polymerase chain reactions (PCRs) were performed in a MyCycler Thermal Cycler System (Bio-Rad Laboratories, Gladesville, NSW, Australia). All sets of PCRs included a negative control to test for contamination, and, in most cases, a positive control was included to test for reagent or protocol errors. Reactions typically included 10 pmol of each primer, 5 mM of each dNTP, 1–2 μ L of extracted DNA, 1.25 units HotStar *Taq* DNA polymerase and its accompanying 10 \times PCR buffer (QIAGEN), 0.5 μ L Fermentas non-acetylated BSA (20 mg mL⁻¹), and 2 mM MgCl₂. These were made up to the 25 μ L final volume with ultrapure water.

Thermo-cycling conditions varied according to the target region. Cycling conditions for *rpl32-trnL* and *trnS-G* were as follows: template denaturing at 95°C for 15 min, followed by 30 cycles of 95°C for 1 min (denaturing), primer annealing at 50°C for 1 min, 65°C extension for 4 min, and then a final 5-min extension at 65°C. Cycling conditions for *trnQ-5'rps16* were as follows: 95°C for 15 min, 30 cycles of 95°C for 1 min, 50°C for 1 min with a 0.5°C temperature increase at each cycle, 65°C for 4 min, and then a final 5-min extension at 65°C. A 'touchdown' protocol was used to amplify *trnL-F*, including 95°C for 15 min,

then six cycles of 95°C for 30 s, primer annealing at 64°C for 30 s, with a 2°C temperature decrease at each cycle, extension for 1 min at 72°C, then a further 30 cycles of 94°C for 30 s, 54°C for 30 s, 72°C for 1 min, and a final extension for 10 min at 72°C.

PCR products were purified using a QIAquick PCR Purification Kit (QIAGEN, Melbourne, Vic., Australia), PureLink Kit (Invitrogen, Melbourne, Vic., Australia), or using ExoSAP-IT (Affymetrix, Santa Clara, CA, USA) or ExoSTAR (GE Healthcare, Freiburg, Germany). PCR products were quantified on agarose gels or using a NanoDrop 2000 UV-Vis spectrophotometer (Thermo-Scientific, Melbourne, Vic., Australia) and directly sequenced using the ABI Prism BigDye Terminator v3.1 Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Foster City, CA, USA). These reactions used the original amplification primers and sometimes the internal sequencing primers d and e (Taberlet *et al.* 1991) for *trnL*-F, and 5'*trnG2G* and 5'*trnG2S* (Shaw *et al.* 2007) for *trnS*-G. Sequences were analysed on an ABI 3730x1 96-capillary automated DNA sequencer (Applied Biosystems) at the Australian Genome Research Facility, Brisbane or Melbourne.

Sequence editing and alignment

Contiguous sequences for each region were assembled and edited using Sequencher v.4.8 (Gene Codes Corporation, Ann Arbor, MI, USA), and aligned manually using Se-AL Sequence Alignment Editor v. 2.0a11 (Rambaut 2002). Insertion–deletion events (indels) were coded for parsimony analysis using a method equivalent to the ‘simple coding’ of Simmons and Ochoterena (2000), with a single character representing each indel whether single- or multi-base. The full data matrix, including indel characters, is deposited in TreeBase (<http://treebase.org/>; accession number S17027).

Phylogenetic analyses

Combined cpDNA sequences were analysed using maximum parsimony (MP) with PAUP* 4.0 β 10 (Swofford 2001) and Bayesian inference (BI) with MrBayes v.3.1.2 (Ronquist and Huelsenbeck 2003). MP analyses were performed using heuristic tree searches, a CLOSEST addition sequence and tree bisection and reconnection (TBR) branch swapping, all characters being equally weighted and gaps treated as missing data. All other settings were left on default.

When initial phylogenetic analysis yielded many thousands of equally parsimonious trees, an expeditious search strategy was employed. An initial heuristic search was commenced using the above settings, and terminated when 50 000 trees were obtained, then a strict consensus of equally parsimonious trees was calculated. This consensus tree was loaded as a constraint in a second analysis that searched only for trees that were as short as or shorter than the shortest tree of the first analysis, but were inconsistent with the constraint tree. This search used 1000 random addition sequences, each followed by TBR branch swapping. Each replicate was aborted when 2000 trees with lengths exceeding that of the first analysis were obtained. When this strategy was used, if trees of equal length to that of the first analysis were obtained (and inconsistent with the consensus from the first analysis), a further consensus was computed including the topology from the new analysis. The

second step of the analysis was repeated until no more new equally short but inconsistent trees were found. The aim of this strategy was to produce a strict consensus tree that was likely to represent the full set of equally most parsimonious trees. Bootstrap support (Felsenstein 1985) was estimated using a full heuristic search with 1000 bootstrap replicates and the search settings as described above. A maximum of 2000 trees was saved per replicate.

The models for BI analyses were GTR+R for *rpl32-trnL* and *trnL*-F, GTR+I for *trnQ-rps16* and GTR+I+G for *trnS*-G, selected using the Akaike information criterion (AIC) as implemented in MrModeltest 2.3 (Nylander 2004). Indels were not separately coded for BI analyses because preliminary analyses indicated that the level of resolution and topology in BI trees was similar to that using MP. Also indels were generally associated with branches of high posterior probability, suggesting that separate coding would add little in the way of extra support or resolution. BI analyses used the default settings of MrBayes, with parameters unlinked between partitions, and each included two runs of four chains, each run for 3 000 000 generations. Trees were sampled every 500 generations and a majority rule consensus was computed, with trees from the first 300 000 generations discarded as burn-in. Tracer v.1.5 (Rambaut 2007) was used to check that the burn-in period was adequate for each analysis and that the runs had converged on a stationary distribution. This was judged by comparing the distribution likelihood values, and the standard deviation of split frequencies, which were <0.01 at the end of the runs.

Results

Overview

Data from the combined chloroplast markers included a total of 4001 characters, of which 581 were variable and 230 were parsimony informative, including 55 parsimony-informative indel characters (statistics from the MP analysis are presented in Table 1). The *rpl32-trnL* and *trnS*-G regions together provided most of the parsimony-informative characters (74%).

The majority-rule consensus tree from the BI analysis was similar to, but slightly better resolved than, the MP strict consensus tree. The two measures of support, posterior probability (PP) for BI and bootstrap support (BS) for MP, were not always well correlated, with some high Bayesian PPs occurring when the corresponding BS values were low. However, there were no conflicting nodes between analyses, and only the Bayesian consensus tree together with both PP and BS values is presented here (Fig. 2).

Letters A–N (Fig. 2) label clades of three or more taxa that were well supported and are discussed in the text (as distinct from pairs of taxa or poorly supported nodes). Australian *Zieria* formed a strongly supported clade (Node 1, PP 1, BS 100%) with the New Caledonian species, *Z. chevalieri*, shown as its sister.

Within Australian *Zieria*, two large Clades A (Node 3) and B (Node 4), a smaller Clade C (Node 6), and a clade of the two subspecies of *Z. veronicea* (Node 5) were each strongly supported in the BI analysis, with PP values of 1. However, the trichotomous Node 2 was poorly supported (PP 0.87, BS 53%), and, therefore, it is not clear whether Clade C and *Z. veronicea* are more closely related to taxa in Clade A or Clade B, or to each other.

Table 1. Details of chloroplast datasets and results from maximum parsimony analyses
Tree statistics are based on equally most parsimonious trees produced by analyses of the combined dataset

Parameter	<i>rpl32-trnL</i>	<i>trnL-F</i>	<i>trnQ-rps16</i>	<i>trnS-G</i>	Combined data
Included characters	975	871	666	1489	4001
Variable characters	186	106	92	197	581
Parsimony-informative characters, total	88	27	32	83	230
Parsimony-informative indel characters	17	8	7	23	55
Parsimony-informative characters as a percentage of variable characters (%)	47	26	35	42	40
Number of steps on shortest trees	253	142	109	296	800
Consistency index (CI)	0.85	0.82	0.89	0.78	0.83
Retention index (RI)	0.93	0.87	0.96	0.90	0.92
Rescaled consistency index (RC)	0.79	0.71	0.86	0.702	0.76
Homoplasy index (HI)	0.15	0.18	0.11	0.22	0.18

Although the large Clade A was well supported in the BI analysis (PP 1) it was poorly supported in the MP analysis (BS 54%). It comprises five subclades, D, E, F, G and H, all strongly supported by BI (PP of 1 for all), but variously well to poorly supported by MP BS. *Zieria tenuis*, *Z. madida*, *Z. littoralis*, *Z. cephalophila* and *Z. boorbunda* formed part of a basal polytomy in Clade A. *Zieria baeuerlenii* and *Z. collina* (MJB2012) were strongly supported as sister (although a second accession of *Z. collina* was resolved in a different well supported clade).

The other large Clade, B, which was strongly supported in both analyses (PP 1, BS 100%), was not well resolved, consisting of a polytomy of seven lineages (Node 4, Fig. 2). Node 41 within Clade B had strong support from the BI analysis (PP 1) but not in the MP analysis where there was no BS support. The relationship of *Z. caducibracteata* (IRT9585) and *Z. smithii* (DJO430) as sister taxa was only poorly supported. *Zieria alata* (KM639) and *Z. arborescens* (MFD2035) were resolved as sister. Samples whose relationships remained unresolved within Clade B are *Z. robusta* (MFD2049), *Z. obcordata* (608324), *Z. citriodora* (the only accession) and *Z. pilosa* (2 accessions). Clade B was further resolved into six subclades, I–N, all being well supported by PP (0.98–1.0), but with variable BS support (53–97%). Other relationships within these clades are discussed in more detail below.

In summary, there was a poor correlation between the cpDNA tree and clades identified in the morphological phylogeny of Armstrong (2002). None of Armstrong's morphological clades was identified as monophyletic and most cpDNA clades contained members of multiple morphological groups (Figs S1 and S2, available as Supplementary material for this paper). The clades C–N resolved here in the cpDNA analysis broadly overlap geographically in eastern Australia, although they include some marked taxon disjunctions. Clade K was the most geographically distinct, being restricted to Victoria and Tasmania.

Monophyly of species and sharing of chloroplast haplotypes between species

Of the species represented by at least two accessions in this analysis, the following were resolved as monophyletic: *Z. veronicea* (Node 5, two subspecies), *Z. laevigata* (Node 8), *Z. ingramii* (Node 9), *Z. littoralis* (Node 20), *Z. baeuerlenii* (Node 28), *Z. pilosa* (Node 39) and *Z. involucrata* (Node 50).

Monophyly of the following species was neither supported nor rejected, with accessions being part of unresolved polytomies that included other species: *Z. lasiocaulis* (Node 32), *Z. prostrata* (Node 53) and *Z. odorifera* (Node 15; including the three sampled subspecies). All other species with multiple accessions were resolved as polyphyletic or paraphyletic. These were *Z. fraseri* (two samples, one from each subspecies, nested in Clade D), *Z. cytisoides* (three samples, in different subclades of Clade A), *Z. obcordata* (two samples from disjunct populations, occurring in different parts of the tree, one in Clade A, one in Clade B), *Z. smithii* (22 samples, some in Clade A, some in Clade B), *Z. collina* (two samples, in different subclades of Clade A), *Z. furfuracea* (three samples, representing three subspecies, one in Clade L, one in Clade M and one in Clade A), *Z. arborescens* (nine samples, in different subclades of Clade B), *Z. oreocena* (four samples, in two subclades within Clade B), *Z. alata* (two samples, in different subclades within Clade B), *Z. caducibracteata* (two samples, one in a well supported clade sister to a sample of *Z. arborescens*, the other weakly supported as sister to a sample of *Z. smithii*), *Z. minutiflora* (a sample of subsp. *trichocarpa* strongly supported as sister to a polytomy including *Z. vagans*, *Z. bifida* and two samples of subsp. *minutiflora*; Clade G), *Z. distans* (two samples in Clade H), *Z. robusta* (one sample in Clade K, one in the basal polytomy of Clade B), and *Z. murphyi* (two samples in Clade M, separated with moderate support).

On the basis of cpDNA markers, widespread species, or species for which samples were collected from highly separated locations, were commonly not found to be monophyletic. However, even some species with narrow distributions or with samples collected from relatively small geographic areas had haplotypes that placed them in different clades. For example, the two specimens of *Z. alata*, a species endemic to the Wet Tropics of Queensland, were collected within 15 km of each other (Clade B), the four specimens of *Z. oreocena* (Clade B) were collected within 50 km of each other in the Grampians in western Victoria, where the species is endemic, and the two samples of *Z. caducibracteata* were collected ~4 km apart in the Budawang Range of New South Wales.

Most chloroplast haplotypes were unique to individual specimens or species. However, the following three haplotypes were shared between specimens of different species: one between *Z. prostrata* and *Z. arborescens* (from samples collected nearly 200 km apart; Clade M, Fig. 5); one between *Z. lasiocaulis* and *Z. southwellii* (across samples collected nearly 200 km apart;

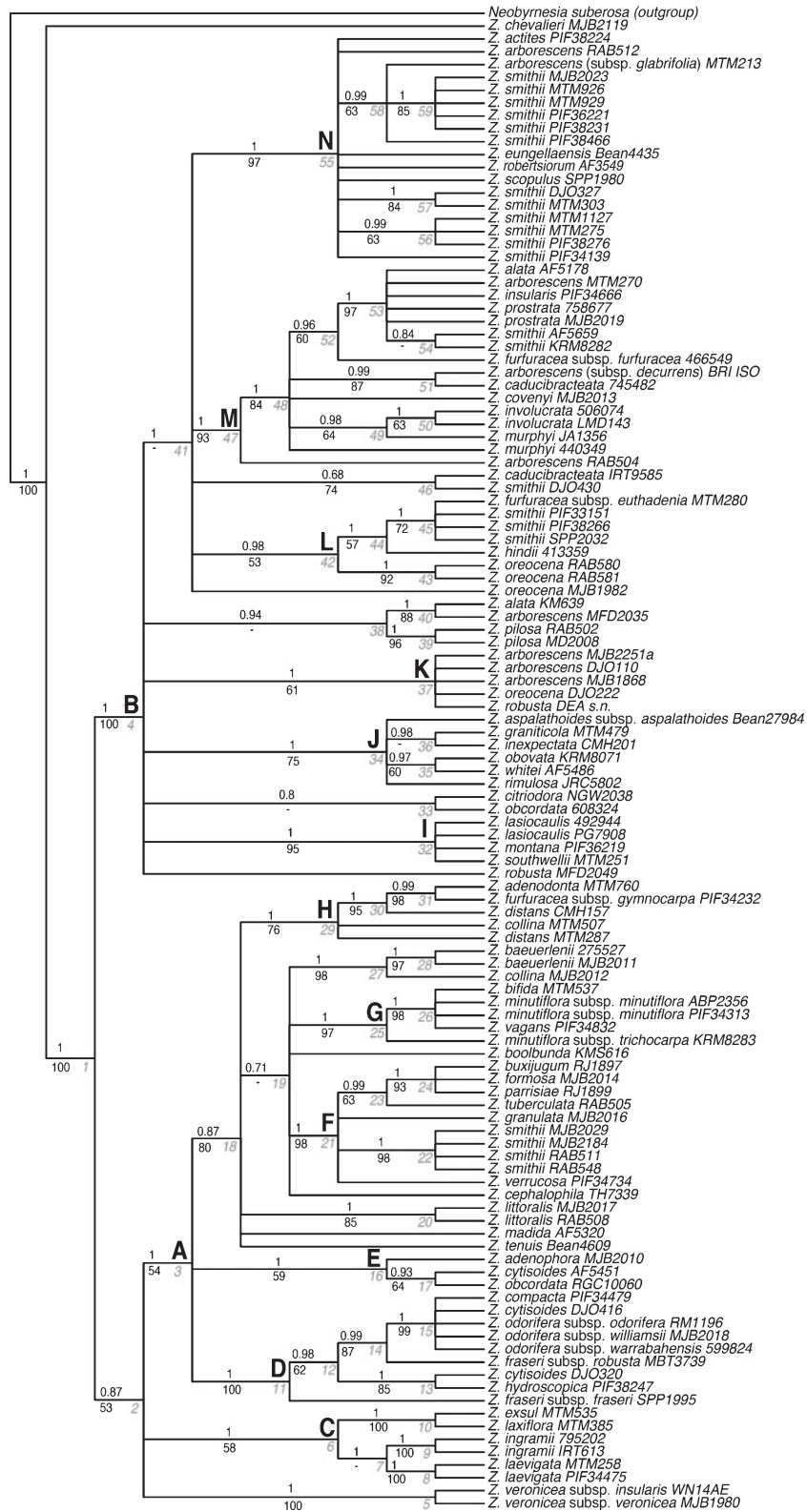


Fig. 2. Bayesian majority-rule consensus tree of combined chloroplast data, with Bayesian posterior probabilities (PP) shown above branches, bootstrap support (BS) values for maximum parsimony analysis below branches, and nodes numbered (in grey). Further details of Clades C–H and I–N are given in Figs 3 and 5 respectively.

Clade I, Fig. 5); and one between samples of *Z. odorifera*, *Z. compacta* and *Z. cytisoides* (across samples collected ~650 km apart; Clade D, Fig. 3).

Composition and distributions of Clades C–H

A portion of the Bayesian tree (Fig. 3) shows branch lengths and support values of Clade A and its subclades, and Clade C. Maps show the location of taxa within those clades (Fig. 4). Together, branch lengths and maps allow visualisation of the degree to which the chloroplast haplotypes are shared, relative divergences, and the provenance of the samples in the clades.

Clade C (PP 1, BS 58%) included *Z. exsul* and *Z. laxiflora* (both from coastal southern Queensland), *Z. ingramii* (inland New South Wales), and *Z. laevigata* (near the New South Wales–Queensland border). Both accessions of *Z. ingramii*, which were from Goonoo State Forest, ~15 km apart, had identical haplotypes. In contrast, in the more common species *Z. laevigata*, haplotypes were resolved as related (Fig. 3) but divergent (differing by 13 steps), despite accessions being collected from populations only ~30 km apart in southern Queensland.

In general, the haplotypes in Clade D were from specimens of taxa that typically occur in more inland locations than do most other *Zieria* taxa, on the western slopes or west of the Great Dividing Range. The accession of *Z. fraseri* subsp. *fraseri* was collected closest to the coast, and was well supported as sister to the other (more inland) specimens in the clade. Both subspecies of *Z. fraseri* were in this clade, but were not resolved as sister. Accessions of the three subspecies sampled of *Z. odorifera* (of four) were in a well supported subclade, with highly similar but not identical haplotypes. *Zieria odorifera* subsp. *williamsii*, *Z. compacta* and one sample of *Z. cytisoides* (DJO416) had identical haplotypes that were highly similar to the haplotypes of the two other *Z. odorifera* subspecies, which differed only by one change each. The samples sharing the identical haplotype were from localities up to 680 km apart. Another sample of *Z. cytisoides* (DJO320) was strongly supported as the sister to *Z. hydrosopica*, although their haplotypes differed by seven changes in the MP analysis. The two divergent samples of *Z. cytisoides* in this clade (differing by 16 steps in the MP analysis) were collected from localities more than 270 km apart in southern Queensland.

Clade E included three samples, one each from *Z. cytisoides*, *Z. obcordata* and *Z. adenophora*. Although it was highly supported by BI, Clade E had poor support in the MP analysis. Branch lengths were long, indicating deep divergences between the three samples, which were remotely separated geographically, from north Queensland to southern New South Wales. Of the three species in Clade E, *Z. cytisoides* is widespread and morphologically very different from the other two species; its taxonomic relationship may be better reflected by the position of two other accessions of *Z. cytisoides* that were resolved in Clade D. In contrast, *Z. obcordata* and *Z. adenophora* of Clade E are rare species that share some morphological affinities. *Zieria adenophora* is known only from a single population, whereas *Z. obcordata* has a disjunct distribution. The accession of *Z. obcordata* (RGC10060) in Clade E was from the more northern population, whereas an accession from a population

~100 km to the south (608324) was placed in major Clade B (Figs 2, 5), with strong support.

Clade F included a group of morphologically very similar species, namely, *Z. verrucosa*, *Z. granulata*, *Z. tuberculata*, *Z. parrisiae*, *Z. formosa* and *Z. buxijugum*, plus four samples of *Z. smithii* from Victoria that had identical or highly similar haplotypes. All of the other accessions of *Z. smithii* in this analysis were resolved in Clade B and were from Queensland or northern New South Wales. The morphologically similar species in this clade occur in southern New South Wales, except *Z. verrucosa*, which occurs only in Queensland, ~1000 km away. The three most closely related haplotypes of that group, representing *Z. buxijugum*, *Z. formosa* and *Z. parrisiae*, were from samples located within ~6 km of each other, but they were not identical.

All accessions in Clade G were from Queensland. *Zieria minutiflora* subsp. *trichocarpa* from northern Queensland was strongly supported as the sister to samples of *Z. bifida*, *Z. minutiflora* subsp. *minutiflora* and *Z. vagans*, which were all from southern Queensland. The haplotypes of the three taxa from southern Queensland were highly similar but not identical; *Z. bifida* and *Z. vagans* are very similar in morphology but different from *Z. minutiflora*.

All accessions in Clade H were also from Queensland. This clade was well supported by BI (PP 1), but less so by MP analysis (BS 76%). It included a sample of *Z. furfuracea* subsp. *gymnocarpa*, which was separated from other subspecies in *Z. furfuracea* in clades L and M. The relationship of *Z. furfuracea* subsp. *gymnocarpa* to *Z. distans* (CMH157) and *Z. adenodonta* was strongly supported (PP 1, BS 95%). However, *Z. distans* included two different haplotypes that did not form a monophyletic group within Clade H. Similarly, *Z. collina* appeared to be polyphyletic with one accession (MTM507) in Clade H and the other haplotype (MJB2012) outside that clade, related to *Z. baeuerlenii* (Node 27, Fig. 2), despite the two accessions of *Z. collina* being collected from populations less than 6 km apart.

Composition and distributions of Clades I–N

A portion of the Bayesian tree (Fig. 5) shows branch lengths and node-support values for Clade B and its subclades, I–N. Maps show the location of taxa within these clades (Fig. 6).

Clade I consisted of three morphologically similar species. *Zieria southwellii* and *Z. montana* are restricted to the area around the New South Wales–Queensland border, and the endangered *Z. lasiocaulis* is restricted to the headwaters of the Wilson River in the North Coast District of New South Wales. Two accessions of *Z. lasiocaulis*, which were collected from populations less than 3 km apart, had slightly different sequences; however, the sequence of *Z. lasiocaulis* (492944) was identical to that of *Z. southwellii*, from more than 300 km away.

Five species in Clade J are narrow endemics, three occurring in northern Queensland (*Z. whitei*, *Z. rimulosa* and *Z. obovata*) and two in southern Queensland (*Z. graniticola* and *Z. inexpectata*). The sixth sample in the clade is *Z. aspalathoides* subsp. *aspalathoides*, a widespread and variable taxon; the accession here was from southern Queensland. BI analysis resolved *Z. graniticola* and *Z. inexpectata* samples as sisters, and *Z. obovata* and *Z. whitei* samples as sisters, both with

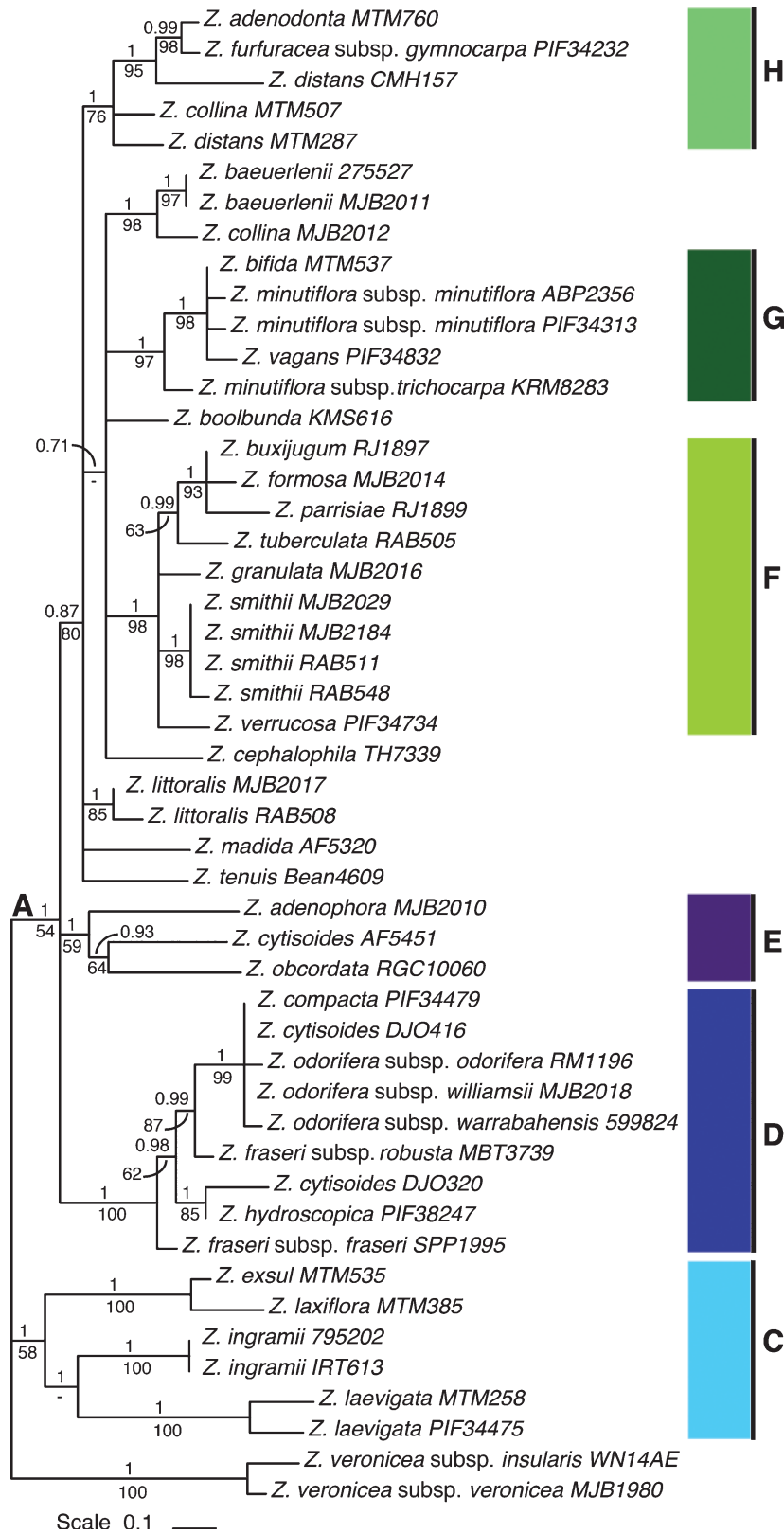


Fig. 3. A section of the Bayesian consensus tree from the combined chloroplast analysis, showing Clades C–H, mean branch lengths and support values. Bayesian inference posterior probability (PP) values are given above branches, maximum parsimony bootstrap (BS) percentages are below branches.

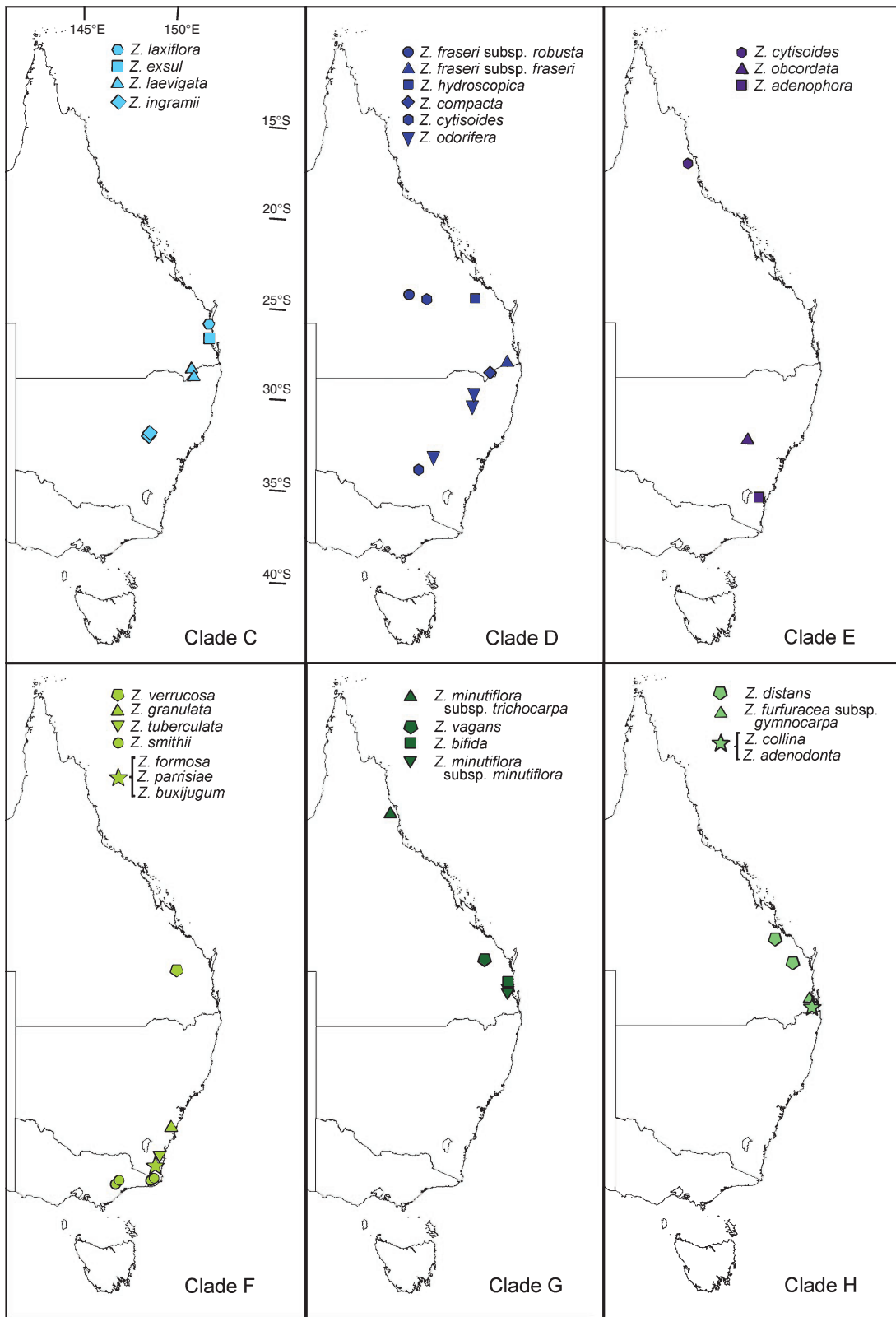


Fig. 4. Maps showing the distribution of samples in Clades C–H.

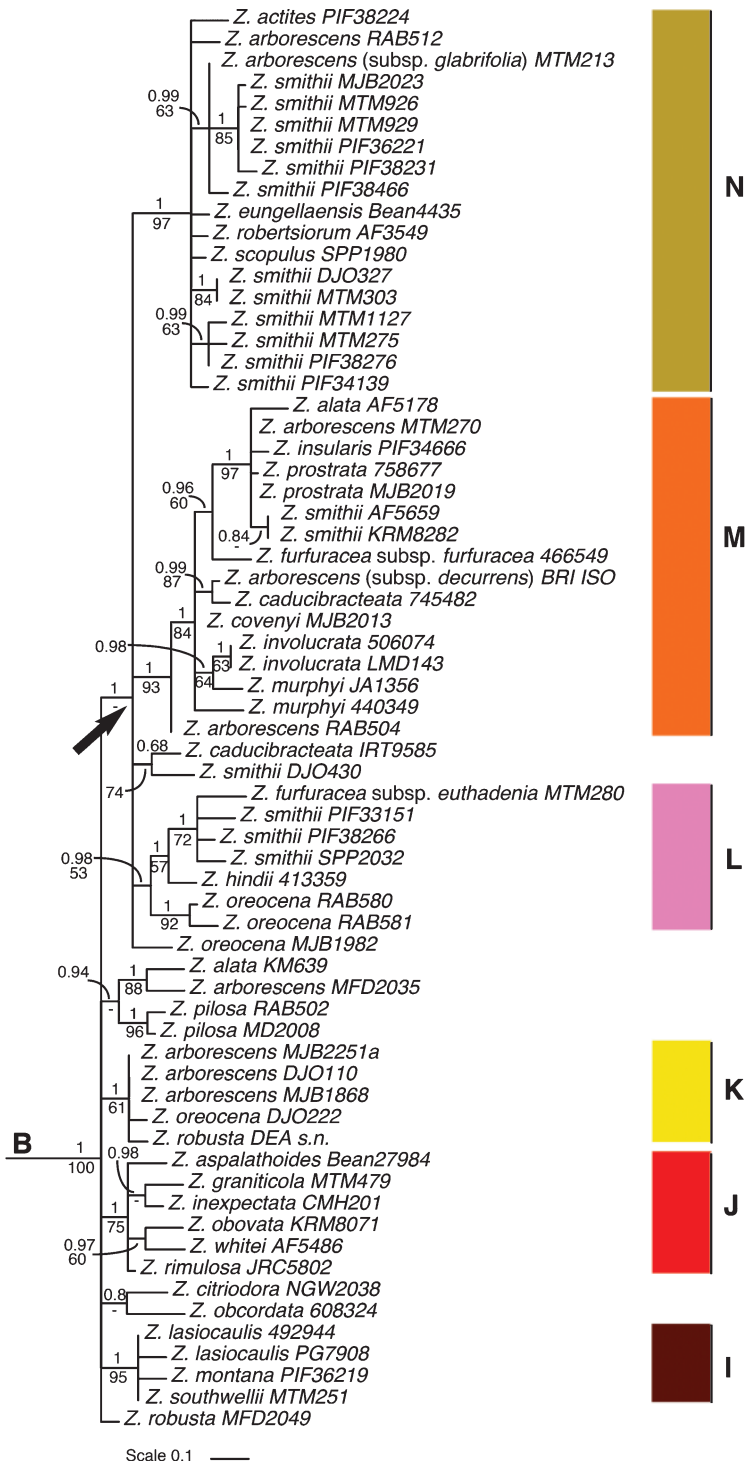


Fig. 5. A section of the Bayesian consensus tree from the combined chloroplast analysis, showing Clades I–N, mean branch lengths and support values. Posterior probability values are given above branches, maximum parsimony bootstrap percentages are below branches.

moderate to strong Bayesian support (respectively PP 0.98 and 0.97), but these relationships were poorly or not at all supported by MP analysis. *Zieria inexpectata*, *Z. graniticola* and *Z. whitei*

(but not *Z. obovata*) have strong morphological affinities with *Z. aspalathoides*. *Zieria whitei*, for instance, was initially described as a variety of *Z. aspalathoides* (var. *intermedia*;

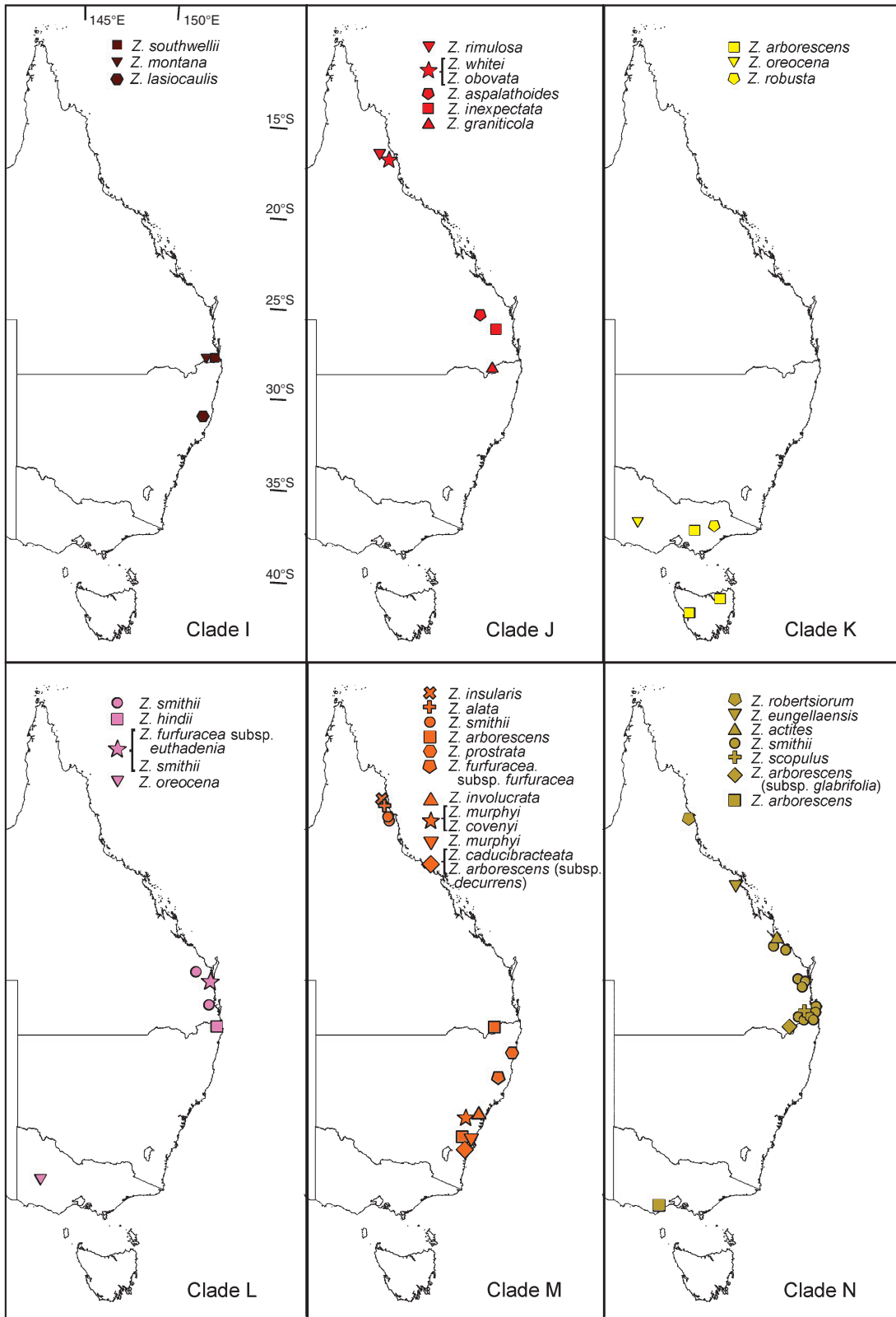


Fig. 6. Maps showing the distribution of samples in Clades I–N.

White 1942). *Zieria obovata* is morphologically very similar to *Z. minutiflora* (not in this clade), and the two species are easily confused. *Zieria rimulosa*, from Mount Mulligan, northern Queensland, is morphologically distinct, although it does have some characters in common with *Z. aspalathoides* and *Z. obovata* (northern Queensland), such as densely pubescent branchlets, and upper lamina leaf surfaces covered exclusively by simple (vs stellate) hairs.

Clade K (PP 1 but BS low at 61%) comprised Victorian and Tasmanian accessions of *Z. arborescens* (identical haplotypes), one accession of *Z. oreocena*, and one accession of *Z. robusta*, a morphologically distinctive species in the genus, very different from *Z. arborescens* and *Z. oreocena*. *Zieria oreocena* is morphologically very similar to *Z. arborescens* but geographically separated, being restricted to the Grampians in western Victoria. *Zieria robusta* has a disjunct distribution, and two accessions were sequenced. The accession in Clade K was from eastern Victoria; the other accession, from nearly 500 km to the north in New South Wales, also fell in Clade B, but at the basal node outside Clade K. All accessions of *Z. arborescens* from outside Victoria and Tasmania were placed elsewhere in Clade B. Surprisingly, *Z. arborescens* (RAB512) from the Otways, Victoria, was also not in this clade. Of the four accessions of *Z. oreocena*, only one occurred in Clade K.

Clade L contained two accessions of *Z. oreocena*, collected from close but distinct habitats at different altitudes in the northern Grampians, Victoria (Fig. 6). One population was in a sheltered valley beside a creek and the other was in a sheltered rocky outcrop near the summit of Hollow Mountain. The accessions were strongly supported as sister to a subclade of *Z. smithii* (three accessions) and *Z. furfuracea* subsp. *euthadenia*, all from southern Queensland, and *Z. hindii*, from northern New South Wales, some 1500 km further north of the Grampians. A third accession of *Z. oreocena* (MJB1982), collected ~40 km to the south, was on the basal node of Clade B, and a fourth accession (DJO222) collected less than 4 km from MJB1982, was resolved in Clade K (PP 1, but low BS of 61%). Thus, phylogenetic relationships here supported by the BI analysis were not necessarily correlated with geographic distance.

Clade M consisted of 11 taxa, including species from a wide geographical range, from the wet tropics in Queensland to the south-east of New South Wales, but with a clear disjunction in the mid- and southern parts of Queensland. Some, but not all, taxa within the clade share morphological affinities. Two accessions of the widespread *Z. arborescens* occurred in this clade (one from Queensland and one from New South Wales), as well as an accession from near the type locality of the highly restricted *Z. arborescens* subsp. *decurrens*, and one accession of *Z. caducibracteata*, a species that is morphologically similar to *Z. arborescens*. *Zieria arborescens* (MTM270) and *Z. prostrata* (MJB2019) had identical haplotypes despite being from locations nearly 200 km apart. Clade M also included the morphologically distinctive species, *Z. involucrata* and *Z. murphyi*, as well as *Z. covenyi*, a putative triploid hybrid (Armstrong 2002). *Zieria insularis* and *Z. smithii* have morphological affinities, although *Z. smithii* is highly variable. The seven samples (representing five species) that were resolved in a well supported subclade of Clade M (PP 1 BS 97%, Node 53, Fig. 2) were all collected in northern New South Wales or Queensland, with *Z. furfuracea*

subsp. *furfuracea* (466549), from further south, moderately supported as the sister. All other accessions of Clade M were from locations even further south, in southern New South Wales.

Clade N consisted of six taxa, including several accessions of *Z. smithii*, all collected from Queensland (but not all accessions of *Z. smithii* from Queensland were in this clade). The clade also included the sample of *Z. arborescens* (subsp. *glabrifolia*), from southern Queensland. Interestingly, one accession of *Z. arborescens* (RAB512), from the Otways, Victoria, was nested in this clade, indicating that this haplotype is more closely related to those of other taxa occurring in Queensland, than to haplotypes of its own species occurring elsewhere in Victoria; this was the only sample from outside Queensland that occurred in this clade.

Discussion

This study presents the first molecular phylogenetic study of *Zieria*, including almost all recognised species and subspecies, based on cpDNA. Interpretation of relationships is complicated because of widespread discordance between the cpDNA gene tree, existing species-level classification and the morphological groups proposed by Armstrong (2002). It is now widely recognised that species trees are not always congruent with gene trees because evolutionary processes often produce discrepancies between gene trees and the phylogenies of the organisms within which the genes evolved (Doyle 1992; Maddison 1997; Mallo *et al.* 2014). We conclude that the cpDNA phylogeny provides useful insight into evolutionary processes in *Zieria* (discussed below) but does not provide a clear basis for assessing phylogenetic relationships of taxa, speciation or biogeographic patterns within Australia, which were among our original aims.

Incongruence between cpDNA phylogeny and species taxonomy

The cpDNA phylogeny showed widespread incongruence with current species taxonomy in *Zieria*. There is a range of possible explanations for such incongruence, including the following: (1) homoplasy in the cpDNA sequence data, i.e. parallel evolution of similar sequences in different taxa; (2) inappropriate taxonomy, confounded by homoplasy of morphological characters; (3) introgression between species (chloroplast capture); and (4) variable retention of ancestral chloroplast lineages across different taxa (incomplete lineage sorting). Homoplasy of molecular characters becomes a less likely explanation as the number of characters supporting different clades of sequences increases (McKinnon *et al.* 1999; Holmes *et al.* 2014), and it is a poor explanation for many of the well supported clades in our dataset. The other three explanations are each more plausible and it is likely that a combination of these factors is at play in *Zieria*.

Introgression and incomplete chloroplast lineage sorting can be expected to leave different genetic and geographic signatures. With introgression, there is a chance that more derived haplotypes (near the tips of trees or networks) will be shared between species, and that interspecific sharing of chloroplast haplotypes or groups will be geographically concentrated, reflecting the area in which introgression has occurred (McKinnon *et al.* 1999; Muir and Schlötterer 2005; Nevill *et al.* 2014). With chloroplast lineage

sorting, there is less chance that tip haplotypes will be shared between species (i.e. there is bias towards sharing of ancestral haplotypes), and interspecific sharing of chloroplast haplotypes or groups need not be geographically concentrated (Schaal *et al.* 1998; Muir and Schlötterer 2005). In the current study, there are few haplotypes shared among different species that might provide evidence for recent introgression between species (discussed below). However, this could be an artefact of low and uneven sampling within species (despite including multiple representatives of most). It could also reflect dilution over time of signals of chloroplast lineage sorting or introgression, e.g. patterns of haplotype distribution could be affected by past range expansions or contractions that might have been considerable (e.g. Mellick *et al.* 2012; Rossetto *et al.* 2012) across multiple glacial or interglacial cycles.

The greatest insight into the processes responsible for the taxonomic incongruence of cpDNA sequences in *Zieria* potentially comes from the two species in our dataset that were the most highly sampled, among the most geographically widespread, and had clearly polyphyletic cpDNA sequences. These two species are *Z. smithii*, which occurs from northern Queensland to eastern Victoria, and *Z. arborescens*, which occurs from southern Queensland to Tasmania and includes three accepted subspecies, although the distinction between the subspecies is not clear cut (see note in Materials and methods).

The cpDNA sequences of *Zieria smithii* show clear geographic patterns. Both samples from northern Queensland group with other taxa from that area in Clade M, all samples from eastern Victoria and southern New South Wales group with other taxa from southern New South Wales in Clade F, and samples from south-eastern Queensland fall in two clades (N and L) with other taxa from that area. This geographic pattern of chloroplast variation and similarity to other taxa would be consistent with regional introgression of chloroplasts. However, it could also be consistent with poor taxonomy, i.e. that *Z. smithii* encompasses multiple, cryptic taxa, yet to be recognised, that are each related to different species. The RAPD data of Hogbin and Crisp (2003), for instance, suggested that the coastal species *Z. prostrata* was incompletely differentiated from nearby populations of *Z. smithii* (although this was not recovered in our cpDNA sampling where one sample of *Z. prostrata* had an identical haplotype to *Z. arborescens* from Mount Norman, almost 200 km away). The considerable morphological variation seen in *Z. smithii*, including the northern Queensland populations previously recognised as subsp. *tomentosa*, was discussed by Duretto and Forster (2007).

Zieria arborescens displays some cpDNA variation that is geographically correlated, but also variation that suggests an influence of chloroplast lineage sorting. Of particular note is the placement of the sample of *Z. arborescens* from the Otway Ranges in south-western Victoria (RAB512) in Clade N, in which all other samples are from Queensland, separated by more than 1200 km. This geographic separation, although it could be reduced with further geographic sampling, is well beyond the realms of plausibility for recent chloroplast introgression, especially in an entomophilous genus that has seeds of limited dispersal (Armstrong 1979, 2002). Placement of the Otway sample in Clade N is well supported (BS 97%, PP 1, and with six characters supporting the node in parsimony reconstructions),

also making homoplasy unlikely. As such, this example provides the best evidence in our dataset that morphologically defined species of *Zieria* could harbour highly divergent chloroplast lineages that pre-date speciation events. In other cases where similar haplotypes in different species are widely geographically separated (e.g. those in clade B of subsp. *arborescens* MFD2035 from New South Wales and *Z. alata* KM639 from north Queensland), the inferred relationships have lower bootstrap or character support.

The patterns of variation in *Z. smithii* and *Z. arborescens* provide good evidence that introgression, lineage sorting and inappropriate taxonomy all potentially account for the observed cpDNA patterns. In other non-monophyletic taxa that are represented by fewer samples, or where divergence of chloroplast haplotypes is not so strong, it is difficult to make firm conclusions. For instance, in the case of *Z. robusta*, the two samples represent disjunct populations in Victoria and New South Wales, and it is not clear whether divergence between them could reflect introgression (e.g. similarity of the Victorian sample of *Z. robusta* to Victorian samples of *Z. arborescens* in Clade K), lineage sorting, or geographic variation associated with morphological differentiation of disjunct populations, e.g. Victorian populations have leaflets that are more deeply crenate, and petioles and undersurfaces of primary veins on leaflets that are more prominently tuberculate. Likewise for *Z. furfuracea*, it is not clear whether the three highly divergent haplotypes in Clades L, M and H, each from a different subspecies, reflect introgression with other species (e.g. they each group with different species from the regions in which they were sampled), variable retention of deeply divergent chloroplast lineages, or that the species is not monophyletic and each of the three subspecies are separate evolutionary lineages. Similarly, contrasting explanations could be plausible for each of the other species in our analysis that are not resolved as monophyletic.

Relationship of Zieria in Eastern Australia and New Caledonia

The chloroplast phylogeny shows the deepest divergence in *Zieria*, with strong support (BS 100%, PP 1.0), to be that between the single New Caledonian species, *Z. chevalieri*, and Australian taxa. As with other taxa, the position of *Z. chevalieri* is inconsistent with the morphological assessment and phylogeny of Armstrong (2002) that grouped *Z. chevalieri* with *Z. laevigata*, *Z. laxiflora* and *Z. fraseri*, which are variously placed in Clades C and D in the cpDNA phylogeny.

An early divergence between plants of these two areas (as opposed to a more nested position of *Z. chevalieri*) potentially lends itself to a vicariant explanation for distribution of the genus. Such an explanation would be consistent with the very limited dispersal capacity of the ant-dispersed seeds and is interesting, given controversy over the history of New Caledonia and its flora (Lowry 1998), and debate over the importance of long-distance dispersal (Grandcolas *et al.* 2008; Swenson *et al.* 2014) versus vicariance (Bauer *et al.* 2006; Ladiges and Cantrill 2007; Heads 2008). Controversy stems from molecular dating of clades where it is concluded that clades are too young to support a vicariance explanation. Molecular dating within Rutaceae by Bayly *et al.*

(2013) estimated that the divergence between *Z. chevalieri* and Australian taxa occurred (6.5) 11.9 (17.9) million years ago. This is younger than the initial rifting of Zealandia from eastern Australia, which commenced ~85 million years ago (McLoughlin 2001), the re-emergence ~37 million years ago of most of present-day New Caledonia after being below sea level from the Late Cretaceous to the Eocene (Aitchison *et al.* 1995; Pelletier 2006), and the likely presence of substantial areas of exposed land between Australia and New Caledonia into the Eocene and Oligocene (De Beauque *et al.* 1998; Exon *et al.* 2006; Ladiges and Cantrill 2007; Sutherland *et al.* 2010; Bache *et al.* 2012). However, it would be unwise to emphasise the molecular dating as a basis for confirming or rejecting biogeographic hypotheses in *Zieria* because, as previously suggested (Bayly *et al.* 2013), large parts of the Rutaceae tree are not supported by good fossil calibrations, including in *Zieria*, and could be prone to substantial underestimates of clade ages. Furthermore, as mentioned above, over water, long-distance seed dispersal is considered highly improbable for *Zieria*.

Because the cpDNA of *Z. chevalieri* in New Caledonia is substantially divergent from that of Australian taxa, the species is significant in terms of the phylogenetic diversity of the genus, making it of conservation concern. It is known only from Mount Kaala in northern Grande Terre (New Caledonia). We have seen only a small number of plants in the field (fewer than 100 in May 2009), and Armstrong (2002) reported a total population of ~200 plants. *Zieria chevalieri* is currently listed as *Vulnerable* under the IUCN Red List of Threatened Species (<http://www.iucnredlist.org>, accessed November 2014) under Criteria B1 and 2C, based on the assessment of Jaffre *et al.* (1998). A population survey and revision of the conservation status of *Z. chevalieri* is warranted, given the high level of mining activity around Mount Kaala and our field observations in 2009 that the population had been affected by road building and recent fire.

Conclusions and prospects for further research

As discussed above, we propose that the cpDNA tree presented here does not overall represent a hypothesis for a species tree in *Zieria*. It largely reflects evolutionary processes other than those of phylogenetic descent, such as introgression between species and chloroplast lineage sorting, as well as inappropriate species-level taxonomy. Gaining further insight into the history and systematics of *Zieria* will require additional data, and priorities should be to obtain phylogenetic data from the nuclear genome, more carefully scrutinise the morphology of some species and more thoroughly sample some species.

Assessing the degree of congruence between phylogenies produced by nuclear and chloroplast markers could help ascertain the underlying causes of observed phylogenetic patterns. For instance, it would be valuable to know how taxa resolved here as polyphyletic might be resolved by nuclear markers. If they were shown to be monophyletic using nuclear markers, current taxonomy would be supported and chloroplast capture or lineage sorting implicated as explanations. A finding of non-monophyly would highlight a need for taxonomic revision.

Additional data on morphology would be useful to compare with genetic variation. This is especially true for widespread and morphologically variable species such as *Z. arborescens*,

Z. aspalathoides, *Z. cytisoides* and *Z. smithii*. *Zieria* contains a striking mixture of a few very widespread species, and a large number of narrowly endemic species. It is possible that widespread taxa could have complicated relationships with a range of endemics that have differentiated through peripheral isolation or that widespread species harbour geographic variants worthy of taxonomic recognition. Correlation of geographic patterns of morphological and genetic variation would allow a more critical assessment of species limits.

A strength of the present study was the inclusion of multiple representatives of many taxa (41% of included species, i.e. 24 of 59). This allowed for the detection of widespread cpDNA polyphyly; more limited sampling would have provided a poorer understanding of the complexity of cpDNA variation. Nonetheless, many taxa in *Zieria* were not well sampled relative to their geographic distributions and morphological variation (e.g. *Z. aspalathoides*, *Z. caducibracteata*, *Z. cytisoides* and *Z. odorifera*). No species represented by more than two samples in our dataset was shown to be monophyletic, although 51 species were represented here by only one or two samples. Further sampling would give a clearer picture of the complexities of cpDNA variation.

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Note added in proof

In the time between acceptance and publication of this paper another phylogenetic study of *Zieria* has been published: Morton CM (2015) Phylogenetic relationships of *Zieria* (Rutaceae) inferred from chloroplast, nuclear, and morphological data. *PhytoKeys* **44**, 15–38.

The chloroplast DNA markers used in that paper were a subset of those used herein. Taxon sampling included 32 species, all of which are also represented here. Because species were each represented only by single accessions, that study did not detect the incongruence between cpDNA variation and species-level taxonomy reported here.

Appendix 1. Details of samples and sequences used in this study

Herbarium abbreviations follow Index Herbariorum. Other abbreviations are as follows: ABG, Australian Botanic Garden; ABP, A.B. Pollock; AF, A. Ford; ANBG, Australian National Botanic Gardens; Bean, A.R. Bean; CMH, C.M. Haskard; DEA, D.E. Albrecht; DJO, D.J. Ohlsen; IRT, I.R. Telford; JA, J. Armstrong; JRC, J.R. Clarkson; KM, K. Muscat; KMS, K.M. Sparshott; KRM, K.R. McDonald; LMD, L. McDougall; MBT, M.B. Thomas; MFD, M.F. Duretto; MJB, M.J. Bayly; MTM, M.T. Mathieson; NGW, N.G. Walsh; NP, National Park; NSW, New South Wales; NT, Northern Territory; PG, P. Gilmour; PIF, P.I. Forster; Qld, Queensland; RAB, R.A. Barrett; RGC, R.G. Coventry; RJ, R. Johnstone; RM, R. Makinson; SA, South Australia; SF, State Forest; SPP, S.P. Phillips; Tas., Tasmania; Vic., Victoria; WN, W. Neal. Collections of *Zieria arborescens* are not identified to subspecies, but those from near the type locations of subsp. *glabrifolia* are indicated (see 'Materials and methods' for details)

Taxon	Collection ID	Location	Voucher	<i>rpl32-trnL</i>	<i>trnL-F</i>	<i>trnQ-rps16</i>	<i>trnS-G</i>
<i>Neohyrcesia suberosa</i> J.A. Armstr.	MJB1904	NT, Kakadu NP, East Alligator area, Bardedjildji Sandstone Walk, ~300 m SW of carpark, near base of sandstone cliff	MEL	KP177988	KP188925	KP188987	KP189143
<i>Z. acatiles</i> Duretto & P.I. Forst.	PIF38224	Qld, Mount Larcom summit area, 2.5 km WSW of Targinie	BRI AQ818047	KP177977	KP188845	KP188995	KP189076
<i>Z. adenodonta</i> (F. Muell.) J.A. Armstr.	MTM760	Qld, Lower Bellbird Circuit, Binna Burra, Lamington NP	BRI AQ756722	KP177997	KP188858	KP188992	KP189110
<i>Z. adenophora</i> (F. Muell.) J.A. Armstr.	MJB2010	NSW, cult. ANBG, ex Araluen ~500 m ESE of Bells Creek Falls on rocky escarpment (same stock as CBG 8805884)	MELU, CBG 8805884	KP178010	KP188886	KP188982	KP189114
<i>Z. alata</i> Duretto & P.I. Forst.	AF5178	Qld, Daintree NP, 'landing rock' headwaters of Roots Creek, SE of topo '1296', site 171	BRI AQ739620	KP178042	KP188874	KP189035	KP189180
<i>Z. alata</i>	KM639	Qld, Mount Lewis NP	MELU	KP178064	KP188885	KP189029	KP189157
<i>Z. arborescens</i> Sims	DJO110	Tas., Saint Patricks River, on the S side of the Mount Barrow road, 10 km from its junction with the Tasman Highway	MELU D 105582	KP177976	KP188883	KP189048	KP189153
<i>Z. arborescens</i>	MFD2035 (AE892158)	NSW, cult. ABG, Mount Annan. Wild source: Blue Mountains NP, Walking track to Wollongambie River, near Mount Wilson	NSW	KP178001	KP188939	KP188986	KP189175
<i>Z. arborescens</i>	MJB1868	Vic., Noojee SF, Starling Gap picnic area	MELU	KP178079	KP188949	KP188969	KP189161
<i>Z. arborescens</i>	MJB2251a	Tas., Strahan	MELU	KP178039	KP188901	KP188965	KP189120
<i>Z. arborescens</i>	MTM270	Qld, Mount Norman, S side, Girraween NP	BRI AQ745993	KP178057	KP188854	KP188958	KP189078
<i>Z. arborescens</i>	RAB504	NSW, Barren Grounds Nature Reserve, next to the entrance gate	MELU	KP177979	KP188941	KP189054	KP189136
<i>Z. arborescens</i>	RAB512	Vic., Otway Ranges, Mount Sabine Benwerrin Road	MELU	KP177972	KP188944	KP189063	KP189112
<i>Z. arborescens</i> (subsp. <i>decurrens</i> J.A. Armstr.)	BRI ISO	NSW, 1.5 miles [2.4 km] along the Caves Beach Road, near Jervis Bay	BRI AQ695444, NSW 458804	KP178014	KP188894	KP189010	KP189144
<i>Z. arborescens</i> (subsp. <i>glabrifolia</i> J.A. Armstr.)	MTM213	Qld, Donnelly's Castle, ~6.5 km W of Thulimbah off Donnelly's Castle Road	BRI AQ745477	KP178052	KP188897	KP189021	KP189147
<i>Z. aspalathoides</i> A. Cunn. ex Benth. subsp. <i>aspalathoides</i>	Bean27984	Qld, near junction of Delubra and Cadarga creeks, 35 km SW of Munduberra	BRI AQ820153	KP178045	KP188903	KP189026	KP189150

(continued next page)

Appendix 1. (continued)

Taxon	Collection ID	Location	Voucher	<i>trp32-trnL</i>	<i>trnL-F</i>	<i>trnQ-rps16</i>	<i>trnS-G</i>
<i>Z. bauerlenii</i> J.A. Armstr.	275527	NSW, Bomaderry Creek Walking Track, cliff top N of number '4'	NSW 275527	KP178069	KP188898	KP188994	KP189104
<i>Z. bauerlenii</i>	MJB2011	NSW, cult. ANBG, ex Bomaderry Creek Reserve, 300 m S of Wier on W side, 10 m behind bench seat (same stock as CBG 9104885)	MELU	KP178048	KP188908	KP188984	KP189085
<i>Z. bifida</i> Duretto & P.I.Forst.	MTM537	Qld, Triunia NP, adjacent to Dulong Road W of Woombye	BRI AQ792099	KP177974	KP188923	KP188951	KP189158
<i>Z. boolbunda</i> Duretto & P.I.Forst.	KMS616	Qld, Boolbunda Rock, ~9 km NE of Mount Perry township	BRI AQ640789	KP178024	KP188857	KP188966	KP189171
<i>Z. buxijugum</i> J.D.Briggs & J.A.Armstr.	RJ1897	NSW, Box Range Farm ~10 km W of Pambula	MEL 2312322	KP178055	KP188930	KP189065	KP189072
<i>Z. caducibracteata</i> J.A.Armstr.	745482	NSW, Budawangs Track to Curong [Corang] River from Wog Wog camping ground	NSW 745482	KP177984	KP188876	KP188988	KP189159
<i>Z. caducibracteata</i> J.A.Armstr.	IRT9585	NSW, northern Budawang Range, Quillys Mountain, 1.5 km SE of Endrick trig	MEL 654142	KP177993	KP188850	KP189024	KP189092
<i>Z. cephalophila</i> Duretto & P.I.Forst.	TH7339	Qld, SE edge of Sydney Heads, Britton Range, 6.3 km NE-ENE of Homevale Homestead	BRI AQ579129	KP178035	KP188913	KP188979	KP189121
<i>Z. chevalieri</i> Virot	MJB2119	New Caledonia, Province Nord (N Province), Mount Kaala near saddle N of summit on S end of range	MEL, BRI, NOU	KP178058	KP188893	KP188960	KP189105
<i>Z. citriodora</i> J.A.Armstr.	NGW2038	Vic., cult. RBG Melbourne, grown from NGW 2038, on S bank of Limestone Creek, 1.5 km direct NE from ford on Limestone Creek track	MEL 222166	KP178038	KP188890	KP189034	KP189148
<i>Z. collina</i> C.T.White	MJB2012	Qld, cult. ANBG. Wild source: Cedar Creek NP, main circuit walking track N side (same stock as CBG 8604923)	MELU	KP178019	KP188934	KP188954	KP189139
<i>Z. collina</i>	MTM507	Qld, Tamborine NP, Panorama Point section, Wongawallan Road, Mount Tamborine	BRI AQ871795	KP178034	KP188914	KP188985	KP189173
<i>Z. compacta</i> C.T.White	PIF34479	Qld, Roberts Range, ascent to Devil's Elbow, Wyberba	BRI AQ745295	KP178046	KP188871	KP189056	KP189127
<i>Z. covenyi</i> J.A.Armstr.	MJB2013	NSW, cult. ANBG ex Narrow Neck Plateau ~5.5 km from Cliff Drive along road to Bushwalkers Hill (same stock as CBG 8411672)	MELU	KP177995	KP188838	KP189053	KP189081
<i>Z. cytisoides</i> Sm.	AF5451	Qld, Great Dividing Range, NW of Mount Emerald near topo '1089', W of Tolga	BRI AQ849111	KP178003	KP188860	KP188952	KP189130
<i>Z. cytisoides</i>	DJO320	Qld, Camarvon Gorge NP, 50 m upstream of the first creek encountered on the Moss Gardens walking track, 15 m above the creek near the base of the sandstone cliffs to the E of the creek	MELU	KP178066	KP188888	KP189030	KP189097

<i>Z. cyttisoides</i>	DJO416	NSW, Weddin Mountains NP, Bertha's Gully, on the N side of the creek next to the walking track, ~500 m E of the junction with the track, W of the gully at the base of a sandstone rock wall	MELU	KP178005	KP188896	KP189052	KP189178
<i>Z. distans</i> Duretto & P.I.Forst.	CMH157	Qld, Coalston Lakes, Walla Range	BRI AQ756300	KP178047	KP188915	KP189037	KP189155
<i>Z. distans</i>	MTM287	Qld, Kroombit Tops NP, Razorback break, ~10 km SW of barracks	BRI AQ813602	KP178009	KP188935	KP189028	KP189115
<i>Z. eungellaensis</i>	Bean4435	Qld, WSW of Mount David, Eungella NP	MEL 2324537, BRI AQ544202	KP178027	KP188892	KP188976	KP189118
<i>Z. exsul</i> Duretto & P.I.Forst.	MTM535	Qld, narrow strip of vegetation adjacent to Sunshine Motorway, Buderim, adjacent to Buderim Waste Landfill Centre	BRI AQ792100	KP177985	KP188911	KP188981	KP189134
<i>Z. formosa</i> J.D.Briggs & J.A.Armstr.	MJB2014	NSW, cult. ANBG. Wild source: Lochiel, 250 m from junction of Pambula-Wyndham road with Back Creek Road, towards Pambula, just S of road (same stock as CBG 8604998)	MELU	KP178015	KP188946	KP188957	KP189172
<i>Z. fraseri</i> Hook. subsp. <i>fraseri</i>	SPP1995	Qld, near the summit of the south peak of Mount Maroon, W of Rathdowney	BRI AQ748157	KP178044	KP188937	KP189017	KP189095
<i>Z. fraseri</i> subsp. <i>robusta</i> (C.T.White) Duretto & P.I.Forst.	MBT3739	Qld, Salvarosa NP, 160 km by road SW of Springsure, at the base of The Sentinel, ~1.5 km W of camping ground	BRI AQ830008	KP178054	KP188932	KP188964	KP189165
<i>Z. furfuracea</i> subsp. <i>euthadentia</i> J.A.Armstr.	MTM280	Qld, Wide Bay, corner of Cooloola Way and Harry's Hut Road, N of Kin Kin	BRI AQ745998	KP177968	KP188900	KP189045	KP189077
<i>Z. furfuracea</i> R.Br. ex Benth. subsp. <i>furfuracea</i>	466549	NSW, ~5 km direct WNW of Yarras, ~700 m E along the Oxley Highway from the Mount Seaview Resort turnoff, towards Wauchope	NSW 466549	KP177990	KP188865	KP188970	KP189146
<i>Z. furfuracea</i> subsp. <i>gymnocarpa</i> J.A.Armstr.	PIF34232	Qld, Belmont Gateway Motorway, thin strip of land between Motorway and Mount Petrie Road, 1.5 km S of Old Cleveland Road	BRI AQ744205, MEL 2324803	KP177998	KP188945	KP189016	KP189131
<i>Z. graniticola</i> J.A.Armstr. ex Duretto & P.I.Forst.	MTM479	Qld, Passchendaele SF, via Carniel Lane Bapaume	BRI AQ792107	KP178070	KP188943	KP188993	KP189109
<i>Z. granulata</i> (F.Muell.) C.Moore ex Benth.	MJB2016	NSW, cult. ANBG. Wild source: Long Brush Road, Kiama (same stock as CBG 8501509)	MELU	KP178063	KP188849	KP188972	KP189083
<i>Z. hindii</i> J.A.Armstr.	413395	NSW, Mount Jersusalem NP, Blackbutt Plateau area	NSW 413359	KP178051	KP188912	KP188977	KP189084
<i>Z. hydroscopica</i> Duretto & P.I.Forst.	PIF38247	Qld, Rocky Gorge Coomingslah SF, Rocky Gorge Waterhole	BRI AQ818058	KP178021	KP188870	KP189066	KP189133
<i>Z. inexpectata</i> Duretto & P.I.Forst.	CMH201	Qld, Burnett District, Pryde's Road, on the southern road reserve, ~700 m from the intersection with the Burnett Highway	BRI	KP177987	KP188853	KP189027	KP189119
<i>Z. ingramii</i> J.A.Armstr.	759202	NSW, Goonoo State Conservation Area, Freeman's Road, ~400 m E of Mount Carl Road	NSW 759202	KP178037	KP188861	KP189007	KP189125

Appendix 1. (continued)

Taxon	Collection ID	Location	Voucher	tp/32-tnL	tmL-F	tnQ-tps16	tnS-G
<i>Z. ingramii</i>	IRT613	NSW, Goonoo SF, ~53 km NE of Dubbo, ~600 m N of Denmore Road from a point 1.75 km E of Mount Carl Road	MEL 2218233	KP178074	KP188843	KP188971	KP189100
<i>Z. insularis</i> Duretto & P.I.Forst.	PIF34666	Qld, Mount Windsor NP, Spencer Creek downstream of forestry barracks	BRI AQ745463	KP178012	KP188848	KP188973	KP189145
<i>Z. involucreata</i> R.Br. ex Benth.	506074	NSW, Maroota, 3.2 km along Laughtondale Gully Road from Old Northern Road	NSW 506074	KP178008	KP188846	KP189013	KP189179
<i>Z. involucreata</i>	LMD143	NSW, Laughtondale Gully Road, ~3 km from Old Northern Road	MEL 2040124	KP178062	KP188940	KP189049	KP189137
<i>Z. laevigata</i> Bonpl.	MTM258	Qld, Passchendaele SF, Forestry Lane	BRI AQ813610	KP177969	KP188950	KP189031	KP189088
<i>Z. laevigata</i>	PIF34475	Qld, Girraween NP, junction of Ramsey and Bald Rock creeks	BRI AQ813611	KP178031	KP188882	KP189006	KP189073
<i>Z. lasiocaulis</i> J.A.Armstr.	492944	NSW, N side of Banda Banda Flora Reserve, 3.4 km by road, N of intersection of Banda Banda Road and Hastings Forest Way	NSW 492944	KP178056	KP188879	KP189060	KP189182
<i>Z. lasiocaulis</i>	PG7908	NSW, ~1 km W of Mount Banda Banda at the headwaters of the Wilson River, Banda Banda Flora Reserve	MEL 2199590	KP178080	KP188942	KP189046	KP189132
<i>Z. laxiflora</i> (Benth.) Domin	MTM385	Qld, Great Sandy NP, adjacent to Cooloola Coast cemetery, Rainbow Beach Road	BRI AQ755776	KP178061	KP188880	KP189064	KP189069
<i>Z. littoralis</i> J.A.Armstr.	MJB2017	Cult. ANBG. Wild source unknown (same stock as CANB 643996)	MELU	KP177982	KP188869	KP188967	KP189079
<i>Z. littoralis</i>	RAB508	NSW, Tathra Head, 50 m from the car park at Tathra Head on the walking track leading to the lookout over the ocean	MELU	KP177980	KP188884	KP188959	KP189138
<i>Z. madida</i> Duretto & P.I.Forst.	AF5320	Qld, Daintree NP, Hilda Creek area near camping area, ~800 m WNW of Thornton Peak Site 190	BRI AQ863277	KP178078	KP188834	KP189023	KP189122
<i>Z. minutiflora</i> Domin subsp. <i>minutiflora</i>	ABP2356	Qld, ~2 km due NE of Landsborough, on margin of private property and Ewen Maddock Council Reserve	BRI AQ815342	KP177983	KP188895	KP189002	KP189093
<i>Z. minutiflora</i> subsp. <i>minutiflora</i>	PIF34313	Qld, Glass House Mountains NP, Mount Coonowrin (Crookneck)	BRI AQ862319	KP177991	KP188919	KP189015	KP189163
<i>Z. minutiflora</i> subsp. <i>trichocarpa</i> J.A.Armstr.	KRM8283	Qld, Lot 5, Webster Road, near Wondeclea	BRI AQ747078	KP178000	KP188931	KP189014	KP189123
<i>Z. montana</i> J.A.Armstr.	PIF36219	Qld, Mount Barney NP, southern slopes (Peasant's Ridge) of Mount Barney, steep S-facing ridge	BRI AQ813884	KP178041	KP188928	KP189001	KP189116
<i>Z. murphyi</i> Blakely	JAI356	NSW, Mount Tomah, on ledge between Gaping Gill and Camels Hump	MEL 2102796	KP178016	KP188878	KP189058	KP189099
<i>Z. murphyi</i>	440349	NSW, Cones Walk, Bundanoon	NSW 440349	KP178068	KP188899	KP189062	KP189166
<i>Z. obcordata</i> A.Cunn.	608324	NSW, 'The Rocks' property, W of Bathurst	NSW 608324	KP178067	KP188933	KP188975	KP189098
<i>Z. obcordata</i>	RGC10060	NSW, 'Bulbudgerie' property, near Wuuluman, 15 km ENE of Wellington	MEL 2067510	KP178026	KP188841	KP188997	KP189126

<i>Z. obovata</i> (C.T.White) J.A.Armstr.	KRM8071	Qld, Grant Creek, Anniversary Falls on Rush Track, W of Herberton	BRI AQ861639	KP178023	KP188924	KP188956	KP189074
<i>Z. odorifera</i> J.A.Armstr. subsp.	RM1196	NSW, ~9 km (direct) SW of Molong Bocoble Gap rocky bluff immediately S of road and railway line in gap near base of bluff	MEL 717377, BRI AQ591376	KP178004	KP188887	KP189018	KP189142
<i>Z. odorifera</i> subsp.	599824	NSW, Warrabah, W of Kingstown, on private property	NSW 599824	KP177970	KP188851	KP189047	KP189096
<i>Z. warrabahensis</i> Duretto & P.I.Forst.	MJB2018	NSW, cult. ANBG. Wild source: 2.4 km from Howell on track to Copeton Lake	MELU	KP178017	KP188864	KP188998	KP189128
<i>Z. odorifera</i> subsp. <i>williamsii</i> Duretto & P.I.Forst.	DJO222	Recreation area (same stock as CBG 8505944)	MELU	KP177975	KP188936	KP189011	KP189149
<i>Z. oreocena</i> J.A.Armstr.	MJB1982	Vic., Grampians NP, Cultivation Creek Gorge, 100 m upstream from where Buandik Falls walking track ends, 1 m W of the creek	MEL	KP178071	KP188904	KP189003	KP189089
<i>Z. oreocena</i>	RAB580	Vic., Grampians NP, Deep Creek, ~150 m upstream of crossing on Harrop Track	MELU	KP178006	KP188889	KP189036	KP189091
<i>Z. oreocena</i>	RAB581	Vic., Hollow Mountain, Northern Grampians, in sheltered rock outcrop. S side of upper cave, just below summit	MELU	KP178002	KP188852	KP189055	KP189164
<i>Z. parrisiae</i> J.D.Briggs & J.A.Armstr.	RJ1899	Vic., Northern Grampians, Hollow Mountain, walking track to Summer Day Valley climbing area	MEL 2312304	KP178073	KP188862	KP188980	KP189152
<i>Z. pilosa</i> Rudge	MFD2008	NSW, Box Range Farm, ~10 km W of Pambula	NSW	KP177981	KP188917	KP189019	KP189174
<i>Z. pilosa</i>	RAB502	NSW, Berowra NP (Sydney Sandstone North) NSW, Georges River NP, Picnic Point on ridge track behind the second block of toilets from the road entrance	MELU	KP177973	KP188921	KP189032	KP189106
<i>Z. prostrata</i> J.A.Armstr.	758677	NSW, Look-at-me-now Headland, ~150 m SE of car park	NSW 758677	KP178075	KP188916	KP188999	KP189101
<i>Z. prostrata</i>	MJB2019	NSW, cult. ANBG. Wild source: Dammerelis Headland (same stock as CBG 8803922)	MELU	KP178032	KP188873	KP189025	KP189070
<i>Z. rimulosa</i> C.T.White	JRC5802	Qld, Mount Mulligan, ~40 km NW of Dimbulah, top of mountain, ~0.5 km SE of dam, rock outcrop	MEL 682024, BRI AQ398829	KP178050	KP188847	KP189059	KP189177
<i>Z. robertsonium</i> J.A.Armstr.	AF5349	Qld, Malbon Thompson Forest Reserve, NE of Bell Peak, North site 194	BRI AQ848776	KP178011	KP188868	KP189022	KP189162
<i>Z. robusta</i> Maiden & Betcher	DEA s.n.	Vic., 3.7 km S of Little Mount Kent, along walking track to Moroka Gorge from Horseyard Flat above N facing sandstone cliff	MEL 2019411 A	KP177966	KP188855	KP189051	KP189135
<i>Z. robusta</i>	MFD2049 (AD 950185)	NSW, cult. ANBG, Mount Amman. Wild source: Kanangra-Boyd NP, Kanangra Brook Falls, Kanangra Walls, below waterfall	NSW	KP178077	KP188842	KP188978	KP189151
<i>Z. scopulus</i> Duretto & P.I.Forst.	SPP1980	Qld, Flinders Peak, ~22 km S of Ipswich	BRI AQ747759	KP178007	KP188926	KP189043	KP189168

Appendix 1. (continued)

Taxon	Collection ID	Location	Voucher	<i>rp/32-trnL</i>	<i>trnL-F</i>	<i>trnQ-rps16</i>	<i>trnS-G</i>
<i>Z. smithii</i> Jacks.	AF5659	Qld, Herberton Range SF, steep upper slope of Mount Misch, W of Tolga	CNS 134680	KP178060	KP188938	KP189050	KP189075
<i>Z. smithii</i>	DJO327	Qld, Kroombit Tops NP, W of Dry Creek, 60 m downstream from the road crossing of Dry Creek which is 300 m E of the Barracks	MELU	KP177986	KP188872	KP189039	KP189154
<i>Z. smithii</i>	DJO430	NSW, Hat Head NP, Korogoro Point, next to the Korogoro Point Track circuit, 100 m from the start when walking the circuit in an anticlockwise direction	MELU	KP178029	KP188947	KP189020	KP189170
<i>Z. smithii</i>	KRM8282	Qld, Lot 5, Webster Road, near Wondecla	BRI AQ747081	KP178053	KP188835	KP189057	KP189129
<i>Z. smithii</i>	MJB2023	Qld, Currieger, South Stradbroke Island	MELU	KP178025	KP188948	KP189044	KP189082
<i>Z. smithii</i>	MJB2029	Vic., Briagolong-Stockdale road, ~300 m W of Stratford-Stockdale Road, Gippsland, Vic.	MELU	KP177999	KP188836	KP188990	KP189080
<i>Z. smithii</i>	MJB2184	Vic., Croaringalong NP, along walking track to Genoa Peak, ridgeline below summit	MELU	KP178013	KP188891	KP189067	KP189141
<i>Z. smithii</i>	MTM1127	Qld, Kureelipa Falls area, Mapleton SF	BRI AQ759541	KP178022	KP188837	KP188974	KP189140
<i>Z. smithii</i>	MTM275	Qld, Kureelipa Falls, South Maroochy River, ~4 km NE of Mapleton via Kureelipa	BRI AQ746002	KP178043	KP188905	KP189009	KP189117
<i>Z. smithii</i>	MTM303	Qld, Clewley's Gap area, Kroombit Tops NP	BRI AQ813593	KP178028	KP188881	KP188968	KP189068
<i>Z. smithii</i>	MTM926	Qld, North Stradbroke Island, E of Amity Point	BRI AQ757196	KP178059	KP188910	KP188961	KP189167
<i>Z. smithii</i>	MTM929	Qld, Caimbable Creek catchment, just W of Caimbable Falls, Lamington NP	BRI AQ757195	KP178065	KP188840	KP189004	KP189181
<i>Z. smithii</i>	PIF33151	Qld, Mount Walsh NP, Palm Valley area, 15 km S of Biggenden Coast Range	BRI AQ729276	KP178020	KP188859	KP189012	KP189090
<i>Z. smithii</i>	PIF34139	Qld, Main Range NP, start of Mount Cordeaux walking track	BRI AQ743453	KP178036	KP188907	KP188991	KP189087
<i>Z. smithii</i>	PIF36221	Qld, Mount Barney NP, southern base of Mount Barney	BRI AQ813882	KP177971	KP188920	KP189042	KP189160
<i>Z. smithii</i>	PIF38231	Qld, Bulburin NP, Dawes Range Road	BRI AQ818053	KP178030	KP188867	KP188953	KP189094
<i>Z. smithii</i>	PIF38266	Qld, Toolara SF (SF 1004), Harrys Hut Road, ~200 m from Cooloola Way	BRI AQ823442	KP178033	KP188918	KP188963	KP189086
<i>Z. smithii</i>	PIF38276	Qld, Conondale NP (formerly Imbil SF 2, Ryan LA)	BRI AQ818086	KP178081	KP188839	KP188996	KP189103
<i>Z. smithii</i>	PIF38466	Qld, Lyrebird Ridge Road, Springbrook	BRI AQ818295	KP178018	KP188906	KP189038	KP189071
<i>Z. smithii</i>	RAB511	Vic., Winging Inlet Croaringalong NP, Rams Head Track	MELU	KP177989	KP188844	KP188983	KP189111
<i>Z. smithii</i>	RAB548	Vic., Moilun Creek Bridge, Stockdale to Glenaladale Road (Beverleys Road), just upstream from crossing	MELU	KP178072	KP188877	KP188989	KP189184
<i>Z. smithii</i>	SPP2032	Qld, Mount Nebo, near Brisbane, Scrub Road ~4 km directly SE of Jollys Lookout, Mount Nebo D'Agular Range	BRI AQ748343	KP178076	KP188922	KP189005	KP189107
<i>Z. southwellii</i> J.A.Armstr.	MTM251	Qld, Boy-ull Creek, ~100 m upstream from Twin Falls, Springbrook NP	BRI AQ745450	KP178049	KP188856	KP189000	KP189113

<i>Z. tenuis</i> Duretto & P.I.Forst.	Bean4609	Qld, Bertya Creek, W of Warang, White Mountains NP	MEL 719859, BRI AQ544935	KP178082	KP188866	KP189061	KP189176
<i>Z. tuberculata</i> J.A.Armstr.	RAB505	NSW, Tilba Central, on the hill with the water tower	MELU	KP177992	KP188902	KP189041	KP189156
<i>Z. vagans</i> Duretto & P.I.Forst.	PIF34832	Qld, Gurgeneena Plateau, SF 172, near Meredith's Road	BRI AQ745514	KP177996	KP188927	KP188955	KP189108
<i>Z. veronicea</i> subsp. <i>insularis</i> J.A.Armstr.	WN14AE	SA, Kangaroo Island, Finders Chase NP, Yacca Flat Road	MELU D 108693	KP177978	KP188863	KP189008	KP189124
<i>Z. veronicea</i> (F.Muell.) Benth. subsp. <i>veronicea</i> <i>verrucosa</i> J.A.Armstr.	MJB1980	SA, Cox Scrub Conservation Reserve	MELU	KP178040	KP188929	KP189040	KP189169
<i>Z. whitei</i> J.A.Armstr. ex Duretto & P.I.Forst.	PIF34734	Qld, Blue Hills, 3 km NNE of Monogorilby	BRI AQ745491	KP177994	KP188875	KP188962	KP189102
	AF5486	Qld, Oaky Creek Falls, ~1 km SW of Mount Emerald	BRI AQ755971	KP177967	KP188909	KP189033	KP189183