SYSTEMATICS AND PHYLOGENY

Widespread morphological parallelism in *Korthalsella* (Santalaceae, tribe Visceae): A molecular phylogenetic perspective

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Abstract *Korthalsella* (Santalaceae, tribe Visceae) mistletoes are hemiparasitic plants that are widespread on islands and continental regions around the Indian and Pacific Oceans. In this study, we add key taxa to a previously generated dataset to produce a more inclusive phylogenetic analysis of the genus. The resulting nuclear ITS and plastid *trnL-F* phylogenies reveal that the historical sectional classifications based on morphology are not supported. Instead, it appears that widespread morphological parallelism has occurred throughout *Korthalsella*. Geographical distribution seems to be a better indicator of phylogenetic relatedness as species found in the same geographic region, island or island group generally are more closely related to one another than species sharing similar morphological characters in other areas. We find greater support for recognition of species as local endemics rather than wide-ranging taxa. Given these results, taxonomic changes that recognise previously described taxa are proposed, but other changes will require further study of broadly distributed taxa.

Keywords biogeography; morphology; Pacific islands; parasitic plants; phylogeny; species concept

Supporting information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Korthalsella Tiegh. (Santalaceae R.Br., tribe Visceae Horan., APGIV, 2016; Viscaceae Batsch, Nickrent & al., 2010) is a genus of approximately 30 scale-leaved, monoecious mistletoe species with cylindrical or flattened stems and diminutive unisexual flowers (Danser, 1937, 1940). The species are distributed widely across the Indo-Pacific region (Fig. 1), with mainland Australia (Barlow, 1983a; Cranfield, 2002), the Hawaiian Islands (six species, Wagner & al., 1999), Malesian region (five species, Barlow, 1997) and Madagascar (four known species, Callmander & al., 2010) having the most species. The flowers are trimerous, comprising three petals that completely enclose the gynoecium in the female flower (with the exception of the sessile umbonate stigma). In the male flower, the anthers are bisporangiate, and the three connate anthers form a disc-like structure called a synandrium (Fig. 2F) (Molvray & al., 1999). Pollen exudes from a central pore in the synandrium via small nectar droplets (Sultan, 2014).

Within *Korthalsella*, the number of recognised species has varied widely from older works that describe more than 60 species (Van Tieghem, 1896) to nearly 30 (Danser, 1937, 1940; Barlow, 1983a) to the most recent treatment that recognises just 8 (Molvray, 1997). The difficulty in defining species results from the diminutive floral features, seemingly simple morphology, and the occurrence of similar morphological forms in different regions/island groups (Figs. 1, 2). Traditionally, the presence or absence of specialised inflorescence branches (spike-like inflorescences), the number of flowers in each floral cluster, the colour of trichomes in the floral clusters, and the emergence of floral cushions from axils have been used in various classification schemes (Danser, 1937; Barlow, 1983a) (Tables 1, 2). However, because of the highly reduced flowers, vegetative characters have been used to delimit species (Danser, 1937; Barlow, 1983a; Molvray, 1997). These features include decussate vs. distichous cladotaxy, flattened vs. cylindrical stems, integration of internodes into phylloclades, the plane of flattening of branches compared to the parent axis

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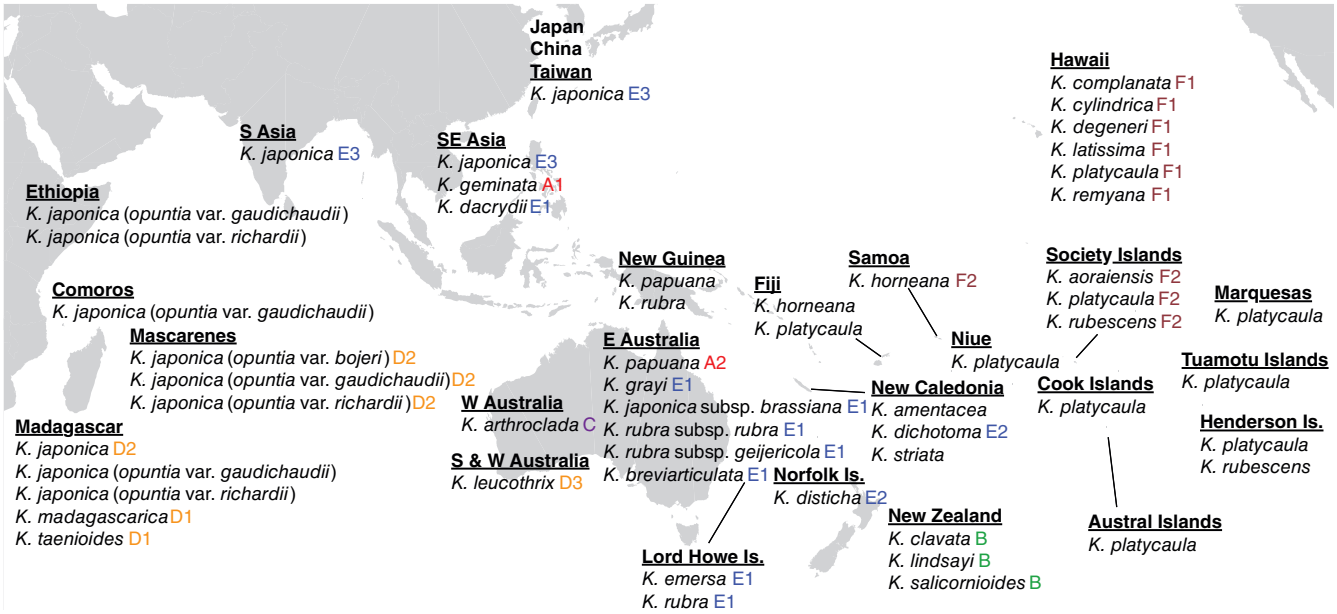

Fig. 1. Geographic distribution of *Korthalsella*. Clade identifications (from Fig. 3) follow taxa sampled from indicated localities.

(transverse vs. flattened in the same plane), the number of prominent veins on the internodes, the presence of an acute or obtuse leaf apex, and the internode shapes and dimensions (Danser, 1937; Barlow, 1983a). Following the concept of Danser (1937, 1940), the term phylloclade relates to the degree of integration of individual internodes. For example, some species (*K. latissima* (Tiegh.) Danser, *K. breviarticulata* (Tiegh.) Danser, *K. taenioides* (Comm. ex Juss.) Engl. [= *K. commersonii* (Tiegh.) Danser] and *K. complanata* (Tiegh.) Danser) have phylloclades where internodes are merely discernible by the presence of sulci between them. Conversely, all other species with flattened stems do not show such integration of internodes and have readily discernible individual internodes.

The taxa currently circumscribed in *Korthalsella* include Van Tieghem's (1896) genera *Korthalsella*, *Heterixia* Tiegh., and *Bifaria* Tiegh. *Heterixia* comprised species bearing flowers on distinct spicate inflorescences and having strongly flattened distichous stems (Fig. 2A, Tables 1, 2). *Korthalsella* and *Bifaria* included species lacking sharply distinct inflorescences and either decussate (*Korthalsella*, Fig. 2B) or distichous cladotaxy (*Bifaria*, Fig. 2C–E). Engler (1897: 138) included *Heterixia* and *Bifaria* as sections within *Korthalsella*. In a monograph of the genus, Danser (1937, 1940) used the same characters to delimit *Korthalsella* sections *Heterixia* (Tiegh.) Engl., *Bifaria* (Tiegh.) Engl. and "*Eukorthalsella* Engl." However, he suggested separating New Zealand's *K. lindsayi* (Oliv. ex Hook.f.) Engl. and *K. clavata* Cheeseman from *Heterixia* into an independent section, because both of these species possess superposed flower-bearing axils, as opposed to the decussate flower-bearing axils found in *K. geminata* (Korth.) Engl. and *K. papuana* Danser. He also used a biogeographic species concept, delimiting species based on geographic distribution, as well as morphology (see key to species in Danser, 1937). For example, *K. disticha* (Endl.) Engl. and *K. dichotoma* (Tiegh.) Engl. are considered to be conspecific by Barlow (1996) but were considered to be distinct species in Danser (1937); these taxa are endemic to Norfolk Island and New Caledonia, respectively. Danser (1940) recognised 23 species in the genus. Barlow (1983a) added two new species (*K. grayi* Barlow, *K. leucothrix* Barlow) and one new subspecies (*K. rubra* subsp. *geijericola* Barlow) from mainland Australia and one new species from Lord Howe Island (*K. emersa* Barlow) (Table 1). More recently, Cranfield (2002) described a new species from Western Australia, *K. arthroclada* Cranfield, which is characterised by cylindrical stems and acute leaf tips.

Molvray (1997) took quite a different view of the circumscription of *Korthalsella* and published a synopsis of the genus recognising just eight species (Tables 1, 2). Her classification was based on an anatomical study (Touw, 1984), taking into account the number of main vascular bundles in the stem, and the results of a molecular study that was published later (Molvray & al., 1999). She placed several species from the Pacific archipelagos, Oceania, mainland Africa and the Indian Ocean Basin as forms in a very broadly circumscribed and highly polymorphic *K. taenioides*. Most of these species were placed in synonymy under the single forma *K. taenioides* f. *taenioides* (Molvray, 1997). She placed *K. madagascarica* Danser (Madagascar) and *K. striata* (New Caledonia) in synonymy under *K. salicornioides* (New Zealand), and placed *K. amentacea*, a poorly known species from Art Island in the Belep archipelago (New Caledonia), under *K. lindsayi* (New Zealand). *Korthalsella clavata* (New Zealand) was also placed under *K. lindsayi* as a variety. Australian *K. rubra* subsp. *rubra* and *K. grayi* were reduced to forms of *K. japonica* (Thung.) Engl., whereas *K. leucothrix*, *K. japonica* subsp. *brassiana* (Blakely) Barlow and *K. opuntia* var. *fasciculata* (Tiegh.) Danser (see below for a comment on the nomenclatural status of this name) were placed under *K. japonica* f. *japonica*.

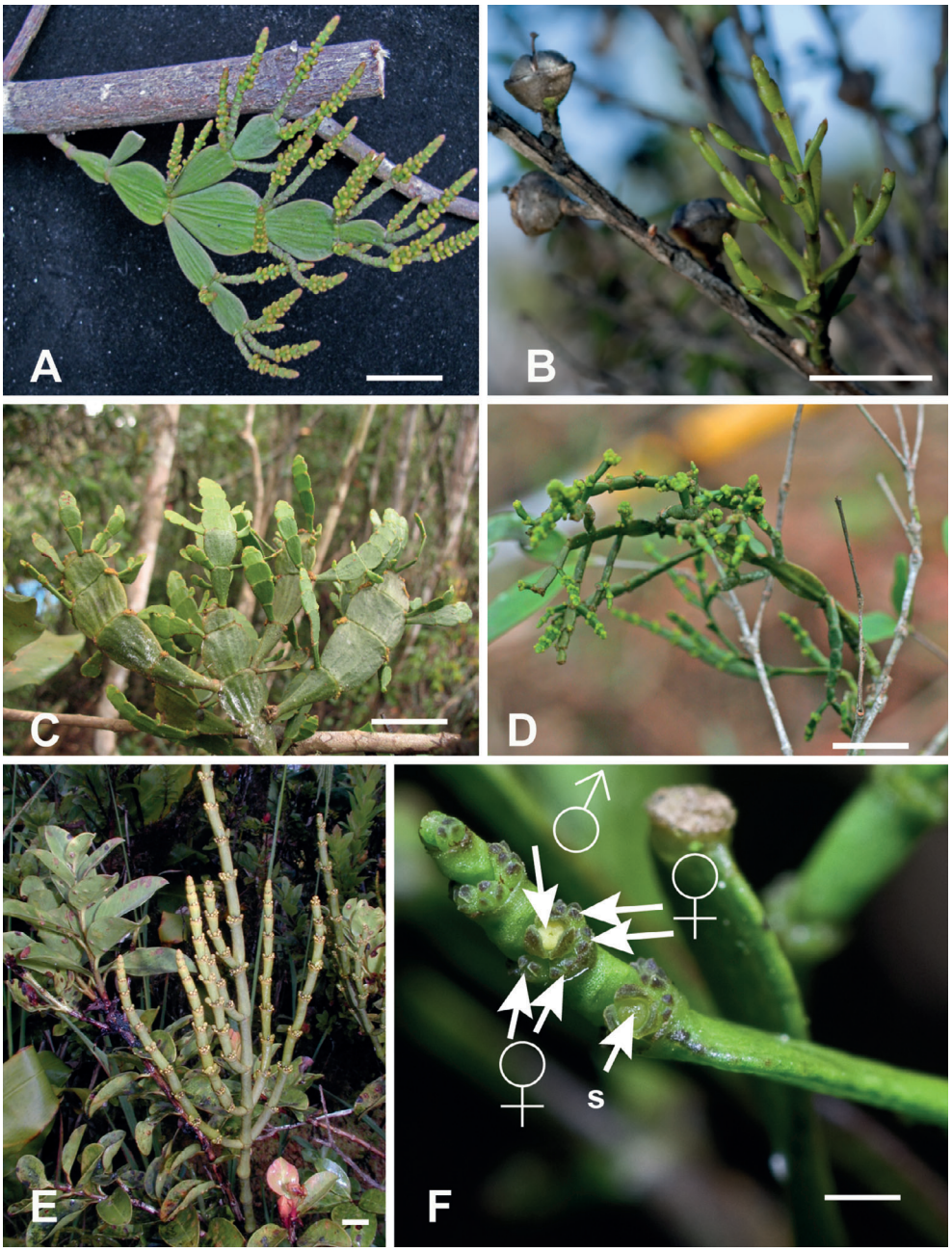

Fig. 2. Representatives of *Korthalsella*. **A**, *K. geminata* from Cambodia representing section *Heterixia* with distinct cylindrical inflorescences and strongly flattened internodes (photo by Philip Thomas, Royal Botanic Garden Edinburgh); **B**, *K. salicornioides* from New Zealand representing section *Korthalsella* with decussate cladotaxy (photo by Alastair Robertson); **C–E**, Section *Bifaria*: **C**, *K. taenioides* from Madagascar with distichous cladotaxy and flattened stems modified into phylloclades (photo by Patrice Antilahimena); **D**, *K. japonica* from Madagascar with distichous cladotaxy and flattened stems not modified into phylloclades (photo by Martin Callmander); **E**, *K. cylindrica* from Hawaii with terete stems (photo by Jean-Yves Meyer, Department of Research, Government of French Polynesia); **F**, *K. clavata* (section *Heterixia*) showing details of male and female floral clusters (photo by Alastair Robertson), s = synandrium. — Scale bar A–E = 1 cm, F = 1 mm.

Curiously, in their published phylogenetic study, Molvray & al. (1999) did not follow the taxonomy proposed as part of the 1997 synopsis. Molecular phylogenies based on nuclear ITS and plastid *trnL-F* spacer sequences revealed that neither of the sectional circumscriptions proposed by Danser (1937) nor Molvray (1997) were monophyletic and that instead biogeographic clusters formed well-supported clades. Previously emphasized morphological characters, such as internode shapes and number of vascular bundles, were homoplastic.

The Molvray & al. (1999) molecular study did not include species from south-eastern Polynesia, New Caledonia, Norfolk Island, Lord Howe Island, Madagascar or mainland Africa. Moreover, two key species from the Malesian region, *K. geminata* and *K. dacrydii* (Ridl.) Danser, were also missing from that study. The species that were not included create a large knowledge gap with regard to infra-generic relationships, especially for geographically wide-ranging taxa, and hinder the ability to evaluate species delimitations, relationships, biogeography, and morphological evolution. Moreover, testing monophyly of the classification scheme as proposed by Molvray (1997) requires much broader sampling than was included in the 1999 study. The goal of this study was to sample more broadly within *Korthalsella* and reconstruct molecular phylogenetic hypotheses to: (1) test the sectional classification scheme of Molvray (1997) (Table 2), and (2) assess intra-generic relationships, especially the species

Table 1. *Korthalsella* species recognised by Danser (1937, 1940) and Barlow (1983a) compared to Molvray (1997).

Danser (1937, 1940) & Barlow (1983a)	Molvray (1997)
Section *Heterixia* (specialised inflorescences, flattened stems)	
K. amentacea (Tiegh.) Engl.	= *K. lindsayi* (Oliv. ex Hook.f.) Engl. var. *lindsayi*
K. clavata Cheeseman	= *K. lindsayi* var. *clavata* (Cheeseman) Danser[a]
K. geminata (Korth.) Engl.	= *K. geminata* (Korthals) Engl.
K. lindsayi (Oliv. ex Hook.f.) Engl.	= *K. lindsayi* (Oliv. ex Hook.f.) Engl. var. *lindsayi*
K. papuana Danser	= *K. papuana* Danser
Section *Korthalsella* (decussate cladotaxy)	
K. dacrydii (Ridl.) Danser	= *K. dacrydii* (Ridley) Danser
K. horneana Tiegh.	= *K. taenioides* f. *horneana* (Tiegh.) Molvray
K. madagascarica Danser	= *K. salicornioides* (A.Cunn.) Tiegh.
K. salicornioides (A.Cunn.) Tiegh.	= *K. salicornioides* (A.Cunn.) Tiegh.
K. striata Danser	= *K. salicornioides* (A.Cunn.) Tiegh.
K. remyana Tiegh.	= *K. taenioides* f. *remyana* (Tieghem) Molvray
K. remyana var. *wawrae* (Tiegh.) Danser	= *K. taenioides* f. *taenioides*
Section *Bifaria* (distichous cladotaxy)	
Stems cylindrical	
K. aoraiensis (Nadeaud) Engl.	–
K. cylindrica (Tiegh.) Engl.	= *K. cylindrica* (Tiegh.) Engl.
K. cylindrica var. *planiuscula* Danser	= *K. taenioides* f. *taenioides*
K. degeneri Danser[b]	= *K. taenioides* f. *horneana* (Tiegh.) Molvray
K. grayi Barlow	= *K. japonica* f. *grayi* (Barlow) Molvray
K. leucothrix Barlow	= *K. japonica* (Thunb.) Engl. f. *japonica*
Stems flattened modified into phylloclades	
K. breviarticulata (Tiegh.) Danser	= *K. taenioides* f. *pendula* (Wawra) Molvray
K. complanata (Tiegh.) Engl.	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*
K. latissima (Tiegh.) Danser	= *K. taenioides* f. *pendula* (Wawra) Molvray
K. latissima var. *crassa* (Tiegh.) Danser	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*
K. taenioides (Comm. ex Juss.) Engl. (= *K. commersonii* (Tiegh.) Danser)[c]	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*
Stems flattened not modified into phylloclades	
K. dichotoma (Tiegh.) Engl.	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*
K. dichotoma var. *balansae* (Tiegh.) Danser	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*
K. disticha (Endl.) Engl.	= *K. taenioides* f. *disticha* (Endl.) Molvray
K. emersa Barlow	= *K. taenioides* f. *emersa* (Barlow) Molvray
K. japonica (Thunb.) Engl. (= *K. opuntia* (Thunb.) Merrill)	= *K. japonica* (Thunb.) Engl. f. *japonica*
K. japonica subsp. *brassiana* (Blakely) Barlow	= *K. japonica* (Thunb.) Engl. f. *japonica*
K. opuntia var. *bojeri* (Tiegh.) Danser	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*
K. opuntia var. *fasciculata* (Tiegh.) Danser	= *K. japonica* (Thunb.) Engl. f. *japonica*
K. opuntia var. *gaudichaudii* (Tiegh.) Danser	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*
K. opuntia var. *richardii* (Tiegh.) Danser	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*

(Continues)

Table 1. Continued.

Danser (1937, 1940) & Barlow (1983a)	Molvray (1997)
K. platycaula (Tiegh.) Engl. var *platycaula*	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*
K. platycaula var. *rapensis* (F. Brown) Danser	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*
K. platycaula var. *vitiensis* (Tiegh.) Danser	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*
K. rubescens (Tiegh.) Lecomte	
K. rubra (Tiegh.) Engl. subsp. *rubra*	= *K. japonica* f. *rubra* (Tiegh.) Molvray
K. rubra subsp. *geijericola* Barlow	= *K. taenioides* (Comm. ex Juss.) Engl. f. *taenioides*

a Danser (1937) considered *K. clavata* to be a variety of *K. lindsayi*, however, later he reinstated species rank for *K. clavata* (Danser, 1940).
b Molvray (1997) placed different forms of *K. degeneri* under *K. taenioides* f. *horneana*, and *K. taenioides* f. *taenioides*.
c *K. taenioides* is the legitimate name for the Malagasy entity *K. commersonii* in Danser (1937, 1940), see Callmander & al. (2010) for details.

Table 2. Sectional arrangement of *Korthalsella* according to Molvray (1997).

Section *Heterixia* (branch vascular bundles 8 or more, rarely 7 or 6; specialised inflorescences)
K. geminata (Korth.) Engl.
K. papuana Danser
Section *Korthalsella* (branch vascular bundles 8 or more, rarely 7 or 6; lacking specialised inflorescences)
K. cylindrica (Tiegh.) Engl.
K. taenioides (Comm. ex Juss.) Engl. f. *taenioides*
K. taenioides f. *disticha* (Endl.) Molvray
K. taenioides f. *emersa* (Barlow) Molvray
K. taenioides f. *horneana* (Tiegh.) Molvray
K. taenioides f. *pendula* (Wawra) Molvray
K. taenioides f. *remyana* (Tiegh.) Molvray
Section *Bifaria* (branch vascular bundles 4 or fewer)
Specialised inflorescences
K. lindsayi (Oliv. ex Hook.f.) Engl.
Lacking specialised inflorescences
K. dacrydii (Ridley) Danser
K. salicornioides (A.Cunn.) Tiegh.
K. japonica (Thunb.) Engl. f. *japonica*
K. japonica f. *grayi* (Barlow) Molvray
K. japonica f. *rubra* (Tiegh.) Molvray

concepts of Molvray (1997) (i.e., that broadly circumscribed entities and similar morphological forms inhabiting different geographical regions are conspecific) versus Danser (1937) and Barlow (1983a) (i.e., that most *Korthalsella* species inhabiting different geographical regions are specialised regional endemics and therefore show morphological parallelism across the distribution).

■ MATERIALS AND METHODS

Taxonomic sampling and DNA extraction. — The taxa sampled are listed in Appendix 1. New sequences of both plastid and ITS markers were generated for 30 *Korthalsella* individuals and the outgroup *Ginalloa linearis* Danser. For two individuals (K175 and K181), only one new sequence was generated. Molecular phylogenetic studies of Santalales indicate that *Korthalsella* is most closely related to *Ginalloa*, a small Indomalayan genus with five species (Nickrent & Soltis, 1995; Der & Nickrent, 2008; Mathiasen & al., 2008; Nickrent & al., 2010; but see also Maul & al., 2019). A further 42 sequences were downloaded from GenBank (Molvray & al., 1999; Papadopulos & al., 2011) (Appendix 1) or taken from our recent study of *Korthalsella* in New Zealand (Sultan & al., 2018), for a total of 106 sequences analysed phylogenetically (53 in each of the plastid and ITS datasets). Seventeen taxa not represented in the study of Molvray & al. (1999) were included here. The names of the taxa correspond to those in Danser (1937, 1940), Barlow (1983a), and Cranfield (2002). However, *K. taenioides* was adopted by Callmander & al. (2010) as a legitimate name for the Malagasy endemic named *K. commersonii* in Danser (1937, 1940). *Korthalsella opuntia* (Thunb.) Merr. is an illegitimate name (see Barlow, 1983a; Molvray, 1997), and the varieties established within this species by Danser (1937, 1940) should have been treated as varieties of *K. japonica*. However, they have never been formally transferred to *K. japonica* or any other species, and it is doubtful whether they conform to the modern concept of variety. Even though these are incorrect names for the taxa concerned, we use them here, following Molvray & al. (1999), to avoid confusion until such time as the species level taxonomy of the group is fully resolved and the necessary nomenclature changes can be made. DNA was extracted from silica gel-dried stem tissue or recent herbarium specimens by a modified CTAB method (Doyle & Doyle, 1987) of Loockerman & Jansen (1996). For older herbarium specimens, DNA was extracted using a Qiagen DNeasy Plant Mini Kit (Qiagen, Valencia, California, U.SA.) followed by multiple displacement amplification (MDA) using a Qiagen REPLI-g kit following the manufacturer's instructions (Brockington & al., 2008).

Nuclear and plastid marker amplification and sequencing. — The nuclear ribosomal internal transcribed spacer region (ITS1, 5.8S, ITS2) was amplified using primers ITS7A (5′-GAGTCATCAGCTCGCGTTGACTA-3′, A. Plovanovich and J. Panero, unpub.) and ITS4 (White & al., 1990). The plastid *trnL-F* intergenic spacer was amplified using primers "e" and "f" of Taberlet & al. (1991). Both ITS and

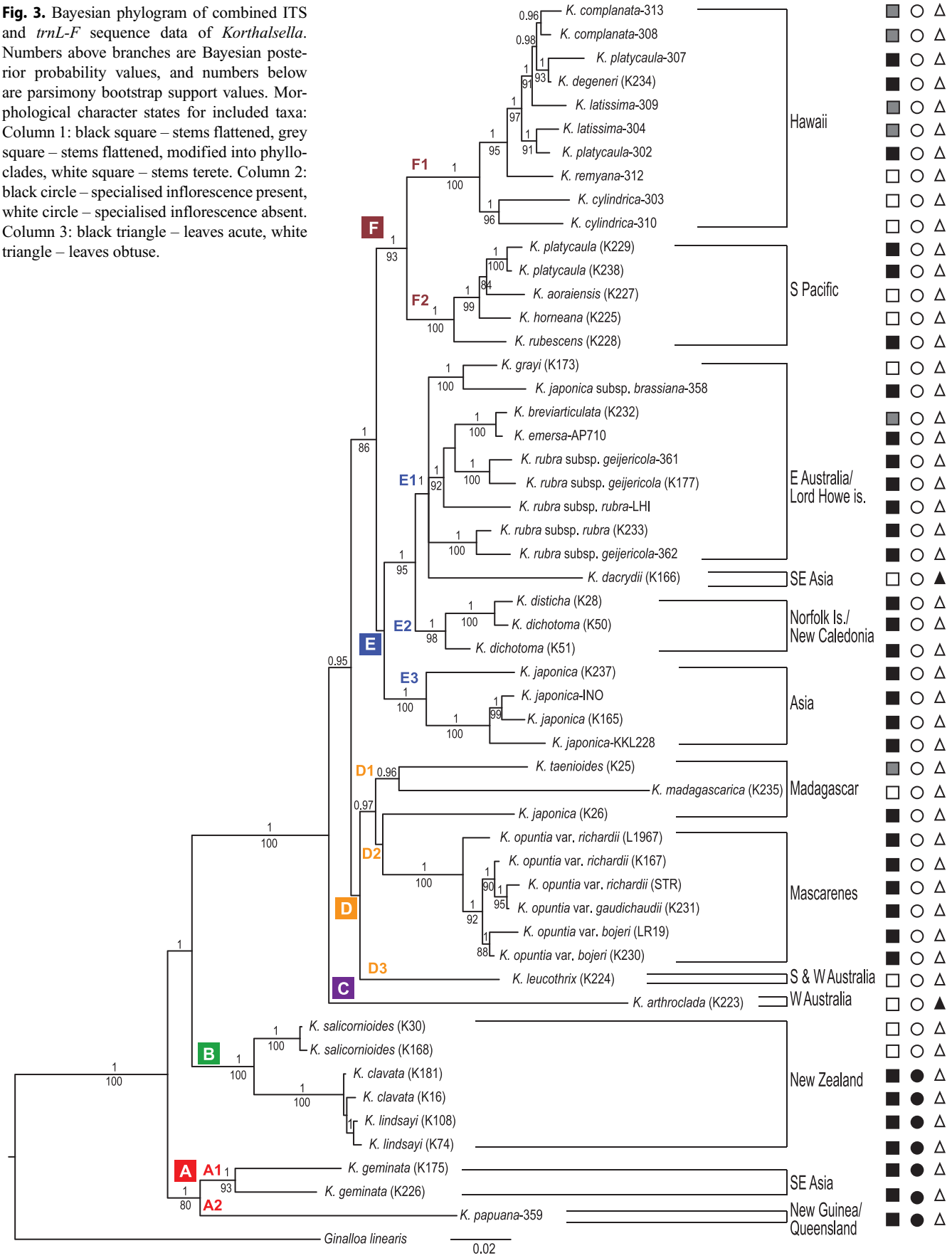

Fig. 3. Bayesian phylogram of combined ITS and *trnL-F* sequence data of *Korthalsella*. Numbers above branches are Bayesian posterior probability values, and numbers below are parsimony bootstrap support values. Morphological character states for included taxa: Column 1: black square – stems flattened, grey square – stems flattened, modified into phylloclades, white square – stems terete. Column 2: black circle – specialised inflorescence present, white circle – specialised inflorescence absent. Column 3: black triangle – leaves acute, white triangle – leaves obtuse.

trnL-F were amplified in a 25 µl total volume comprising 10× ThermoPol reaction buffer (New England BioLabs, Ipswich, Massachusetts, U.S.A.), 10 mM dNTPs, 4 µM forward and reverse primers, 5 µM Betaine, 0.5 units NEB Taq polymerase and ~50 ng template. A step-down PCR profile was employed for amplification of ITS at 95°C for 1 min, 53°C for 1 min and 72°C for 1 min for five cycles, followed by a decrease in the annealing temperature to 48°C for another 44 cycles, and with a 7 min final extension at 72°C. The plastid region was amplified using 95°C for 1 min, 50°C for 1 min followed by 65°C for 4 min for 34 cycles, and a 5 min final extension at 72°C. Amplification products were separated on a 1% agarose gel, stained with ethidium bromide and visualised with UV on a trans-illuminator. For amplifying the ITS region from older herbarium specimens, internal primers were used to amplify ITS in two overlapping fragments: ITS1: ITS7A and ITS2B (CTCGATGGAACACGGGATTCTGC, based on Kim & Jansen, 1994); ITS2: ITS3 (GCATCGATGAAGAACGCAGC, Kim & Jansen, 1994) and ITS4 (White & al., 1990). Bovine serum albumin (BSA) was used as an adjuvant at a concentration of 1% to avoid mis-amplification from fungal contamination in the ITS reaction of sample K26 (De Miranda & al., 2010). Without the addition of BSA, amplification resulted in a smeared product.

Unincorporated dNTPs and excess primers were removed by adding 5 units of exonuclease I (Fermentas, Glen Burnie, Maryland, U.S.A.) and 0.5 units shrimp alkaline phosphatase (Fermentas) to 8 µl of PCR product and incubating at 37°C for 30 min followed by 80°C for 15 min. PCR products were sequenced using forward and reverse primers. Cleaned products were sequenced on an ABI 3770 sequencer at the Massey Genome Service (Massey University, Palmerston North, New Zealand) following the manufacturer's recommendation (Applied Biosystems, Foster City, California, U.S.A.). Sequences were edited by generating contigs from forward and reverse sequences in Sequencher v.4.8 (Gene Codes, Ann Arbor, Michigan, U.S.A.) or Geneious v.6.1 (Biomatters, Auckland, New Zealand). Edited sequences were aligned in Geneious using MUSCLE (Edgar, 2004), with manual adjustments. Alignments are available in TreeBase under study accession S25318 (http://purl.org/phylo/treebase/phylows/study/TB2:S25318).

Phylogenetic analyses. — Parsimony analyses were conducted in PAUP* v.4.10 (Swofford, 2002) initially on separate nuclear and plastid datasets using heuristic searches with tree-bisection-reconnection (TBR) branch-swapping, 1000 random addition replicates, and gaps coded as missing. A number of insertion-deletion events were identified in the nuclear and plastid alignments that seemed to unite biogeographical groups (see Results). We conducted analyses with and without these regions coded as a presence/absence character but found no resulting differences in the topologies or support for those clades. Therefore, in the final analyses, the indels were ignored. Bootstrap support for clades was determined on the basis of 10,000 replicates (Felsenstein, 1985). Visual inspection of phylogenies from separate datasets revealed no hard incongruences. Therefore, combined ITS and *trnL-F* datasets were analysed using the same search criteria as for the separate regions.

Bayesian analyses were conducted on separate and concatenated ITS and *trnL-F* datasets using MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001). The best-fit model for each region (ITS1, 5.8S, ITS2, *trnL-F*) was determined using MrModeltest v.2.3 (Nylander, 2004) prior to Bayesian phylogeny estimation. ITS1, 5.8S and ITS2 were analysed together, specifying the best-fit model for each partition (GTR+Γ for ITS1 & 2, K80+I+Γ for 5.8S). For the *trnL-F* dataset, the best-fit model selected was GTR+Γ+I. Combined ITS and *trnL-F* datasets were analysed using the same search criteria as for the separate regions. MrBayes was allowed to run for at least 20 million generations or until the average standard deviation of the split frequencies approached 0.001. Trees corresponding to the burn-in period (the first 25%) were discarded and a majority-rule consensus constructed from the remaining trees.

■ RESULTS

The ITS matrix had a total aligned length of 745 bp with 236 parsimony-informative characters (including the outgroup). The aligned length included ITS1: 290 bp, 5.8S: 164 bp, ITS2: 291 bp. *Korthalsella arthroclada* had the longest sequence, comprising 685 bp (ITS1: 256 bp, ITS2: 262 bp). *Korthalsella leucothrix* had the shortest sequence length of 626 bp (ITS1: 219 bp, ITS2: 240 bp). All New Zealand taxa have an 11 bp deletion at positions 90–100 and another 6 bp deletion at 208–213. A 6 bp deletion was common to *K. grayi* and *K. japonica* subsp. *brassiana* at 86–91. A 27 bp deletion at positions 232–258 was common to all Mauritius and Réunion taxa. *Korthalsella platycaula* (Tiegh.) Engl. from Tahiti had a 10 bp deletion beginning at position 114 relative to other *Korthalsella*. All Hawaiian species except *K. remyana* Tiegh. have a 6 bp deletion at positions 121–126.

The *trnL-F* matrix had a total aligned length of 1216 bp with 166 parsimony-informative characters (including the outgroup). *Korthalsella leucothrix* had the longest sequence, comprising 894 bp; *Korthalsella arthroclada* had the shortest sequence length of 638 bp. *Korthalsella madagascarica*, *K. japonica* subsp. *brassiana*, *K. dacrydii*, *K. grayi*, *K. rubra* subsp. *geijericola* (361 & 362), and *K. rubra* subsp. *rubra* also have relatively short sequences (lengths of 749, 756, 761, 765, 785, 789 and 803 bp, respectively). All Mauritius and Réunion taxa share an 8 bp deletion beginning at position 358 relative to other *Korthalsella* species. *Korthalsella japonica* from Asia, *K. dichotoma*, *K. disticha* and *K. taenioides* share a 4 bp deletion at 381–384, whereas all *Korthalsella japonica* accessions from Asia have a 6 bp insertion at 671–676. Similarly, all Hawaiian species have a 6 bp deletion at 423–428. A 10 bp insertion at 811–820 is common to *K. geminata*, *K. papuana*, *K. leucothrix* and all New Zealand species. A 5 bp deletion at 882–886 is shared by *K. rubra* subsp. *geijericola* (361 & 362) and *K. rubra* subsp. *rubra*.

The parsimony ITS analysis returned 240 equally parsimonious trees of 861 steps (consistency index [CI] excluding uninformative characters = 0.53, rescaled consistency index [RC] = 0.49), while the parsimony analysis of the *trnL-F* data resulted in 201 equally parsimonious trees of 582 steps (CI = 0.58, RC = 0.55). The resulting trees from the two datasets were highly congruent, although the *trnL-F*-based trees were much less resolved than those derived from ITS (data not shown). The combined ITS+*trnL-F* strict consensus is presented as supplementary Fig. S1. ITS and *trnL-F* datasets were concatenated as there was not significant conflict between them as determined by the incongruence length difference test (P = 0.236). Although *trnL-F* sequences were not obtained from *Korthalsella japonica* from Madagascar (K26), we included this taxon in the combined analyses to determine its overall placement. Analyses that excluded this taxon resulted in trees that did not differ substantially from the ones presented here (data not shown). The combined ITS and *trnL-F* data matrix included 402 parsimony-informative characters. The parsimony analysis resulted in 12 equally parsimonious trees of 1453 steps (CI = 0.54, RC = 0.51).

Because the individual and concatenated parsimony trees were very similar to the results from Bayesian phylogeny estimation, the resulting species relationships are presented from the latter analyses. The main difference between the parsimony and Bayesian analyses was the lack of resolution for some clades, which was reflected in the lack of support as indicated in the resulting trees (suppl. Figs. S1–S3, Fig. 3). Otherwise, there were no supported differences between the two datasets (nuclear vs. plastid) nor trees resulting from the different analyses (parsimony vs. Bayesian).

The resulting topologies of the Bayesian consensus for individual ITS (suppl. Fig. S2), *trnL-F* (suppl. Fig. S3), and concatenated datasets (Fig. 3) were largely congruent with the results of Molvray & al. (1999), where species grouped according to geographic region and not by morphological characters (Fig. 1). Sections *Bifaria* and *Korthalsella* of Danser (1937) and Molvray (1997) were not monophyletic, but the two species of section *Heterixia* (*K. geminata*, *K. papuana*; Table 2) as defined by Molvray (1997) did form a well-supported clade (Clade A in Fig. 3; posterior probability [PP] = 1.00, bootstrap support [BS] = 80%). This clade was sister to the rest of the genus, followed by a clade of New Zealand endemics (*K. clavata*, *K. lindsayi*, *K. salicornioides*) (Clade B in Fig. 3; PP = 1.00, BS = 100%). The recently described *Korthalsella arthroclada* from Western Australia (lineage C, PP = 0.95) was sister to the rest of the genus.

Within the main large clade, a number of sub-clades emerge that generally reflect geographic proximity. *Korthalsella leucothrix* from southern and western Australia was sister to an Indian Ocean Basin clade (Fig. 3; PP = 0.97) with species from Madagascar and the Mascarenes (Clade D in Fig. 3). The Malagasy species *K. taenioides* and *K. madagascarica* formed a clade (Clade D_1; PP = 0.96). Another Malagasy collection, identified as *K. japonica* (K26) was sister to a well-supported clade of species from the Mascarenes (Clade D_2; PP = 1.00, BS = 100%). These latter specimens are part of the species group referred to the illegitimate name *K. opuntia* (sensu Danser, 1937). Asian populations referred to *K. japonica* formed a well-supported clade (Clade E_3 in Fig. 3; PP = 1.00, BS = 100%), quite separate from the collections from Australia and the Mascarenes identified as subspecies or varieties within this species. This material included a collection identified as *K. japonica* from Japan, another collection from Java although most of the material available for inclusion in the study was from India or Pakistan.

Clade E (Fig. 3) contains taxa from Australia, Asia, and the western Pacific. *Korthalsella dacrydii* from Southeast Asia and taxa from eastern Australia and Lord Howe Island formed a clade that is unresolved at the base (Clade E_1 in Fig. 3; PP = 1.00). Within this clade, *K. rubra* subsp. *rubra* and *K. rubra* subsp. *geijericola* were both polyphyletic. *Korthalsella grayi* and *K. japonica* subsp. *brassiana* from Queensland, Australia formed a strongly supported sub-clade (PP = 1.00, BS = 100%). Another sub-clade (PP = 1.00, BS = 92%) comprised a *K. rubra* subsp. *rubra* collection from Lord Howe Island, two *K. rubra* subsp. *geijericola* collections from New South Wales, Australia, *K. emersa* from Lord Howe Island and *K. breviarticulata* from Queensland. Within this latter clade *K. emersa* and *K. breviarticulata* formed a strongly supported sub-clade (PP = 1.00, BS = 100%) sister to a *K. rubra* subsp. *geijericola* sub-clade (PP = 1.00, BS = 100%). Sister to clade E_1 was *Korthalsella disticha* from Norfolk Island and two collections of *K. dichotoma* (K51, K50) from New Caledonia, which formed a well-supported clade (Clade E_2 in Fig. 3; PP = 1.00, BS = 98%), within which *K. disticha* and a collection of *K. dichotoma* (K50) formed a strongly supported sub-clade (PP = 1.00, BS = 100%). Sister to clades E_1 and E_2 was a clade of *K. japonica* collections from Asia (Clade E_3; PP = 1.00, BS = 100%).

All Hawaiian species cluster together (Clade F_1 in Fig. 3; PP = 1.00, BS = 100%), and this clade is sister to species from Samoa and the Society Islands (Clade F_2; PP = 1.00, BS = 100%) to form a well-supported South Pacific clade (Clade F; PP = 1.00, BS = 93%). *Korthalsella platycaula* collections from Tahiti cluster together in the Society Islands clade with *K. aoraiensis* (Nadeaud) Engl. from Tahiti (Clade F_2); *Korthalsella horneana* Tiegh. from Samoa was sister to this Tahitian sub-clade. The *K. platycaula* individuals from Hawaii occur in the Hawaiian clade (Clade F_1). Within this Hawaiian clade, two *K. cylindrica* (Tiegh.) Engl. samples (303-Kauai, 310-Oahu) grouped together (PP = 1.00, BS = 96%), while *Korthalsella complanata*, *K. latissima* and *K. platycaula* were polyphyletic. *Korthalsella latissima* (304) and *K. platycaula* (302) from Kauai formed a clade. The remaining collections in the Hawaiian clade were from Oahu.

Morphological characters plotted onto Fig. 3 reveal widespread homoplasy for those characters previously used to delimit the sections and species boundaries as defined by Molvray (1997). This result in consistent with that of Molvray & al. (1999), who plotted other morphological characters onto

the tree, including the number of internode vascular bundles and internode shape (fig. 6 in Molvray & al., 1999).

■ DISCUSSION

Biogeographical species concept and morphological parallelism. — The phylogenetic results presented here strongly support the species concepts of Danser (1937, 1940) and Barlow (1983a) in recognising numerous regional endemic species rather than the fewer wide-ranging taxa Molvray (1997) advocated. Thus, the similar morphology of certain widespread species (e.g., *Korthalsella taenioides* or *K. japonica* as defined by Molvray, 1997) is due to either the retention of plesiomorphic features or to convergent or parallel evolutionary trends within the genus. As a result, we find that the traditional sections based on morphology are not supported. The one exception is Molvray's (1997) section *Heterixia*, for which we confirm the sister relationship of *K. papuana* and *K. geminata* as indicated by Molvray & al. (1999).

Barlow (2018) suggested that the distribution of *Korthalsella* on remote Pacific and Indian Ocean archipelagos conformed to the movement of wide-ranging, island-dwelling seabirds that are potential long-distance dispersal agents of these mistletoes, whereas the continental distribution patterns of other species conform to movement of dispersing land birds that move through tropical and temperate forests in these regions. However, some of the wide-ranging species also inhabit remote oceanic islands and geographical regions so it does not appear that we have support for two clades with different dispersal histories as implied by Barlow (2018).

For most of the species, ITS, plastid, and combined ITS and plastid reconstructions strongly support biogeographical affinities within the genus (Fig. 3). The cause of the patchy distribution of these mistletoes on remote Indian Ocean and Pacific islands remains elusive. The origins of Visceae have been controversial – either being considered of Laurasian (Barlow, 1983b) or Gondwanan origin (Vidal-Russell & Nickrent, 2008). A more recent study by Maul & al. (2019) reconstructed the biogeographic history of *Viscum* L. and related genera (including *Korthalsella*). That study concluded that the ancestral distribution for Viscaceae was Australasia. Like *Korthalsella*, *Viscum* has a complex biogeographic history. The genus originated in Africa, but dispersed to Australia, Asia, and Europe at different times during its evolutionary history (Maul & al., 2019). Most of these events correlate with known migratory bird patterns, although some (e.g., to Australia) do not. Similarly, Liu & al. (2018) showed recently that long-distance dispersal of Loranthaceae mistletoes was facilitated by birds (between Australasia and Asia, Africa and Asia, and Africa and Madagascar). Molvray & al. (1999) considered the Malesian region to be the centre of origin of *Korthalsella*, and this is supported by our phylogeny which places the Malesian section *Heterixia* as sister group to the rest of the genus with a similar distribution to the sister genus *Ginalloa* (Barlow, 1997). Under this scenario, we envisage *Korthalsella* evolving in SE Asia, then colonising New Zealand and later spreading west to Australia and the Indian Ocean reaching Madagascar and Africa and east across the Pacific to Samoa, Tahiti and Hawaii. However, further biogeographic analyses with additional outgroup sampling, especially for *Ginalloa*, are needed to discern these large-scale patterns.

Carlquist (1967), Burrows (1996), and Barlow (2018) proposed that migratory birds are potential vectors of long-distance dispersal in *Korthalsella*, carrying seeds by adherence to plumage after weakly explosive discharge of seeds. Speciation in this genus then most likely followed independent introductions and specialisation on different hosts. For example, *Korthalsella breviarticulata* from eastern Australia, *K. latissima* from Hawaii and *K. taenioides* from Madagascar represent examples of parallelism in different geographical regions, with stems modified into phylloclades and an overall close resemblance in gross morphology. These species group with their biogeographic counterparts in different clades/sub-clades. Thus, phylloclades evolved independently in at least three different lineages (Clades D_1, E_1, and F_1 in Fig. 3). Based on these apparent similarities, Molvray (1997) reduced *K. breviarticulata* and *K. latissima* to synonyms of *K. taenioides* f. *pendula* (Table 1), while the Malagasy material of *K. taenioides* was placed under a broadly circumscribed *K. taenioides* f. *taenioides* (Table 1). Molvray's forma *taenioides* contained taxa from clades D, E and F that are spread across the range from Madagascar, Australia and across the Pacific to Hawaii. Similarly, *Korthalsella aoraiensis* from Tahiti and Moorea (Society Islands) and *K. cylindrica* from the Hawaiian Islands both have distichous cylindrical stems and are usually parasitic on *Metrosideros* (Myrtaceae) species, yet, in our analysis, they grouped with other neighbouring species from the South Pacific and Hawaiian Islands, respectively.

Korthalsella madagascarica, *K. striata* and *K. salicornioides*, with decussate cladotaxy, cylindrical stems and a relatively small overall size, represent another example of parallelism in the genus. Danser (1937, 1940) recognised *K. madagascarica*, *K. striata* and *K. salicornioides* as distinct species endemic to Madagascar, New Caledonia and New Zealand, respectively. However, Barlow (1996) considered *K. striata* and *K. salicornioides* to be conspecific and placed New Caledonian *K. striata* in synonymy under the New Zealand *K. salicornioides*. Molvray (1997) also treated *K. striata* and *K. madagascarica* as synonyms of *K. salicornioides*, rendering the latter species with a highly disjunct distribution. *Korthalsella striata* is missing from our molecular dataset, as it is known only from a few isolated records. Despite considering *K. striata* to be conspecific with *K. salicornioides*, Barlow (1996) noted differences like thinner basal internodes and more pronounced ribs on New Caledonian material compared to specimens from New Zealand. *Korthalsella madagascarica* groups with the other Malagasy taxa in the analysis of both molecular markers (Clade D_1 in Fig. 3). Moreover, examination of original material of *K. madagascarica* (*Humbert 14060* [B, G, P]; *Perrier de la Bâthie 12363* [P]) revealed a significant number of morphological characters

that differ from *K. salicornioides*. Flowering in *K. madagascarica* is continuous, whereas in *K. salicornioides*, flowering time is restricted to summer. Female flowers in *K. madagascarica* are pedicellate, while these are sessile in *K. salicornioides*. The inflorescence trichomes in *K. salicornioides* are fewer and reddish-brown, while in *K. madagascarica* these are colourless and more numerous. In *K. madagascarica* flowers originate as a cluster of three (two female, one male) or five (four female, one male), and more female flowers continue to develop below these (Fig. 4A,B); thus, the number of flowers in each axil is variable, while the number of flowers in each floral cluster of *K. salicornioides* is always five (four female, one male). *Korthalsella salicornioides* shares this characteristic (number of flowers) with the other New Zealand species, which means that each node bears a maximum of eight fruits all of the same age (Fig. 4C). Thus, closer examination of inflorescence/floral micro-morphology within the genus could potentially reveal more taxonomically important characters.

Furthermore, the occurrence of *K. madagascarica* on non-Myrtaceous hosts (Balle, 1964), including species of *Erica* L. (Ericaceae), *Leptolaena* Thouars (Sarcolaenaceae) and *Diospyros* L. (Ebenaceae) as well as *Cynometra* L. (Fabaceae) (specimen of *Jongkind & al. 3529* in MO and WAG), as opposed to predominantly Myrtaceous hosts for *K. salicornioides* (*Kunzea* spp. and *Leptospermum scoparium* J.R.Forst. & G.Forst. s.l.) (Sultan & al., 2018) also suggests divergence in terms of host preferences. Thus, *K. madagascarica* is not conspecific with *K. salicornioides* given the genetic affinity between the Malagasy specimens, distinct ecology, and differences in floral morphology. Instead, we interpret both of these species as specialised regional endemics.

Korthalsella arthroclada from Western Australia, which is parasitic on *Melaleuca lanceolata* Otto (Myrtaceae) (Cranfield, 2002), was considered to be possibly conspecific with *K. dacrydii* (Watson, 2011), as both species have acute leaves. However, *K. dacrydii* uses quite different hosts, being the only species in the genus that parasitizes gymnosperms (*Dacrydium* Sol. ex G.Forst. and *Podocarpus* L'Her ex Pers.). The ITS and plastid phylogenies show that these species are not closely related (lineage C and clade E_1 in Fig. 3). *Korthalsella arthroclada* is a much larger species with distinctive yellowish-green branches (Fig. 5A) compared to the smaller *K. dacrydii* (Fig. 5B). *Korthalsella arthroclada* has a single row of female flowers in each axil (Cranfield, 2002) compared to several female flowers developing in more than one row in *K. dacrydii* (Fig. 5C). Morphological examination of *K. dacrydii* flowers shows that male flowers in this species have a distinctive synandrium with a raised central pore (Fig. 5D), whereas the central pore in *K. arthroclada* is not raised.

Molvray's (1997) concept of *Korthalsella japonica* is also not supported by the molecular phylogenetic results. For example, *K. japonica* subsp. *brassiana* and *K. grayi* (both Clade E_1) from Queensland, and *K. leucothrix* (Clade D_3) from southern and western Australia are not conspecific with Asian collections of *K. japonica* (Clade E_3) as considered by Molvray

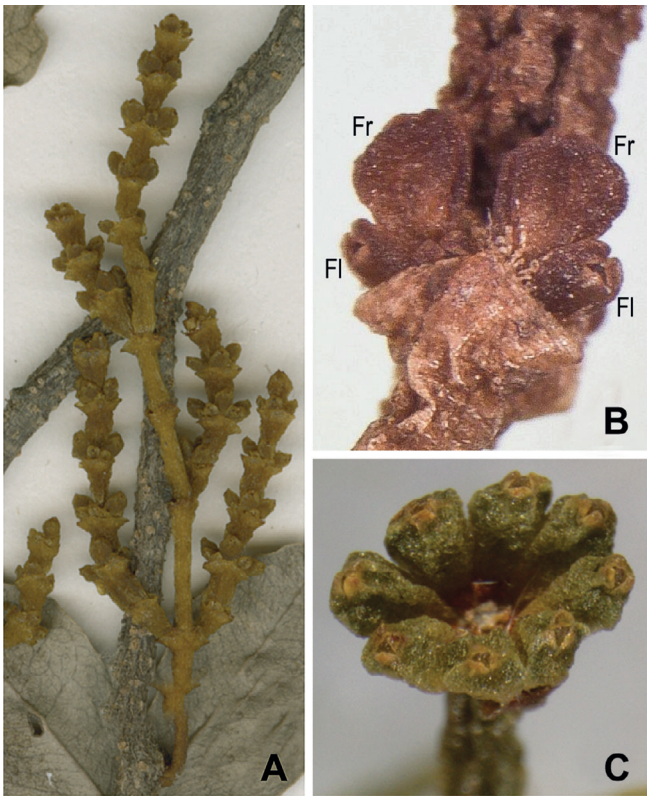

Fig. 4. *Korthalsella madagascarica* is distinct from *K. salicornioides*. **A**, *K. madagascarica* parasitic on *Cynometra* (Fabaceae) (*Jongkind & al. 3529* [MO], photo courtesy of Folkert Aleva); **B**, Developing fruits (Fr) and newly emerging flowers (Fl) of *K. madagascarica* (photographed by Sarah Bollendorf from *Humbert 14060* isosyntype [B]); **C**, Developing fruits of *K. salicornioides* (apical part of stem removed, photo by Amir Sultan). — Scale bars = 1 mm.

(1997). Specimens identified as *Korthalsella japonica* (K26) from Madagascar and the *K. japonica* (including *K. opuntia*) collections from the Mascarenes (Clade D_2 in Fig. 3) are also separated from the Asian *K. japonica* collections. We propose that the name *K. japonica* should be restricted to the Asian material (Clade E_3). Certain taxa thus require nomenclatural changes, but these will be dealt with in a separate article.

Collections of New Caledonian *K. dichotoma* were paraphyletic within the Norfolk Island–New Caledonia clade. *Korthalsella disticha* from Norfolk Island has overall larger dimensions with larger, dark olive-green internodes compared to smaller, yellow/green internodes in *K. dichotoma*. Danser (1937) recognised two forms of *K. dichotoma*. The typical form has obovate to lanceolate-obovate internodes, whereas *K. dichotoma* var. *balansae* (Tiegh.) Danser has oblong-lanceolate internodes (Danser, 1937). A collection from New Caledonia included in the current study (*Munzinger 643g*, K51) matches the description of *K. dichotoma* var. *balansae*, whereas another collection (*Callmander 911*, K50) matches the typical form of this species. *Korthalsella disticha* and *K. dichotoma* were considered conspecific by Barlow (1996), however, he noted that New Caledonian

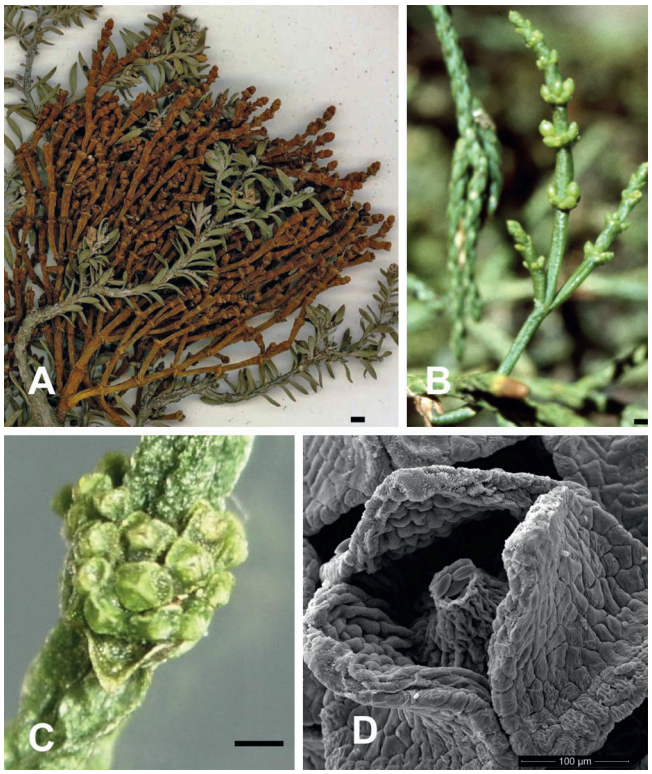

Fig. 5. *Korthalsella arthroclada* and *K. dacrydii* are not conspecific. **A**, *K. arthroclada* (*Marchant 76/127* [PERTH], photo courtesy of David Watson and Raymond Cranfield); **B**, *K. dacrydii* parasitic on *Podocarpus imbricata* (Podocarpaceae) in Gunung Gede Pangrango National Park, West Java (photo by John Dransfield); **C**, Floral cluster of *K. dacrydii* showing multiple female flowers associated with male flowers (photo by Amir Sultan); **D**, SEM of *K. dacrydii* male flower showing raised synandrium (photo by Amir Sultan and Doug Hopcroft). — Scale bars A–C = 1 mm, D = 100 µm.

collections were polymorphic. *Korthalsella disticha* and *K. dichotoma* possibly share a common ancestry followed by speciation on Norfolk Island and New Caledonia. We propose that Danser's (1937) taxonomy be followed regarding the distinction of *K. disticha* and *K. dichotoma*, including the recognition of varieties within the latter.

Additional complexities arise within taxa from islands of the eastern Pacific (Clade F). Danser (1937, 1940) recognised distinct morphological varieties within Hawaiian *K. latissima* and *K. cylindrica* and also considered *K. complanata* to be a highly polymorphic species. A collection of *K. latissima* (304) and a collection of *K. platycaula* (302) cluster together and are both from Kauai, while the *K. latissima* (309) and *K. platycaula* (307) from Oahu are in another clade along with *K. complanata* and *K. degeneri* Danser, which are also from Oahu. The present study shows that Hawaiian material identified as *K. platycaula* is phylogenetically distinct from material identified as this species collected in Tahiti (the type locality). Thus, there are apparently taxa in the *K. platycaula* complex found in the North Pacific (Hawaii) that are different from those in the South Pacific (from Fiji, Niue, the Cook Islands to the Austral, Society, and Marquesas Island groups in French Polynesia). Further studies of this widespread species (Fig. 1) might necessitate the reinstatement of certain *Korthalsella* species described by Brown (1935) that were placed in synonymy under *K. platycaula* by Danser (1937, 1940). Additional collections and study of *K. platycaula* throughout the Pacific are needed before taxonomic changes are made.

In some cases, collections with distinct morphology from the same geographical region were genetically very similar. For example, *Korthalsella lindsayi* (New Zealand) has obovate internodes and produces single axillary and apical inflorescences mostly in twos and threes, while *K. clavata* (New Zealand) has much narrower spathulate internodes and a solitary apical inflorescence. Despite these very different morphologies, genetic data indicate they are not strictly monophyletic. This may be the result of occasional gene flow between populations when the two species occur in sympatry. Both of these species also significantly differ in their host preferences (Sultan & al., 2018).

This study confirms that most *Korthalsella* species are specialised regional endemics and geographically proximal species are more closely related to one another than morphology suggests given the frequent instances of parallelism in this group. In a phylogenetic study of *Arceuthobium* M.Bieb. (Viscaceae), Nickrent & al. (2004, using ITS and *trnT-L-F* data) also found that Old and New World species were phylogenetically distinct, thus rendering the subgenus *Arceuthobium* paraphyletic. Similarly, Maul & al. (2019) showed that morphology, geographic distribution and host preference in *Viscum* L. were all poor indicators of phylogenetic relatedness.

Danser's (1937, 1940) sectional arrangement is not supported because these do not form clades within any of the molecular phylogenies, consistent with the findings of Molvray & al. (1999). For example, within the New Zealand clade, *K. salicornioides* has decussate cladotaxy and inflorescences that are not sharply distinct from the vegetative branches (section *Korthalsella* in Danser, 1937, 1940), whereas *K. clavata* and *K. lindsayi* (section *Heterixia* in Danser, 1937, 1940) have distichous cladotaxy and specialised inflorescences (Fig. 3). Molvray & al. (1999) considered *K. salicornioides* to be a specialised form of the section *Heterixia* in which vegetative branches have secondarily become terete. Similarly, within the eastern Australian/Lord Howe Island, South Pacific and Hawaiian clades, *K. dacrydii*, *K. horneana* and *K. remyana* have decussate cladotaxy (section *Korthalsella* in Danser, 1937, 1940), and the remaining taxa have distichous cladotaxy (section *Bifaria* in Danser, 1937, 1940) (Fig. 3). The New Zealand, Indian Ocean Basin, eastern Australia/Lord Howe Island, South Pacific, and Hawaiian clades have both flattened-stemmed and cylindrical-stemmed forms. Thus, flattened- and terete-stemmed forms have evolved independently multiple times in several clades. Mistletoes in the tribe Phoradendreae (Viscaceae) also have defied classification based on morphology. Ashworth (2000b) found that the three major clades identified in the molecular study of this tribe could not be readily characterised

morphologically. Similarly, in a molecular phylogenetic study of the North American species of *Phoradendron* Nutt., Ashworth (2000a) found that species lacking cataphylls were polyphyletic given the divergent position of *P. californicum* Nutt. relative to other species lacking cataphylls. That study also showed a sister relationship between *P. rhipsalinum* Rzed. and *P. brachystachyum* (DC.) Nutt. that was not evident from morphology or host associations.

This study shows that there is need for extensive further sampling of *Korthalsella* throughout its range, but especially from the South Pacific islands including south-eastern Polynesia and New Caledonia, mainland Africa, Madagascar and the Comoros, and that a complete taxonomic revision of the genus will be needed, as was also suggested by Molvray & al. (1999). While cladotaxy and internode characteristics are not reliable characters in terms of determining phylogenetic affinities within the genus, these can still be useful in regional identification. Additional characters, such as flower number in each floral cluster and inflorescence characters, may prove to be useful in conjunction with the host range of each species.

Taxonomic implications. — Based on the current evidence, the species concepts of Danser (1937, 1940) and Barlow (1983a) are generally supported rather than those of Molvray (1997). As an attempt to clarify species delimitations in the genus, we suggest here a number of taxonomic conclusions grouped by geographical regions based on the molecular results and following the careful study of existing specimens at B, G, MO and P. Formal taxonomic changes will occur in a separate manuscript.

Africa, Madagascar and western Indian Ocean islands. — As mentioned above, *Korthalsella japonica* is restricted to Asia and is not present in this region. Danser (1937) noted that amongst the specimens of *K. opuntia* var. *gaudichaudii* (Tiegh.) Danser and of *K. opuntia* var. *richardii* (Tiegh.) Danser that he studied, there were several that showed transitions towards other varieties. In the Mascarene Islands, Philcox (1982) also accepted three varieties within *Korthalsella opuntia*: var. *gaudichaudii*, var. *bojeri* (Tiegh.) Danser and var. *richardii*. *Korthalsella opuntia* var. *gaudichaudii* and var. *richardii* differ by having much broader internodes in the former, with usually 5 prominent ribs as opposed to much narrower internodes and fewer (1–3) ribs in the latter. Both of these taxa have similar ITS sequences. Perhaps these morphologies have evolved recently. *Korthalsella opuntia* var. *gaudichaudii* and var. *richardii* were also recorded from Madagascar (Balle, 1964) where two endemic species are also recorded: *K. madagascarica* and *K. taenioides* s.str. (Callmander & al., 2010). The collection *Callmander & al. 640* (K26) from NW Madagascar, previously determined as *K. japonica* (Callmander & al., 2010), may possibly represent a new taxon. The status of *K. humblotii* (Tiegh.) Engl. described from the Comoro archipelago remains to be studied.

Very few *Korthalsella* collections exist from mainland Africa, and none were able to be included in the phylogenetic analyses. While *K. opuntia* var. *gaudichaudii* and var. *richardii* are very likely present (Polhill & Wiens, 1998), the status of *K. binii* Pic.Serm. (placed in synonymy with *K. japonica* by Polhill & Wiens, 1998) described from Ethiopia remains to be studied.

Australia. — The treatment of the Australian species of Barlow (1983a) is mainly supported except that we suggest that *Korthalsella brassiana* Blakely should be accepted at the species level and not as a subspecies of *K. japonica* as this species is distinct from the core of *K. japonica* from Asia. The *Korthalsella rubra* complex still needs further investigation to better understand the status of *K. rubra* subsp. *geijericola*. The recently described *K. arthroclada* from Western Australia (Cranfield, 2002) should be considered a good species endemic to Australia.

Pacific Islands. — Nelson & Friday's (2009) illustrated account for Hawaii largely agrees with the results of this study. Six species occur on the archipelago (Fig. 1). However, *Korthalsella platycaula* is probably restricted to the South Pacific and is likely not in Hawaii, but further study of this widespread species is needed. Additional study of species in the Pacific islands is needed to better understand their morphological diversity in the region. *Korthalsella salicornioides* is restricted to New Zealand. At least two species occur in New Caledonia, but these also require further investigation. *Korthalsella amentacea* is an enigmatic species collected on Île Art (Belep archipelago), a micro-hotspot bearing high plant micro-endemism (Gâteblé & al., 2019). Its affinity with related *K. papuana* needs to be investigated.

■ AUTHOR CONTRIBUTIONS

AS, AWR, and JAT designed the study. AS and JAT generated sequence data and conducted phylogenetic analyses. JYM contributed specimens to the study and provided input on the manuscript. MWC contributed specimens to the study and with PBP provided input on the manuscript, especially on the taxonomic implications of the phylogenetic analyses. AS wrote the paper with contributions from AWR, JYM, PBP, MWC, and JAT.

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Appendix 1. Voucher information for *Korthalsella* and *Ginalloa* species included in the study.

Taxon, DNA extraction code Kxxx for newly sequenced *Korthalsella* samples, collector and collection number (herbarium code), locality, host species, ITS, and *trnL-F* GenBank accession numbers, respectively. An asterisk (*) indicates a sequence from Molvray & al. (1999), Papadopulos & al. (2011), or Sultan & al. (2018); all other sequences are new.

Ginalloa linearis Danser, *Coode 6811* (L 200671), Malaysia, Brunei, Belait District, Host: *Croton* sp. (Euphorbiaceae), MK497830, MK514226. ***Korthalsella aoraiensis*** (Nadeaud) Engl., K227: *Meyer 3175* (MPN 44716), Society Islands, Tahiti, trail to Mt. Aorai, Host: *Metrosideros collina* A.Gray (Myrtaceae), MK497818, MK514227. ***K. arthroclada*** Cranfield, K223: *Marchant 76/127* (PERTH 7399081), Western Australia, Lake Logue, Host: *Melaleuca lanceolata* (Myrtaceae), MK497805, MK514228. ***K. breviarticulata*** (Tiegh.) Danser, K232: *Cause s.n.* (BRI AQ0771489), Australia, Queensland, Boonah, Host: *Citrus* sp. (Rutaceae), MK497824, MK514229. ***K. clavata*** Cheeseman, K16: *Sultan & Robertson s.n.* (MPN 47748), New Zealand, South Island, Castle Hill Basin, Host: *Coprosma propinqua* A.Cunn. (Rubiaceae), MK500048, MK514230; K181: *P.J. de Lange 7839* (AK 304816), New Zealand, North Island, Whakamaru, Mangakowhiriwhiri Gorge, Host: *Coprosma propinqua*, MG229899*, MK514231. ***K. complanata*** (Tiegh.) Engl., *Molvray 308* (MO), Hawaii, Oahu, Waialae ridge, Host: *Eugenia* sp. (Myrtaceae), AF051966*, AF055688*; *Molvray 313* (MO), Hawaii, Oahu, Kooau Mountains, Niu ridge, Host: *Eugenia* sp. (Myrtaceae), AF051967*, AF055689*. ***K. cylindrica*** (Tiegh.) Engl., *Molvray 303* (MO), Hawaii, Kauai, Pihea ridge trail, Host: *Metrosideros* (Myrtaceae), AF051960*, AF055682*; *Molvray 310* (MO), Hawaii, Oahu, Waianae Mountains, Kaala summit, Host: *Metrosideros* (Myrtaceae), AF051959*, AF055681*. ***K. dacrydii*** (Ridl.) Danser, K166: *Iskandar & al. EA 315* (MPN 47715), Java, Gunung Gede Pangrango National Park, trail above Cibodas Mountain Gardens, Host: *Podocarpus imbricatus* Blume (Podocarpaceae), MK497815, MK514233. ***K. degeneri*** Danser, K234: *Lau s.n.* (MPN 47722), Hawaii, Oahu, Host: *Sapindus oahuensis* Hillebr. ex Radlk. (Sapindaceae), *Pouteria* sp. (Sapotaceae), MK497814, MK514232. ***K. dichotoma*** (Tiegh.) Engl., K50: *Callmander 911* (MO), New Caledonia, Port Boisé. Host: *Halfordia kendack* Guillaumin (Rutaceae), MK497822, MK514234; K51: *Munzinger 643g* (NOU), New Caledonia, Province Nord, Hienghène, La Guen. Host: unknown, MK497820, MK514235. ***K. disticha*** (Endl.) Engl., K28: *Petterson & McCoy s.n.* (MPN 24043), Norfolk Island, Mt Pitt, Host: Norfolk Island "bush lemon" [*Citrus jambhiri* Lush.] (Rutaceae), MK497821, MK514236. ***K. emersa*** Barlow, *Papadopulos AP710* (NSW970409), Australia, Lord Howe Island, Max Nichols track, Host: *Cryptocarya triplinervis* (Lauraceae), JF950771*, JF950942*. ***K. geminata*** (Korth.) Engl., K175: *Awa & Lee S50969* (KEP), Borneo, Sarawak, Bario, Gunung Batu Buli, Host: unknown, MG229893*, MK514237; K226: *Thomas s.n.* (E), Cambodia, Cardamon Mountains near Phnom Samkos, Host: *Garcinia* sp. (Clusiaceae), MK497808, MK514238. ***K. grayi*** Barlow, K173: *Zich & Harrington 652* (CNS 130825), Australia, Queensland, Mt Bellenden Ker, Host: *Symplocos ampulliformis* C.T.White (Symplocaceae), MK497823, MK514239. ***K. horneana*** Tiegh., K225: *Sultan & Asotasi s.n.* (MPN 47714), Samoa, Upolu, Mt Sina'ele, Host: *Dysoxylum huntii* Merr. ex Setch. (Meliaceae), MK497817, MK514240. ***K. japonica*** (Thunb.) Engl., K165: *Iskandar & al. EA314* (MPN 47713), Java, Cibodas Mountain Gardens, Host: *Altingia excelsa* Noronha (Altingiaceae), MK497827, MK514241; K237: *Sultan s.n.* (MPN 48363), Pakistan, Athmuqam, Neelum valley, Azad Jammu and Kashmir, Host: *Quercus* sp. (Fagaceae), MK497826, MK514245; K26: *Callmander & al. 640* (MO), Madagascar, Antsiranana, DIANA region, Host: *Vaccinium* sp. (Ericaceae), MK497831, –; KL228: *Klackenberg & Lundin 228* (K), India, Western Ghats, Tamil Nadu, Host: *Rhododendron* sp. (Ericaceae), AF051974*, AF055696*; INO: *Inouye s.n.* (K), Japan, Oshina Island, Host: unknown, AF051975*, AF055697*. ***K. japonica*** subsp. ***brassiana*** (Blakely) Barlow, 358: *Molvray 358a* (MO), Australia, Queensland, Mt Lewis, Host: *Rapanea* (Primulaceae), *Uromyrtus* (Myrtaceae), AF051968*, AF055690*. ***K. japonica*** (***K. opuntia*** var. ***bojeri*** (Tiegh.) Danser), K230: *Pynee & Bone s.n.* (MAU 24845), Mascarenes, Mauritius, Mt Le Pouce, Host: *Eugenia* sp. (Myrtaceae), MK497811, MK514243; LR19: *Lorence R19* (K), Mascarenes, Réunion, Cilaos near les Thermes, Host: *Eugenia* sp. (Myrtaceae), AF051972*, AF055694*. ***K. japonica*** (***K. opuntia*** var. ***gaudichaudii*** (Tiegh.) Danser), K231: *Pynee & Chitbauhaal s.n.* (MAU 24307), Mascarenes, Mauritius, Plaine Champagne, Host: *Nuxia verticillata* Lam. (Stilbaceae), MK497813, MK514244. ***K. japonica*** (***K. opuntia*** var. ***richardii*** (Tiegh.) Danser), K167: *Pynee & Beetun s.n.* (MAU 24938), Mascarenes, Mauritius, Mt. Cocotte, Host: *Nuxia verticillata* (Stilbaceae), MK497812, MK514242; STR: *Strasberg s.n.* (K), Mascarenes, Réunion, Host: unknown, AF051973*, AF055695*. L1967: *Lorence 1967* (K), Mascarenes, Mauritius, Piton de la Rivière Noire, Host: *Nuxia* sp. (Stilbaceae), AF051971*, AF055693*. ***K. latissima*** (Tiegh.) Danser, 304: *Molvray 304* (MO), Hawaii, Kauai, Pihea-Alakai trail, Host: *Clermontia* (Campanulaceae), *Pelea* (Rutaceae), AF051965*, AF055687*; 309: *Molvray 309* (MO), Hawaii, Oahu, Waianae Mountains, Kaala summit, Host: *Myrsine* (Myrsinaceae), AF051962*, AF055684*. ***K. leucothrix*** Barlow, K224: *D.J. Edinger & al. DJE2479A* (PERTH 05853818), Western Australia, Track to Baker Lake, Host: *Acacia aneura* F.Muell. ex Benth. (Fabaceae),

Appendix 1. Continued.

MK497810, MK514246. ***K. lindsayi*** (Oliv. ex Hook.f.) Engl., K74: *Sultan & al. s.n.* (MPN 47934), New Zealand, North Island, Coles Bush, near Rongotea, Host: *Coprosma rigida* Cheeseman (Rubiaceae), MK500047, MK514247; K108: *Sultan & Mahmood s.n.* (MPN 47730), New Zealand, South Island, Aramoana, Host: *Myrsine australis* (A.Rich.) Allan (Primulaceae), MK497807, MK514248. ***K. madagascarica*** Danser, K235: *Jongkind & al. 3529* (MO), Madagascar, Mahajanga, Tsingy de Bemaraha, South of Manambolo river, Host: *Cynometra* sp. (Fabaceae), MK497804, MK514249. ***K. papuana*** Danser, 359: *Molvray 359* (MO), Australia, Queensland, Mt Lewis, Hosts: *Acmena* sp., *Syzygium* sp. (Myrtaceae), AF051951*, AF055673*. ***K. platycaula*** (Tiegh.) Engl., K229: *Meyer 3177* (MPN 47712), Society Islands, Tahiti, Anaorii Plateau, Papenoo Valley, Host: *Crossostylis biflora* J.R.Forst. & G.Forst. (Rhizophoraceae), MK497828, MK514250; K238: *Meyer 3238* (MPN 48364), Society Islands, Tahiti, trail to the Mille Sources, Tuauru valley, Host: *Neonauclea forsteri* (Seem. ex. Havil.) Merr. (Rubiaceae), MK497829, MK514251; 302: *Molvray 302* (MO), Hawaii, Kauai, Waininiua trail, Host: *Nestegis* (Oleaceae), AF051963*, AF055685*; 307: *Molvray 307* (MO), Hawaii, Oahu, Waianae Mountains, Kaala, Host: *Planchonella* sp. (Sapotaceae), AF051964*, AF055686*. ***K. remyana*** Tiegh., 312: *Molvray 312* (MO), Hawaii, Oahu, Koolau Mountains, Host: *Diospyros* sp. (Ebenaceae), AF051961*, AF055683*. ***K. rubescens*** (Tiegh.) Lecomte, K228: *Meyer 3178* (MPN 47721), Society Islands, Moorea, Paoroa valley, trail to Mt Tohiea, Host: *Metrosideros collina* A.Gray (Myrtaceae), MK497816, MK514252. ***K. rubra*** subsp. ***rubra*** (Tiegh.) Engl., K233: *Jensen 1325* (BRI AQ771312), Australia, Queensland, Gadgarra, Host: *Elaeocarpus grandis* F.Muell. (Elaeocarpaceae), MK497819, MK514254; LHI: *Papadopulos AP284* (NSW786344), Australia, Lord Howe Island, lower road, Host: unknown, JF950772*, JF950891*. ***K. rubra*** subsp. ***geijericola*** Barlow, K177: *Brown & al. 2002/42* (AK 297162), Australia, New South Wales, 52 km SE of Coonamble, Host: *Acacia* sp. (Fabaceae), MK497825, MK514253; 361: *Molvray 361* (MO), Australia, New South Wales, Croppa Creek, Hosts: multiple hosts, AF051970*, AF055692*; 362: *Molvray 362* (MO), Australia, New South Wales, Robertson, Host: *Doryphora* (Atherospermataceae), AF051969*, AF055691*. ***K. salicornioides*** (A.Cunn.) Tiegh., K30: *Sultan s.n.* (MPN 49550), New Zealand, North Island, Bay of Islands, Kerikeri Inlet Road, Host: *Leptospermum scoparium* s.l. (Myrtaceae), MK497806, MK514255; K168: *Robertson s.n.* (MPN 49551), New Zealand, South Island, Kaiteriteri, Host: *Kunzea ericoides* s.l. (Myrtaceae), MK500046, MK514256. ***K. taenioides*** (Comm. ex Juss.) Engl., K25: *Antilahimena & al. 7526* (MO), Madagascar, Ambotavy near Moramanga, Host: *Rhodolaena bakeriana* Baill. (Sarcolaenaceae), MK497809, MK514257.