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An Expanded *Metrosideros* (Myrtaceae) to Include *Carpolepis* and *Tepualia* Based on Nuclear Genes

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Abstract−The genus *Metrosideros* (Myrtaceae) comprises 50-60 species found largely across the Pacific Islands. The relationships within this genus, including the circumscriptions of the subgenera *Mearnsia* and *Metrosideros* and their relationships with the other members of the tribe Metrosidereae (namely the New Caledonian endemic genus *Carpolepis* and the South American *Tepualia*), are poorly understood. Phylogenetic analyses were carried out using previously published ITS sequences, covering most species of the tribe, and new sequences of five single-copy nuclear genes with a reduced taxon sampling. The independent and combined analyses of the five nuclear genes using a range of approaches, including Bayesian single-gene, concatenated (MrBayes), concordance (BUCKy) and coalescent (*BEAST) analyses, yielded different topologies, indicating important conflicts among phylogenies based on individual genes. The deep relationships within the tribe Metrosidereae remain poorly resolved, but our results indicate that the species of *Carpolepis* and *Tepualia* are likely nested in the genus *Metrosideros*. A broad circumscription of the genus *Metrosideros* is therefore adopted, and the new combinations ***Metrosideros laurifolia* var. *demonstrans***, ***Metrosideros tardiflora*** and ***Metrosideros vitiensis*** are here published.

Keywords−*Carpolepis*, *Metrosideros*, Myrtaceae, Pacific, phylogeny, *Tepualia*

Myrtaceae is a large family of predominantly tropical trees and shrubs with ca. 140 genera (Wilson, 2011) and over 5000 species (Govaerts et al., 2015), including many economically important species used for timber, fruit, spices, and as ornamentals. Generic limits are still unresolved for some members of this family, e.g. *Syzygium* Gaertn. (Biffin et al., 2006), *Rhodomyrtus* (DC) Rchb. (Snow et al., 2011). Recent molecular phylogenetic studies at the family level have delimited a number of tribes (Wilson et al., 2005; Biffin et al., 2010; Wilson, 2011) that allow more targeted follow-on studies at the tribal level to assess generic limits. Such approaches have already been applied to tribe Syzygieae (Biffin et al., 2006), Myrteae (Lucas et al., 2007), Melaleuceae (Edwards et al., 2010) and Backhousieae (Harrington et al., 2012), leading to changes in generic boundaries, often broadening some genera to include other smaller ones.

Metrosideros Banks ex Gaertn. (tribe Metrosidereae) is a medium-sized genus (ca. 52 species) found primarily on the Pacific islands, including the Philippines and New Guinea, with an outlying species in South Africa (Govaerts et al., 2015). The genus is interestingly absent from mainland Australia. Most species have potential as ornamentals, particularly pōhutukawa (*Metrosideros excelsa* Sol. ex Gaertn.) from New Zealand. *Metrosideros* is particularly ecologically important in Hawai'i, where the widespread and highly variable *M. polymorpha* Gaudich. dominates the canopies of most native forests. The genus is also emerging as a model for the study of speciation in trees, in particular sympatric speciation on Lord Howe Island (Papadopulos et al., 2011) and incipient ecological speciation in Hawai'i (Stacy et al., 2014).

Despite a number of phylogenetic works published on *Metrosideros*, its relationships with other genera of Metrosidereae remain poorly understood. Besides *Metrosideros*, the tribe Metrosidereae also includes the New Caledonian endemic *Carpolepis* (J. W. Dawson) J. W. Dawson (three species) and the monotypic *Tepualia* Griseb. from southern Chile and

Argentina. The genus *Mearnsia* Merr. sometimes is segregated from *Metrosideros* (Wilson, 2011), although regional monographs did not recognize this genus (Allan, 1961; Dawson, 1992). Besides recognizing *Mearnsia*, Briggs and Johnson (1979) also suggested splitting *Metrosideros* in a number of smaller genera that have never been formally described with one exception. The species of *Metrosideros* subgenus *Mearnsia* section *Adnatae* J.W. Dawson are now included in the genus *Thaleropia* Peter G. Wilson (Wilson, 1993), which has been excluded from the tribe Metrosidereae and placed in the tribe Tristanieae (Wilson, 2011).

Most phylogenetic studies carried out on the genus *Metrosideros* have not addressed taxonomic issues. For example, Wright (2000a) focused on dispersal of *Metrosideros* subgenus *Metrosideros* across the Pacific using ITS sequence data, whereas a later study (Wright, Gray, and Gardner, 2003) focused on the rate of molecular evolution in ITS and ETS sequences within the subgenus *Mearnsia*. A phylogenetic study based on ITS data focusing on the New Caledonian *Metrosideros* (Wright et al., 2000b), including a single species from New Zealand, suggested that *Carpolepis* may be nested within *Metrosideros*, and that subgenus *Mearnsia* may not be monophyletic. The first comprehensive phylogeny of the genus *Metrosideros* not restricted to a subgenus or archipelago focused on dating the Cape endemic *Metrosideros angustifolia* (L.) Sm. (Warren and Hawkins, 2006, supplementary data, ITS sequence). *Tepualia* was included in a later molecular phylogenetic study using ITS, ETS *matK*, and *psbA-trnH*, and found to be close to *Metrosideros* (Lucas et al., 2007). More recently, Papadopulos et al. (2011, supplementary data) conducted a phylogenetic analysis of *Metrosideros* using ETS, ITS, 5S, *rps16*, and *trnL-trnF* with broad sampling across taxa that included *Tepualia*, but which focused primarily on the origin of the two species endemic to Lord Howe Island. No previous molecular phylogenetic study included comprehensive sampling of *Metrosideros* (subgenera *Metrosideros* and *Mearnsia*), as well as both *Carpolepis* and *Tepualia*. In addition, previous studies (Wright et al., 2000a;

Wright et al., 2001) revealed two distinct and distant clades within *M. collina* (J.R. Forst. & G. Forst.) A. Gray, the only species of *Metrosideros* found on multiple archipelagoes. The taxonomic limits of this widespread species warrant further study.

In this study we re-analyzed ITS sequence data from GenBank available for most species of tribe Metrosidereae. We also sequenced five single-copy nuclear genes for a subset of taxa to address the monophyly of *Metrosideros* subgenus *Metrosideros* and subgenus *Mearnsia*, and the distinctiveness of *Carpolepis* and *Tepualia*. In addition, we aimed to assess the delimitation of *M. collina*, including its possible division into multiple species.

MATERIALS AND METHODS

ITS Sequence Analysis−We downloaded ITS sequences from GenBank for all species of tribe Metrosidereae (*Metrosideros*, *Carpolepis*, and *Tepualia*), including multiple accessions for *M. collina* (Appendix 1). Sequences were available for all species of the tribe currently recognized in the World checklist of Myrtaceae (Govaerts et al., 2015) with the exception of *M. arfakensis* Gibbs, *M. parallelinervis* C.T. White, and *M. regelii* F. Muell., all from New Guinea, which have never been included in any molecular phylogenetic analysis. In Wright et al. (2003) all species from New Guinea and the Philippines are part of a well-supported monophyletic group, and the three unsampled species may be expected to fall in this clade. Samples of *Thaleropia*, *Tristania* R. Br. (tribe Tristanieae) and *Cloezia* Brongn. & Gris were included as outgroups and the tree was rooted with *Syzygium*.

ITS sequences were aligned with MUSCLE within MEGA6 (Tamura et al., 2013), and the alignment was deposited in TreeBASE (study number TB2:S16972). The best-fit evolution model was GTR + I + γ according to jModeltest analysis (Posada, 2008). Phylogenetic analysis

was conducted in MrBayes (Ronquist and Huelsenbeck, 2003) running one-million generations of Markov Chain Monte Carlo (MCMC), sampling one tree every 1,000 generations, using the gene-specific substitution model and default settings otherwise. Convergence of runs and adequate MCMC sampling were checked using Tracer (Rambaut and Drummond, 2007). The burn-in period per run was then set to 250,000 generations, and the remaining trees were used to construct a half-compatible consensus tree and its associated estimated posterior probabilities.

Single-Copy Nuclear Genes—

SEQUENCING−As part of a larger study on the phylogenomics of *Metrosideros*, five single-copy nuclear genes (exon-primed intron crossing) were used here on a smaller sample of tribe Metrosidereae (Appendix 2). We included all genera of tribe Metrosidereae and both subgenera of genus *Metrosideros*; the same accessions were used for all five genes. Primers (Table 1) were designed following the protocols described in a previous study (Pillon et al., 2014). The loci were amplified using Fluidigm access arrays (48 × 48 well fluidigm chip) and sequenced on a quarter Miseq plate (sequencing v3, 600 cycles) at the Institute for Bioinformatics and Evolutionary Studies (IBEST, University of Idaho) as part of a larger study involving additional genes and accessions from the Hawaiian Islands. With this sequencing procedure, alleles of heterozygote accessions were readily separated (phased). DNA extracted from silica-dried leaves of *Carpolepis laurifolia* (Brongn. & Gris) J. W. Dawson and *Metrosideros cacuminum* J. W. Dawson was too degraded or diluted for successful sequencing with the above procedure, so was amplified and sequenced using standard Sanger sequencing (see Pillon et al., 2014, for full protocols for DNA extraction and PCR amplification). Those sequences were subsequently phased using DnaSP (Librado and Rozas, 2009) using the default settings.

INDIVIDUAL-GENE BAYESIAN PHYLOGENETIC ANALYSIS–All analyses were executed with phased alleles. The best-fit evolution models for each locus were HKY (*MeNu40*), HKY + I (*MeNu42*), HKY (*MeNu55*), HKY + γ (*MeNu68*), and HKY (*MeNu74*). Analyses in GARD (Kosakovsky Pond et al., 2006), assuming no site-to-site rate variation, did not reveal any sign of recombination in any of the individual alignments. We ran one-million generations of MCMC in MrBayes (Ronquist and Huelsenbeck, 2003), sampling one tree every 1,000 generations and using gene-specific substitution models for each locus. Convergence of runs and adequate MCMC sampling were checked using Tracer, and the burn-in period per run was then set to 250,000 generations.

CONCATENATED BAYESIAN PHYLOGENETIC ANALYSIS–Multiple alleles within individuals were combined into a single sequence using IUPAC nucleotide codes. We ran one-million generations of MCMC in MrBayes, sampling one tree every 1,000 generations using gene-specific substitution models for all loci, unlinking substitution models, discarding a burn-in period of 250,000 generations, and default settings otherwise.

CONCORDANCE ANALYSIS– We carried out a concordance analysis in BUCKy (Ané et al., 2007; Larget et al., 2010) to detect common phylogenetic signals among the different nuclear genes that may display some conflicts. Alleles in heterozygotes were combined using IUPAC codes for ambiguous bases. We ran phylogenetic analyses in MrBayes for each gene independently, running 1,200,000 generations, sampling every 100 generations and discarding the first 200,000 generations. We ran four parallel concordance analyses in BUCKy with 10-million generations with priors (α) set to 2 for the analysis with four genes (*MeNu40*, *MeNu42*, *MeNu68*, and *MeNu74*) and 3 for the analysis with all five genes (as *MeNu55* was missing for *Carpolepis*), and default settings otherwise. A number of preliminary analyses were run to determine the number of concordant trees present in each dataset. Optimal values for α were determined as the ones yielding the highest prior

probability for the actual numbers of trees observed using R code available from http://ane-www.cs.wisc.edu/bucky/prior.html.

*BEAST ANALYSIS–We ran a phylogenetic analysis using phased alleles for all five genes in *BEAST within BEAST 2 (Bouckaert et al., 2014). The analysis was run twice using default settings (strict clock, population function constant, tree prior Yule), a chain of 200 million generations sampling every 20,000 generations, and a burn-in of 20 million generations. Adequate sampling and convergence of the two runs were checked in Tracer, and the two runs were then combined.

NETWORK ANALYSIS–We measured the pairwise genetic distance (number of substitutions) between phased alleles for each of the five single-copy nuclear genes using MEGA6 (Tamura et al., 2013). A single pairwise standardized distance matrix between taxa accounting for all five genes was obtained using POFAD (Joly and Bruneau, 2006), which was then used to build a network using the NeighborNet analysis in Splitstree (Huson and Kloepper, 2005; Huson and Bryant, 2006).

Taxonomic treatment–Type specimens were examined at K, and other type images were viewed online.

RESULTS

In the phylogenetic analysis based on ITS sequence data (Fig. 1), the tribe Metrosidereae is a well-supported monophyletic group with a deep polytomy. *Carpolepis* and subgenus *Metrosideros* (when including section *Neocaledonica*) are well-supported monophyletic groups, but subgenus *Mearnsia* (sections *Mearnsia*, *Calyptropetala*, and *Crystalla*) is not supported as a monophyletic group: taxa form multiple lineages that are unresolved with respect to the basal polytomy in the tribe, along with some samples

grouped with weak support with Carpolepis (Fig. 1). Section *Mearnsia* (including *M. albiflora* Sol. ex Gaertn., *M. halconensis* (Merr.) J. W. Dawson, and *M. porphyrea* Schltr.) and section *Calyptropetala* J.W. Dawson (including *M. operculata* Labill. and *M. perforata* (J. R. Forst. & G. Forst.) Druce) sensu Dawson (1976) are not monophyletic. As anticipated, *M. collina* is composed of two distinct groups, one comprising accessions from French Polynesia and the Cook Islands that are closely related to all Hawaiian and some New Zealand species, and the other comprising accessions from Vanuatu, Fiji, and Samoa.

All of the nuclear genes were successfully amplified and sequenced for our reduced taxon sampling, except *MeNu55* for *Carpolepis laurifolia*. Individual-gene analyses yielded somewhat different topologies (Fig. 2), particularly with respect to the relative positions of *Carpolepis*, *Tepualia*, and *Metrosideros angustifolia*, and the relative positions of *M. collina* (Samoa), *M. excelsa*, and *M. nervulosa* C. Moore & F. Muell. The three Hawaiian species (*M. macropus* Hook. & Arn., *M. polymorpha*, and *M. rugosa* A. Gray) and the Tahitian *M. collina* (east Polynesian *Metrosideros*) have almost identical sequences for all five genes, thus leaving their relationships unresolved. The BUCKy analysis indicated that three different tree topologies (i.e. three different gene groups) were present in both of the four-genes analysis (mean number of groups = 3.1, standard deviation = 0.249) and the five-gene analysis (mean = 3.0, SD = 0.016). *MeNu68* and *MeNu74* yielded concordant topologies in both analyses. *MeNu40* and *MeNu55* (not included in the four-gene analysis) yielded concordant topologies in the five-gene analysis.

Despite conflicts in tree topology based on the individual-gene analyses, the concatenated analysis (Fig. 2) yielded an almost fully resolved tree with all nodes supported by strong posterior probabilities, with just two exceptions: the unresolved relationships between Hawaiian and Tahitian *Metrosideros*, and the weakly supported position of *M. boninensis* (Hayata ex Koidz.) Tuyama. The latter species appeared as sister to the rest of the

tribe Metrosidereae, a relationship not recovered in any of the individual-gene analyses. The concatenated phylogenetic tree and primary concordance tree (Fig. 3) agreed at a number of nodes: a monophyletic group that includes species from Tahiti and the Hawaiian Islands (east Polynesian *Metrosideros*), and a monophyletic group including *Carpolepis*, *Tepualia*, *M. angustifolia*, and *M. cacuminum* (Figs. 2, 3). The three analyses (those based on concatenation, *BEAST and BUCKy) yielded different topologies for the relationships among *M. collina* from Samoa, *M. excelsa*, *M. nervulosa*, and the East Polynesian *Metrosideros*, as well as for the relationships among *Carpolepis*, *Tepualia*, *M. angustifolia*, and *M. cacuminum*. *Metrosideros boninensi*s was sister to the rest of the genus *Metrosideros* in the concatenated analysis, sister to the rest of the subgenus *Metrosideros* in the *BEAST analysis, and sister to the Samoan *M. collina* in the BUCKy analysis.

The Splitstree network (Fig. 4) further supported the conflicts observed among the various phylogenetic analyses. *Metrosideros boninensis* has an intermediate position between the rest of the subgenus *Metrosideros* and the group composed of *Carpolepis*, *Tepualia*, *M. angustifolia*, and *M. cacuminum*. The relatively large loop observed in the network between the Samoan *M. collina* and *M. excelsa* indicates that there are conflicts regarding their relative positions. *Carpolepis* also branches on a loop of the network between *M. angustifolia* (sister group in the concordance analysis) and *M. cacuminum* (sister group in the *BEAST analysis).

DISCUSSION

Our study reveals important conflicts among the tree topologies derived from different single-copy nuclear genes, thus illuminating the importance of careful analysis of such loci, particularly in combination. The blind concatenation of conflicting genes can yield

an almost fully resolved topology that is not recovered in any single-gene analysis. The different total-evidence analyses yielded different topologies, and none of them appears clearly preferred over the others. Bayesian coalescent analyses tend to yield low posterior probabilities (see Arbizu et al., 2014; Folk and Freudenstein, 2014, for other case studies). The concordance factor in Bayesian concordant analysis (BUCKy) tends to be well below 1 (see also Arbizu et al., 2014), and it is not clear beyond what threshold a node can be considered well supported. The network analysis may be more conservative since it is not entirely dichotomous, but it does not provide measures of confidence. A high frequency of gene conflicts in *Metrosideros* suggests that a large number of genes will be necessary to fully understand phylogenetic relationships within this genus, possibly because of ancient hybridization events (see Pillon et al., 2013, for another similar case in Gesneriaceae).

Despite significant conflicts among the nuclear genes, some patterns are consistently recovered that are in agreement with, or at least not contradicted by, the ITS-only phylogenetic analysis. *Carpolepis* is nested within *Metrosideros* although its sister group differs between ITS, *MeNu42*, and *MeNu74*. Dawson (1984) segregated *Carpolepis* from *Metrosideros* because of its yellow flowers and sympodial growth, two characters occasionally found in *Metrosideros* (Dawson, 1992); and its winged seeds, a character that is quite homoplasious within Myrtaceae (Wilson, 2011). *Tepualia* is recovered as either sister to *Metrosideros angustifolia* with strong support in analyses based on *MeNu40* and *MeNu55*, sister to *Metrosideros angustifolia* + *Carpolepis* with moderate support in analysis based on *MeNu74,* or as having an unresolved position within *Metrosideros* in analyses with other genes, including ITS. *Tepualia* was never recovered as sister to *Metrosideros*. The sister group relationship between *Tepualia* and *M. angustifolia* had previously been recovered in a cladistic analysis based on morphological characters (Wilson, 1996). Both have indeed white flowers, but so does the New Caledonia *M. operculata*, which is is not closely related to these two species. The genus *Tepualia* was distinguished from *Metrosideros* due to the

absence of broad protective scales in the vegetative bud, which are also missing in some species of subgenus *Mearnsia* (Dawson, 1972a, 1976). It is now known to also differ by its dicolporate pollen (Thornhill et al., 2012a), a character also found in the more distantly *Acmena* DC. (syn. *Syzygium*) and *Pileanthus* Labill. (Thornhill and Crisp, 2012); and the pairs of spherical vesicles flanking leaf bases (Dawson, 1972b), a character that is likely autapomorphic.

Maintaining *Carpolepis* and *Tepualia* as independent genera would likely require the splitting of *Metrosideros* into several smaller genera, some yet to be described, as has been recommended previously based on morphology (Briggs and Johnson, 1979). However, even in a narrow sense (*Metrosideros* subgen. *Mearnsia* sect. *Mearnsia* sensu Dawson, 1976), *Mearnsia* is not monophyletic according to ITS data, and most other groups distinguished by Briggs and Johnson (1979) are small if not monotypic, and have never been formally described taxonomically. Currently, little morphological or phylogenetic evidence supports the splitting of *Metrosideros* into numerous monophyletic groups, and the conflicts among the five nuclear genes examined here suggest that an improved understanding of evolutionary relationships with this genus will require data from a large number of loci. Adopting a broad concept of *Metrosideros* on the other hand would have a number of advantages. The genus would be clearly defined as the equivalent of the well-circumscribed tribe Metrosidereae. In terms of nomenclatural stability, only two combinations for names in *Carpolepis* are needed since the name *Metrosideros stipularis* (Hook. & Arn.) Hook. already exists for the species of *Tepualia*. A broadly defined *Metrosideros* would still be of moderate size (50-60 species), whereas narrow generic concepts would require the recognition of many small genera (some monotypic, e.g. *Tepualia*), many of which remain undescribed (e.g., probably at least one to accommodate the South African *M. angustifolia*). Proposed taxonomic changes associated with the expanded concept of *Metrosideros* are provided below.

Analyses of the single-copy nuclear genes also agree with the ITS analysis in the distinction of two components within the widespread *Metrosideros collina*. The plants from French Polynesia (where the type of the species was collected) and the Cook islands are close genetically to the plants from the Hawaiian Islands. Samples from Vanuatu, Fiji, and Samoa occur in a different part of the trees, although their closest relatives are yet unknown. The oldest name described for a plant in this area is *Metrosideros collina* var. *vitiensis* A. Gray (Smith, 1973), which is raised here to the species rank.

As newly circumscribed, *Metrosideros* includes ca. 60 species, mostly on the Pacific Islands, including New Guinea and the Philippines, with outlier species in South Africa and South America. The geographical origin of *Metrosideros* is difficult to determine with currently available data. Deep relationships within *Metrosideros* are poorly resolved, and the closest relatives of the African and American species are unknown. Relationships between Metrosidereae and the related tribes Backhousieae, Kanieae, Myrteae, Syzygieae and Tristaneae are also poorly resolved (Biffin et al., 2010). *Metrosideros* originated some time during the Cenozoic (Thornhill et al., 2012b), and its occurrence on most high Pacific islands, South Africa, and South America is likely explained by the capacity of its seeds to disperse by wind over long distances (Drake, 1992; Wilson, 1996).

TAXONOMIC TREATMENT

METROSIDEROS Banks ex Gaertn., Fruct. Sem. Pl. 1: 170 (1788), nom. cons.−TYPE. *Metrosideros spectabilis* Sol. ex Gaertn. (*typ. cons*.).

> *Agalmanthus* (Endl.) Hombr. & Jacquinot in J. S. C. Dumont d'Urville, Voy. Pôle Sud, Atlas (Dicot.): t. 1 (1843).−TYPE: *Agalmanthus umbellatus* (Cav.) Hombr. & Jacquinot. ("*umbellata*").

Ballardia Montrouz., Mém. Acad. Imp. Sci. Lyon, Sect. Sci., sér. 2, 10: 204 (1860). non *Balardia* Cambess. (1829). –TYPE: *Ballardia elegans* Montrouz.

Carpolepis (J.W.Dawson) J.W.Dawson, Bull. Mus. Natl. Hist. Nat., B, Adansonia 1984: 466 (1984 publ. 1985).–TYPE: *Carpolepis elegans* (Montr.) J. W. Dawson. syn. nov.

Mearnsia Merr., Philipp. J. Sci., C 2: 283 (1907).–TYPE: *Mearnsia halconensis* Merr.

Microsideros Baum.-Bod., Syst. Fl. Neu-Caledonien 5: 77 (1989), nom. inval. (no replaced synonym reference, Govaerts et al., 2015).

Tepualia Griseb., Abh. Königl. Ges. Wiss. Göttingen 6: 119 (1854).–LECTOTYPE (designated here): *Tepualia stipularis* (Hook. & Arn.) Griseb. syn. nov.

Under this new circumscription, *Metrosideros* is the sole member of tribe Metrosidereae (see Wilson et al., 2005, Wilson 2011, for a morphological description) and contains ca. 60 species. Apart from Dawson's (1992) revision for New Caledonia, recent revisions are unavailable for the Solomon Islands or New Guinea, the latter of which has the third-highest level of diversity after New Caledonia and New Zealand.

Metrosideros laurifolia Brongn. & Gris. var. **demonstrans** (Tison) Pillon comb. nov. Basionym: *Metrosideros demonstrans* Tison, Compt. Rend. Assoc. Franc. Avanc. Sci., Clermont-Ferrand 5: 462 (1877). –TYPE: NEW CALEDONIA. Mt Humboldt, feb. 1972, *Balansa 3407* (lectotype: by Dawson 1992, P [P00057638]!; isolectotypes: P [00057639, P00057640]!). *Carpolepis laurifolia* (Brongn. & Gris.) J. W. Dawson var. *demonstrans* (Tison) J. W. Dawson, Bull. Mus. Natn. His. Nat., Paris, ser. 4, sect. B, Adansonia 6(4): 468 (1984, publ. 1985).

METROSIDEROS STIPULARIS (Hook. & Arn.) Hook. f., Bot. Antarct. Voy. I. (Fl. Antarct.). 2: 275 (1846). *Myrtus stipularis* Hook. & Arn., Bot. Misc. 3: 316 (1833). *Tepualia stipularis* (Hook. & Arn.) Griseb., Sys. Bemerk. 31 (1854). *Nani stipularis* (Hook. & Arn.) Kuntze, Revis. Gen. Pl. 1: 242 (1891). –TYPE: CHILE. Chiloe, *Cuming 32* (lectotype: designated here, K [000565021]!; isolectotypes: K!, E!; remaining syntypes: *Cuming 33*, K!, E!).

Tepualia philippiana Griseb., Sys. Bemerk. 32 (1854). –TYPE: CHILE. March 1852, *Philippi 89* (lectotype: designated here, GOET!; Isolectotypes: K! GOET!, P [P05235964, P05235947]!, S!, SGO!)

Tepualia philippii Griseb. ex Phil., Linnaea 28: 637 (1857). –TYPE: "Ad radicales borealem vulcani de Osorno dicti Februario 1852 legi", collector unknown (location unknown).

Tepualia patagonica Phil., Anales Univ. Chile 84: 755 (1893).

Cuming 32 was chosen over *Cuming 33* as the lectotype for *Tepualia stipularis* because more material is available (three specimens rather than two). Both gatherings are equally representative of the species and are highly similar morphologically; both are from Valdivia, Chile. Regarding lectotypification of *P. philippiana*, Taxonomic Literature 2 (Stafleu and Cowan, 1976) describes GOET as being a primary deposit for Philippi material and Grisebach worked mostly in Göttingen. We therefore select *Philippi 89* at GOET as the lectotype for *Tepualia philippiana* as it likely to be the original material on which the taxon was based. No type material was cited in the protolog of *Tepualia philippii*, only the locality 'Osorno Volcano.' No material with this name or locality has yet been located.

Metrosideros tardiflora (J.W. Dawson) Pillon comb. nov. Basionym: *Carpolepis tardifora* J.W. Dawson, Bull. Mus. Natn. His. Nat., Paris, ser. 4, sect. B, Adansonia 6(4): 468 (1984, publ.

1985).–TYPE: NEW CALEDONIA. Mt Mandjélia, 17 Feb. 1977, *MacKee 32843* (holotype: P [P00057633]!, isotypes: P [P00057634]!, NOU [NOU006244]!).

Metrosideros vitiensis (A. Gray) Pillon comb. et stat. nov. Basionym: *Metrosideros collina* (J. R. Forst. & G. Forst.) A.Gray var. *vitiensis* A. Gray, U.S. Expl. Exped. , Phan. 1: 559 (1854).–TYPE: FIJI. Wilkes Explor. Exped., United States Exploring Expedition, 1838-1842, *US 47896 & US 47895* (lectotype [first-step] designated by Smith (1973: 486); lectotype [second-step], here designated: *US 47896*, US [US00118308]!, remaining syntype: *US 47895*, US [US00118309]!).

Smith (1973) typified *Metrosideros collina* var. *vitiensis* by "a U. S. Exploring Expedition collection (US 47895 & US 47896 holotype)". The two sheets are similar and may be a single gathering, *US47896* is chosen as a lectotype because it is has more material.

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TABLE 1. Primers used to amplify single-copy nuclear genes.

Locus	Putative *Arabidopsis* homolog	Putative product	Primers
MeNu40	*At5g63960*	DNA-directed DNA polymerase	F: AGCGAAGCAGAAGAACCTTG R: TTTCATAGAAACCTGCCTTGG
MeNu42	*At1g02410*	cytochrome c oxidase assembly protein	F: GTCAAGCCTGGAGAAAGTGC R: AGTAGCCGCTGCTCTTCAAA
MeNu55	*At1g32200*	chloroplast glycerol-3-phosphate acyltransferase	F: ACGAAGCTTGAAGGAAATGG R: AGGATCTGGACGATCTCTGC
MeNu68	*At2g17510*	embryo defective 2763 (EMB2763), ribonuclease	F: GGCAGATGTGGAGAGACTGG R: ACAGAGCTGCACATGATTTGA
MeNu74	*At2g31440*	positive regulation of catalytic activity	F: AGGTGCTCAAAGATGCCATT R: CAAAGGCAAGAGCGATCAAT

APPENDIX 1. List of DNA sequences used for the phylogenetic analysis based on ITS sequences with GenBank accession number and literature reference for original publication.

Metrosideros albiflora[8], DQ328799; *Metrosideros angustifolia*[8], DQ 328795; *Metrosideros bartlettii*[6], AF172740; *Metrosideros boninensis*[5], AF172734; *Metrosideros brevistylis*[5], AF211496; *Metrosideros cacuminum*[6], AF211497; *Metrosideros carminea*[8], AF211498; *Metrosideros cherrieri*[5], AF172768; *Metrosideros colensoi*[8], AF211499; *Metrosideros collina* (Vanuatu)[5], AF172735; *Metrosideros collina* (Fiji)[5], AF172757; *Metrosideros collina* (Samoa)[5], AF172737; *Metrosideros collina* (Tahiti)[5], AF172739; *Metrosideros collina* (Rurutu)[7], AF328070; *Metrosideros collina* (Marquesas)[7], AF328069; *Metrosideros collina* (Cook)[7], AF172741; *Metrosideros cordata*[4], JF950776; *Metrosideros diffusa*[8], AF211500; *Metrosideros dolichandra*[6], AF211501; *Metrosideros engleriana*[5], AF172736; *Metrosideros excelsa*[5], AF172738; *Metrosideros fulgens*[8], DQ328800; *Metrosideros gregoryi*[5], AF172769; *Metrosideros halconensis*[8], DQ328797; *Metrosideros humboldtiana*[5], AF172744; *Metrosideros kermadecensis*[5], AF172743; *Metrosideros longipediolata*[6], AF211502; *Metrosideros macropus*[5], AF172745; *Metrosideros microphylla*[5], AF172746; *Metrosideros nervulosa*[5], AF172747; *Metrosideros nitida*[5], AF172770; *Metrosideros ochrantha*[5], AF172748; *Metrosideros operculata*[5], AF172733; *Metrosideros oreomyrtus*[5], AF172749; *Metrosideros ovata*[8], DQ328793; *Metrosideros paniensis*[6], AF211503; *Metrosideros parkinsonii*[8], DQ328796; *Metrosideros patens*[6], AF211504; *Metrosideros perforata*[5], AF172732; *Metrosideros polymorpha*[5], AF172753; *Metrosideros porphyrea*[6], AF211505; *Metrosideros punctata*[5], AF172755; *Metrosideros ramiflora*[8], DQ328798; *Metrosideros robusta*[5], AF172758; *Metrosideros rotundifolia*[6], AF211507; *Metrosideros rugosa*[5], AF172759; *Metrosideros salomonensis*[5, 9], AF172766; *Metrosideros sclerocarpa*[5], AF172760; *Metrosideros tetragyna*[8, 9], DQ328801; *Metrosideros tetrasticha*[5], AF172762; *Metrosideros tremuloides*[5], AF172763; *Metrosideros umbellata*[5], AF172764; *Metrosideros waialealae*[5], AF172765; *Metrosideros whitakeri*[6], AF211506; *Metrosideros whiteana*[8], DQ328794; *Carpolepis elegans*[6], AF211492; *Carpolepis laurifolia*[6], AF211494; *Carpolepis tardiflora*[6], AF211495; *Tepualia stipularis*[3], AM234071; *Thaleropia queenslandica*[2], AY264945; *Tristania neriifolia*[1], EF026608 ; *Cloezia floribunda*[5], AF172767; *Syzygium malaccense*[2], AY187199.

[1]Biffin et al. (2007), [2]Harrington & Gadek (2004), [3]Lucas et al. (2007), [4]Papadopulos et al. (2011), [5]Wright et al. (2000b), [6]Wright et al. (2000a), [7]Wright et al. (2001), [8]Wright et al. (2003), [9]Two ITS sequences labeled *Metrosideros* cf. *salomonensis* in GenGank are clearly distinct. We have inferred one, ascribed to subgenus *Metrosideros*, to correspond to *M. salomonensis* (AF172766). The other, DQ328801, ascribed to subgenus *Mearnsia*, is here tentatively relabeled as *Metrosideros tetragyna* J.W. Dawson, a new name created by Dawson (1976) to combine *Mearnsia salomonensis* C.T. White into *Metrosideros* since *Metrosideros salomonensis* C.T. White was already taken. No voucher information was available to validate this determination, but these are the only two species of *Metrosideros* recorded in the Solomon islands (Govaerts et al., 2015).

APPENDIX 2. List of of samples used for the phylogenetic analysis based on single-copy nuclear genes, with geographical origin, voucher reference, and GenBank accession numbers (*MeNu40*, *MeNu42*, *MeNu55*, *MeNu68* and *MeNu74*).

Metrosideros angustifolia, South Africa, *Forest & Manning 527* (NBG), KP231653, KP231668, KP231684, KP231698, KP231715; *Metrosideros boninensis*, Ogasawara (cult. at K), *Chase 2455* (K), KP231652, KP231667, KP231683, KP231697, KP231714; *Metrosideros cacuminum*, New Caledonia, *Pillon 1401* (NOU), KP231665, KP231681, KP231689, KP231712,

KP231723; *Metrosideros collina* (Tahiti), French Polynesia, Tahiti, sommet Aorai, 2070m, *Meyer s.n.* (PAP), KP231656, KP231671, KP231688, KP231705, KP231720; *Metrosideros collina* (Samoa), American Samoa, Tutuila, Alava, *Pillon 1429* (BISH), KP231654, KP231679 & KP231680, KP231685, KP231699 & KP231700, KP231716; *Metrosideros excelsa*, New Zealand, Auckland (cult.), *Cuttriss s.n.* (PTBG), KP231661 & KP231662, KP231677 & KP231678, KP231690 & KP231691, KP231701 & KP231702, KP231717; *Metrosideros macropus*, Hawaiian islands ,O'ahu, Ko'olau, Poamoho, *Johansen 62* (PTBG), KP231655, KP231669, KP231686, KP231703, KP231718; *Metrosideros nervulosa*, Lord Howe Island (cult. at K), *Chase 2451* (K), KP231651, KP231666, KP231682, KP231696, KP231713; *Metrosideros polymorpha* var. *incana*, Hawaiian islands, Hawai'i, Hilea, *Johansen 61* (PTBG), KP231660, KP231674 & KP231675, KP231692, KP231707, KP231724 & KP231725; *Metrosideros rugosa*, Hawaiian islands, O'ahu, Ko'olau, Poamoho, *Johansen 63* (PTBG), KP231659, KP231676, KP231693, KP231708 & KP231709, KP231726; *Carpolepis laurifolia*, New Caledonia, *Barrabé 1165* (NOU), KP231658, KP231673, –, KP231706, KP231722; *Tepualia stipularis*, Chile, Chiloe, Castro (cult. at RBGE 19952370), *Rae & Gardner 1* (E), KP231657, KP231672, KP231694 & KP231695, KP231710 & KP231711, KP231721; *Psidium guajava,* Hawaiian Islands, Hawai'i (naturalized), *Pillon 1432* (NOU), KP231663 & KP231664, KP231670, KP231687, KP231704, KP231719.

FIG. 1. Half-compatible Bayesian phylogenetic tree of the tribe Metrosidereae based on ITS sequences. Numbers at nodes are posterior probabilities. Section *Mearnsia* (black bars) is composed of subsection *Crassinervis* and subsection *Trivalvis*; section *Calyptropetala* (white bars) is composed of subsection *Exsertis* and subsection *Inclusis*. The two groups of *Metrosioderos collina* are highlighted in grey.

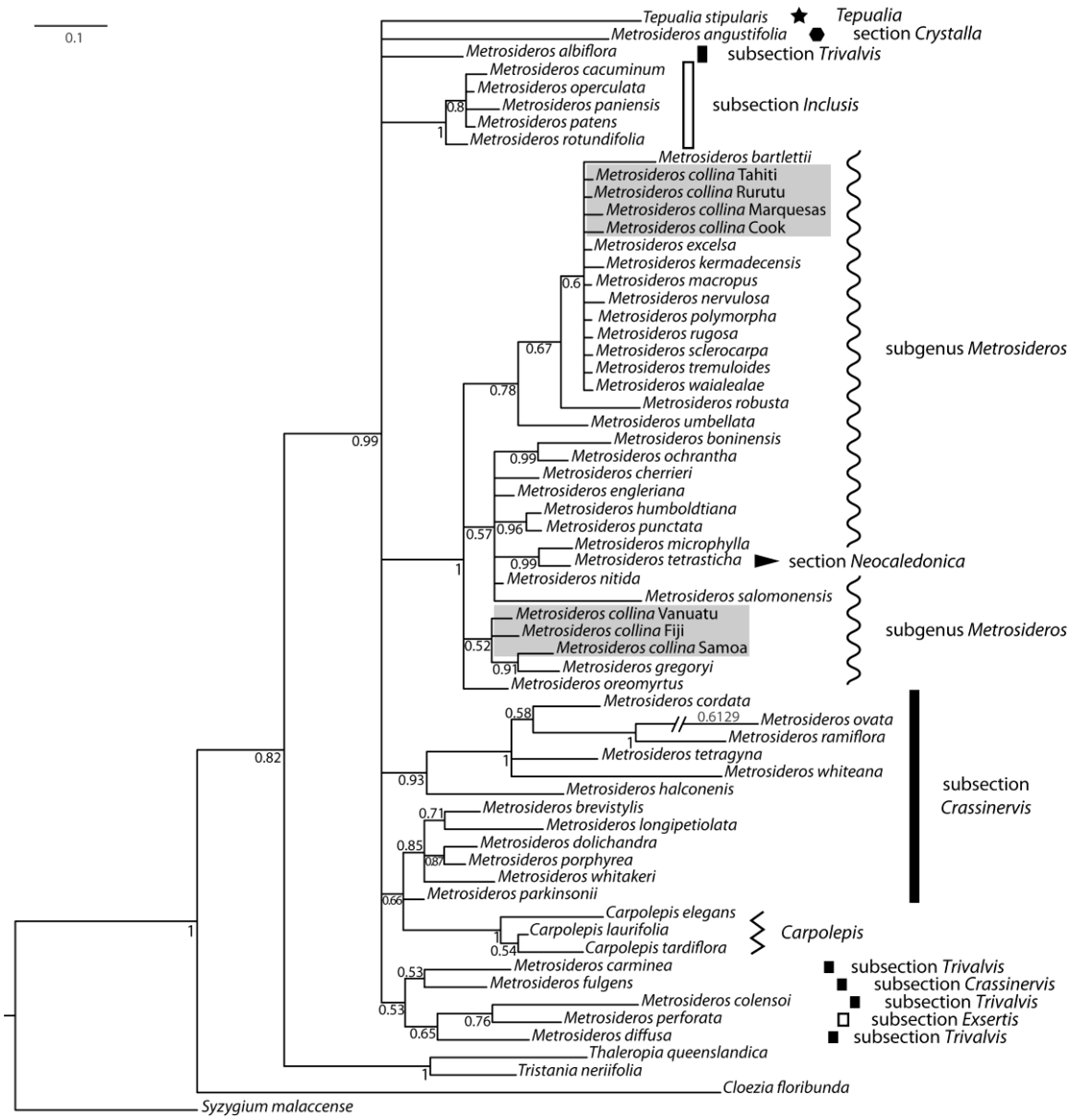


FIG. 2. Half-compatible Bayesian phylogenetic tree of the tribe Metrosidereae based on individual nuclear gene data and the combined analysis of five nuclear genes. Numbers at nodes are posterior probabilities. The number 1 and 2 after species name refers to different alleles of the same accession. Species of subgenus *Metrosideros* are indicated by a black dot (●).

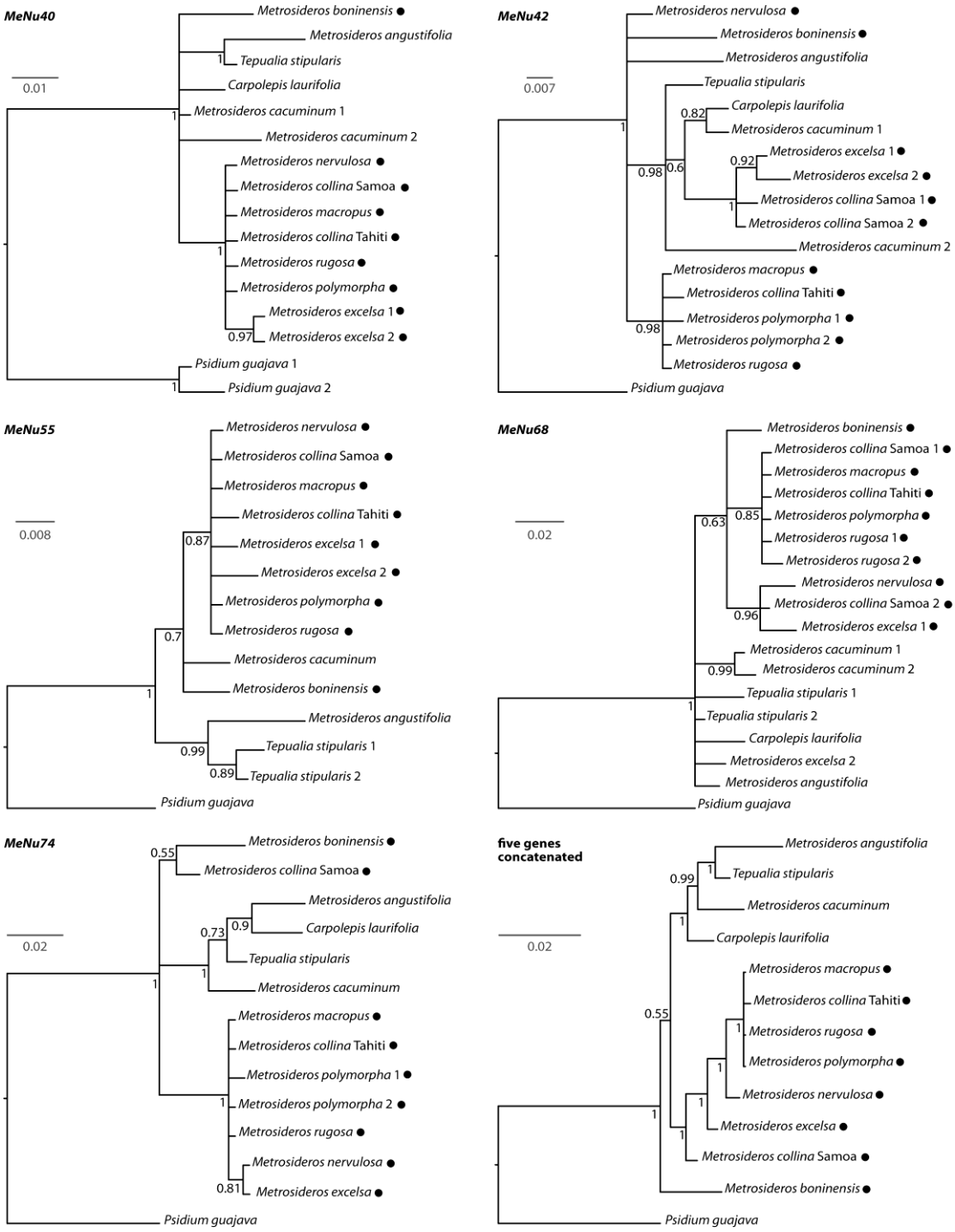


FIG. 3. Half-compatible phylogenetic tree of the tribe Metrosidereae after Bayesian coaslescent analysis (*BEAST) and primary concordance tree (BUCKy). Numbers at nodes are posterior probabilities (left) and concordance factor (right). Species of subgenus *Metrosideros* are indicated by a black dot (●).

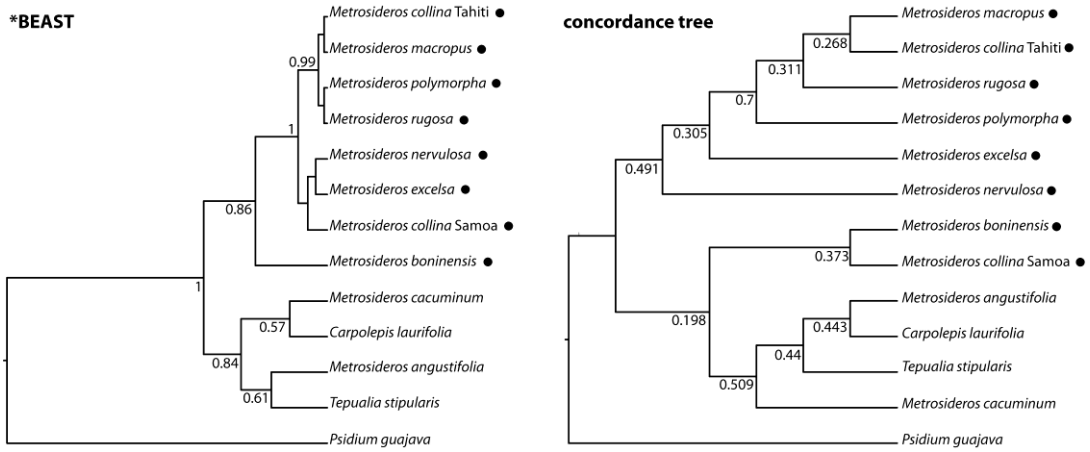


FIG. 4. Splitstree network of the tribe Metrosidereae based on the combined analysis of five nuclear genes.

