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NEW WORLD ORIGINS OF SOUTHWEST PACIFIC GESNERIACEAE: MULTIPLE MOVEMENTS ACROSS AND WITHIN THE SOUTH PACIFIC

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Coronanthereae is a tribe of ~20 species with a suite of unique morphological characters and a disjunct geographic distribution in the Southern Hemisphere. Three species are found in southern South America and the remainder in the southwest Pacific. It has been suggested, because of this distribution and disjunction, that Coronanthereae represents a relictual Gondwanan group from which the two major lineages in the family, the Old World Cyrtandroideae and the New World Gesnerioideae, originated. We tested this hypothesis by using phylogenetic analyses of nuclear and chloroplast DNA sequences, ancestral-area reconstruction, and molecular dating. The tribe is placed within the mostly Neotropical subfamily Gesnerioideae and comprises three lineages, treated here as subtribes. Two events of dispersal from South America explain the presence of the tribe in the South Pacific. Negriinae, newly recognized here, comprises arborescent genera: Australian *Lenbrassia*, New Caledonian *Depanthus*, and *Negria* from Lord Howe Island. Mitrariinae groups facultatively epiphytic Australian *Fieldia* with epiphytes from South America, a finding inconsistent with recent placement of *Lenbrassia* in synonymy of *Fieldia*. Coronantherinae consists of the arborescent *Coronanthera* from New Caledonia and the shrub *Rhabdothamnus* from New Zealand. Ancestral-area reconstruction and molecular dating of the clades support long-distance dispersal mechanisms, rather than Gondwanan vicariance, for explaining geographic distributions.

Keywords: biogeography, Coronanthereae, long-distance dispersal, molecular phylogeny, New Caledonia, New Zealand.

Introduction

The relationships of the biotas of the Southern Hemisphere have fascinated biogeographers for more than a century. Early accounts of southern disjunct plant distributions proposed land connections (Hooker 1853) and long-distance dispersal (Darwin 1859) as mechanisms. Brundin (1966), in a paper that stimulated vicariance biogeographic hypotheses, related distributions of chironomid midges to the fragmentation sequence of the Gondwana continents, and explanations that involve Gondwanan vicariance (Skipworth 1973) and ancient origins (Heads 1999) have become cultural icons of the Southern Hemisphere biota (McGlone 2005). Many plant genera found in temperate South America, Australia, and New Zealand give at least the impression of Gondwanic vicariance, e.g., *Veronica* sect. *Hebe* (Wagstaff et al. 2002, as *Hebe* and relatives), *Fuchsia* (Berry et al. 2004, in Australia as fossils only), *Ourisia* (Meudt and Simpson 2006), *Oreobolus* (Seberg 1988), *Tetrachondra* (Wagstaff et al. 2000), and *Abrotanella* (Swenson and Bremer 1997). However, in the past 20 years, molecular ages (Wagstaff et al. 2002, 2007; Smissen et al. 2003; Pfeil and Crisp 2008; Tay et al. 2010) have indicated that many southern disjunct plant groups are too recent for their distributions to be explained by Gondwanic vicariance. Further, cladogram topologies often do not match the order of vicariance events (see Pole 1994, 2001; Linder and Crisp 1995; and McGlone et al. 2001 for overviews). Although similar distribution patterns might be inferred to have similar causes, modern methods that allow estimates of the relative ages of the branching events and even of their actual ages (Knapp et al. 2005) can show that similar patterns may result from different processes. For instance, in *Veronica*, the grade of taxa basal to the Australasian clade (subg. *Pseudoveronica*) is found in Eurasia (Albach and Meudt 2010), whereas the grades of taxa basal to the Australasian clades of *Ourisia* and *Fuchsia* are found in South America (Berry et al. 2004; Meudt and Simpson 2006).

Dispersal patterns and processes can be most clearly investigated on oceanic island chains (Baldwin et al. 1995; Funk and Wagner 1995; Clement et al. 2004; Cronk et al. 2005; Clark et al. 2008, 2009), whereas older and larger continental islands have more complex histories and more diverse processes, with the added possibility of vicariance to explain current distributions. New Zealand and New Caledonia are associated continental islands that have important similarities and differences in their histories and environments. Trans-Tasman affinities between New Zealand plants and the Australian flora have drawn attention because evidence of directionality for the dispersal events has been evaluated

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(Cook and Crisp 2005), and New Zealand's history includes either complete (discussed by Pole 1994) or at least substantial (Campbell 1985; Cooper and Cooper 1995) drowning in Oligocene times. The origins of the New Caledonian flora have also indicated long-distance dispersal mechanisms as a major factor in diversity (e.g., Sapotaceae: Bartish et al. 2005; Rutaceae: Pfeil and Crisp 2008). New Caledonia and New Zealand might have been connected at times through the Lord Howe Ridge (Lee et al. 2001), and some New Zealand plant groups appear to be related to those of New Caledonia.

Here we describe molecular phylogenetic analyses for a group of species distributed in what may appear to be a classic Gondwanan vicariant pattern. This is the small southern temperate tribe Coronanthereae (Gesneriaceae), which spans the Old and New Worlds. Species are found in temperate South America, Australia, New Zealand, New Caledonia, and several islands in the southwest Pacific. The tribe has at times been placed in either subfamily Cyrtandroideae (Fritsch 1893–1894) or the Gesnerioideae (Burtt 1963) or, alternatively, as a small third subfamily, Coronantheroideae (Wiehler 1983). We test monophyly of the tribe and evaluate its evolutionary relationships. These analyses provide a temporal framework for understanding the biogeographic origins, species distributions, taxonomy, and character evolution of the group.

The Taxonomy of Gesneriaceae

Gesneriaceae [Rich. & Juss. ex] DC., a member of Lamiales (APG III 2009), is a primarily tropical family containing ~150 genera and 3000–3500 species (Weber 2004; Skog and Boggan 2006). Within Gesneriaceae, some higher-level relationships remain ambiguous, most notably the placement and resolution of relationships within Coronanthereae.

Molecular studies have clarified the phylogenetic relationships of many genera and tribes, providing evidence that supports (1) the monophyly of Gesneriaceae as one of three families sister to "core" Lamiales (Oxelman et al. 1999, 2005; Backlund et al. 2000; Olmstead et al. 2001; Bremer et al. 2002; Wortley et al. 2005; APG III 2009); (2) the monophyly of the New World subfamily Gesnerioideae and the presence within it of at least six or seven tribes (Smith et al. 1997; Zimmer et al. 2002; Roalson et al. 2005*a*); (3) the presence of a distinct, perhaps relictual, tribe, Epithemateae, sister to the rest of the tribes within Cyrtandroideae (Mayer et al. 2003); (4) the incongruence between traditional classification and tribal relationships suggested by molecular data within subfam. Cyrtandroideae excluding Epithemateae (Möller et al. 2009); and (5) the internal relationships and monophyly of several tribes (Episcieae: Smith and Carroll 1997; Smith 2000*b*; Clark et al. 2006; Gloxinieae: Smith and Atkinson 1998; Roalson et al. 2005*a*, 2005*b*, 2008; Beslerieae and Napeantheae: Smith 2000*a*; Sinningieae: Perret et al. 2003; Gloxinieae and Gesnerieae: Smith et al. 2004*a*, 2004*b*;) and genera (*Columnea*: Smith and Sytsma 1994*a*, 1994*b*; *Saintpaulia*: Möller and Cronk 1997; Smith et al. 1998; *Streptocarpus*: Möller and Cronk 2001; *Aeschynanthus*: Denduangboripant and Cronk 2001; *Achimenes*: Roalson et al. 2003; *Alloplectus*: Clark and Zimmer 2003; *Cyrtandra*: Bramley et al. 2004; Cronk et al. 2005). Despite this large body of work, strongly supported placement of Coronanthereae has not been examined.

Tribe Coronanthereae

The ingroup of our study, tribe Coronanthereae, is found mostly in the Southern Hemisphere of the Old World. It is an anomalous group in the family because it combines isocotylous embryos characteristic of the otherwise New World Gesnerioideae with superior ovaries characteristic of the Old World Cyrtandroideae. The tribe contains nine genera, all monospecific except *Coronanthera*, which has up to 20 species (V. L. Woo and P. J. Garnock-Jones, unpublished data). Morphological synapomorphies of Coronanthereae include a nectary embedded at the base of the ovary, high chromosome numbers (n=±37, ±40, and ±45, whereas most other Gesneriaceae range from n=8 to n=17 [Weber 2004]), and woody habit (Wiehler 1983; Burtt and Wiehler 1995, as Coronantheroideae). The tribe is diverse (fig. 1), containing trees, shrubs, facultative and obligate epiphytes (Fernanda Salinas et al. 2010), and lianas with a range of vegetative and reproductive morphologies. Its members formerly belonged to two tribes: Mitrarieae, made up of species with indehiscent fleshy fruits, and Coronanthereae, characterized by dehiscent capsular fruits (Burtt 1963).

Fritsch (1893–1894) originally placed Coronanthereae within subfamily Cyrtandroideae on the basis of ovary position. Burtt (1963) placed the same species within the New World subfamily Gesnerioideae because of their isocotylous seedling morphology but raised the subgroups to the rank of tribes on the basis of fruit type, with the indehiscent fleshy–fruited species as Mitrarieae and the dry, dehiscent capsular–fruited ones as Coronanthereae.

The combination of South American and South Pacific species into a single tribe or subfamily (Wiehler 1983; Burtt and Wiehler 1995) has intrigued researchers interested in the origin and evolution of the family, because Gesneriaceae otherwise splits almost exclusively into Old and New World subfamilies (Smith 1996; Weber 2004). Coronanthereae was raised to subfamily rank, as Coronantheroideae, by Wiehler (1983) and Burtt and Wiehler (1995), but this has not been accepted by all authors. Because of the inclusion of a few members of Coronanthereae in molecular studies, its placement at subfamily rank (as Coronantheroideae) has been questioned (Mayer et al. 2003; Smith et al. 2004*b*; Wang et al. 2004). As the Coronanthereae have been little studied until now, are seldom collected, and are difficult to cultivate, questions about their relationships have not been definitively answered. Molecular studies by Smith et al. (1997, 2004*b*), Smith (2000*c*), Mayer et al. (2003), Wang et al. (2004), and Möller et al. (2009) have all found Coronanthereae to be allied to the New World Gesnerioideae, although its placement within the subfamily has varied. However, finer details of the phylogenetic relationship of Coronanthereae to Gesnerioideae have been poorly resolved because of limited taxon sampling. First, on the basis of chloroplast genes *ndhF* and *rbcL* and morphology, Coronanthereae has been placed as sister to the rest of Gesnerioideae (Smith 2000*c*). Second, a postulated position of Coronanthereae as sister to the rest of

Fig. 1 Morphological diversity within tribe Coronanthereae. *A*, Epiphytic creeper *Sarmienta repens*; *B*, divaricating shrub *Rhabdothamnus solandri*; *C*, large tree *Depanthus glaber*. Photographs by Serge Aubert of Le Jardin Botanique Alpin du Lautaret (*A*) and Vincent Woo (*B*, *C*).

Gesnerioideae except Beslerieae and Napeantheae (Smith et al. 2004*b*; Wang et al. 2004) was inferred from studies using data sets that combined low-copy-number nuclear G-*CYCLOIDEA* (GCYC), nuclear ITS, and chloroplast spacer markers *trnL-trnF* and *atpB-rbcL*.

In addition to that from molecular systematics, there is other evidence to connect Coronanthereae with Gesnerioideae. The rare 3-deoxyanthocyanins, found usually in mosses and ferns but only rarely in flowering plants, are present in *Sarmienta repens* (Silva et al. 1971) and other Gesnerioideae. These compounds might provide another link to this subfamily, although they were not found in *Fieldia australis* (Harborne 1967) or *Rhabdothamnus solandri* (Lowry 1972).

Gondwanan Origins of Gesneriaceae

Burtt (1998) proposed that the Gesneriaceae are a family of Gondwanan origin that arose in Australasia and invaded South America and Asia. He saw the current coronantheroid Gesneriaceae as a relictual group that had a continuous presence in the area for 80 million years and gave rise to the Asian Cyrtandroideae and the American Gesnerioideae. In many other angiosperm families, molecular phylogenetic studies have enabled reexamination of theories regarding the evolution of major lineages. The hypothesis proposed by Burtt (1998) would be falsified if Coronanthereae did not form a basal grade in the family or at least a clade sister to the rest of the family.

Our study, with the most comprehensive sampling of Coronanthereae thus far, was undertaken to evaluate phylogenetic relationships within the tribe and to test Burtt's (1998) hypothesis that Coronanthereae represent the relictual ancestors of both subfamilies of Gesneriaceae. We have used maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) analyses of the nrDNA ITS region and several chloroplast DNA regions, as well as GCYC, for all genera and most of the species. We employ ancestral-area reconstruction and molecular dating to better understand the pattern and timing of species distributions. This study complements other phylogenetic investigations that focused primarily on subfamily Gesnerioideae (Smith et al. 2004*b*) and showed a close relationship of Coronanthereae to Gesnerioideae but sampled minimally from Coronanthereae. We address three main questions: (1) Is the current circumscription of Coronanthereae accurate in reflecting a monophyletic assemblage? (2) What are the generic relationships among members of Coronanthereae, and do they support the current morphologically based classification? (3) What are the biogeographical relationships among members of Coronanthereae, and is there support for a Gondwanan origin for the Gesneriaceae?

Material and Methods

Species Sampling

A complete list of samples, voucher specimens, and GenBank accession numbers can be found in appendix A. Our sampling

was at two levels. For the full analysis, we sampled comprehensively among species and populations of species within Coronanthereae as a means of testing generic and species monophyly. For the reduced analysis, one individual per genus of Coronanthereae was used, along with two (one for Sphaerorrhizeae) species for each of the tribes of Gesnerioideae, but with increased sampling of DNA regions to improve support for resolved nodes.

Our ingroup sample for the full analysis included all nine genera of Coronanthereae and 17 of the 20 species described within the tribe. In addition, we included three individuals of *Coronanthera* that likely represent new species. Suitable material was lacking for three species: *Coronanthera pinguior* C. B. Clarke and *Coronanthera pulchra* C. B. Clarke, both from New Caledonia, and *Coronanthera grandis* G. W. Gillett, from the Solomon Islands.

Our outgroup samples were chosen on the basis of previous phylogenetic studies, and we follow Roalson et al. (2005*a*) in recognizing seven distinct tribes within subfamily Gesnerioideae: Beslerieae, Episcieae, Gesnerieae, Gloxinieae, Napeantheae, Sinningieae, and Sphaerorrhizeae. We included as many samples as possible from within Napeantheae (three species) and Beslerieae (10 species), as well as eight species representing the remaining five tribes of Gesnerioideae. Two members of Cyrtandroideae tribe Didymocarpeae, *Chirita gemella* from Vietnam and *Boea hygroscopica* from Australia, were used as outgroups in analyses that examined the position of Coronanthereae relative to the tribes of Gesnerioideae.

The reduced sampling included three representatives of Cyrtandroideae designated as the outgroup (app. A). Ideally, sequences would have been obtained for all individuals used in the full analysis. However, the reduced sampling is justified on the basis that (1) our goal was to maximize our understanding of relationships and biogeography within Coronanthereae, (2) many of the sequences we wished to use to add support to our trees were already published, and (3) the tribe Coronanthereae and each genus within the tribe that included more than a single sequence had been resolved as monophyletic with strong support in the full sampling (fig. 2).

DNA Extraction, Amplification, Sequencing, and Alignment

DNA was extracted from silica-dried or herbarium leaf material of one individual plant with Qiagen DNeasy Plant Mini Kits (Valencia, CA) according to manufacturer's instructions. Double-stranded DNA was amplified via PCR; each 25-μL reaction contained 5 μL of 5× Qiagen Q-solution, 2.5 μL of 10× Qiagen PCR buffer, 250 pmol of each dNTP (Roche Diagnostics, Auckland, New Zealand), 10 pmol of each amplification oligonucleotide primer (Invitrogen, Auckland, New Zealand), 0.75 U of Taq DNA Polymerase (5 u/μL; Qiagen), and 1–10 ng of genomic DNA. Thermal cycling was conducted in thin-walled tubes in an Applied Biosystems (Carlsbad, CA) GeneAmp PCR system 2700 thermal cycler with the following temperature profile: a denaturation step of 94°C for 3 min, followed by 30 cycles of 94°C denaturation for 30 s, 50°C for 30 s for annealing, and 72°C for 2 min of extension, and a final extension phase at 72°C for 10 min. Amplifications were run on 1% low-melting-point gels stained with ethidium bromide, and the fragment of expected size was cut from the gel and purified using the Qiagen MinElute gel extraction kit according to the manufacturer's protocols. Amplifications failed for several species. In *Besleria* and *Coronanthera barbata*, PCR products failed to amplify for any of the regions, despite multiple extractions from different accessions.

The same regions used by Zimmer et al. (2002) were chosen for sequencing, as they were useful in resolving relationships within Gesnerioideae, with the addition of the *psbA-trnK* spacer region (Winkworth et al. 2002*a*). The ITS and *trnL-trnF* data sets have been shown to have great utility in generic and family limitations (Baldwin et al. 1995; review in Shaw et al. 2005).

The nrDNA ITS region (ITS1, ITS2, and the 5.8S gene) was amplified with ITS5 forward primer (White et al. 1990) and a modified reverse primer, ITS28CC (Wagstaff and Garnock-Jones 1998). Two internal primers, ITS2 and ITS3, were used during sequencing to provide additional overlapping sequences for confirmation of precise sequencing (White et al. 1990). The chloroplast DNA primers of Taberlet et al. (1991) were used to generate a fragment that included both the *trnL* intron and the *trnL-trnF* intergenic spacer. The primers trnE and trnTr (Doyle et al. 1992) were used to amplify the *trnE-trnT* intergenic spacer. The intergenic spacer *psbA-trnK* was amplified with trnK3F and PSBAR (Winkworth et al. 2002*a*).

Amplified products were cycle sequenced initially with 4-μL half-reactions of Applied Biosystems Big Dye Terminator v. 2.0 and later with 2-μL quarter-reactions of Big Dye Terminator v. 3.1, with equal success. Sequencing was accomplished by gel slab sequencing, initially on an Applied Biosystems ABI 377 sequencer and later on an ABI 3730 capillary sequencer.

For the reduced analysis, we used sequences for the ITS and the cpDNA *trnL-trnF* spacer region. We also obtained sequences for the *trnL* intron (Taberlet et al. 1991), *ndhF* (Smith and Carroll 1997; Smith et al. 1997; Smith and Atkinson 1998), the *rpl20-rps12* spacer (Hamilton 1999), and the low-copy-number nuclear gene G*CYC* (Smith et al. 2004*a*, 2004*b*, 2006). Amplification, cloning, and sequencing procedures followed those of Smith et al. (2004*a*) for these latter DNA regions.

Test of Incongruence

The partition homogeneity test (Farris et al. 1994) was performed as implemented in PAUP*4.0 b10 (Swofford 2002) with 10,000 bootstrap replicates (using a heuristic search, simple addition, and no branch swapping). The cpDNA and ITS were treated as separate partitions for both full and reduced analyses. For the reduced sampling, additional partitions were used for each of the two paralogs of G*CYC*. As an additional measure of congruence among partitions, bootstrap analyses were performed on each partition separately to assess areas of conflict and to determine whether any conflict was strongly supported (Seelanen et al. 1997).

Phylogenetic Analyses: Full Analysis

Sequences were initially aligned with SEQMAN (DNASTAR 1999) and ClustalX 1.83 (Thompson et al. 1997) and corrected manually with event-based criteria (Morrison 2006). Sequence boundaries for the contiguous ITS region, the *trnL* intron and *trnL-trnF* spacer, and the *trnE-trnT* spacer were de-

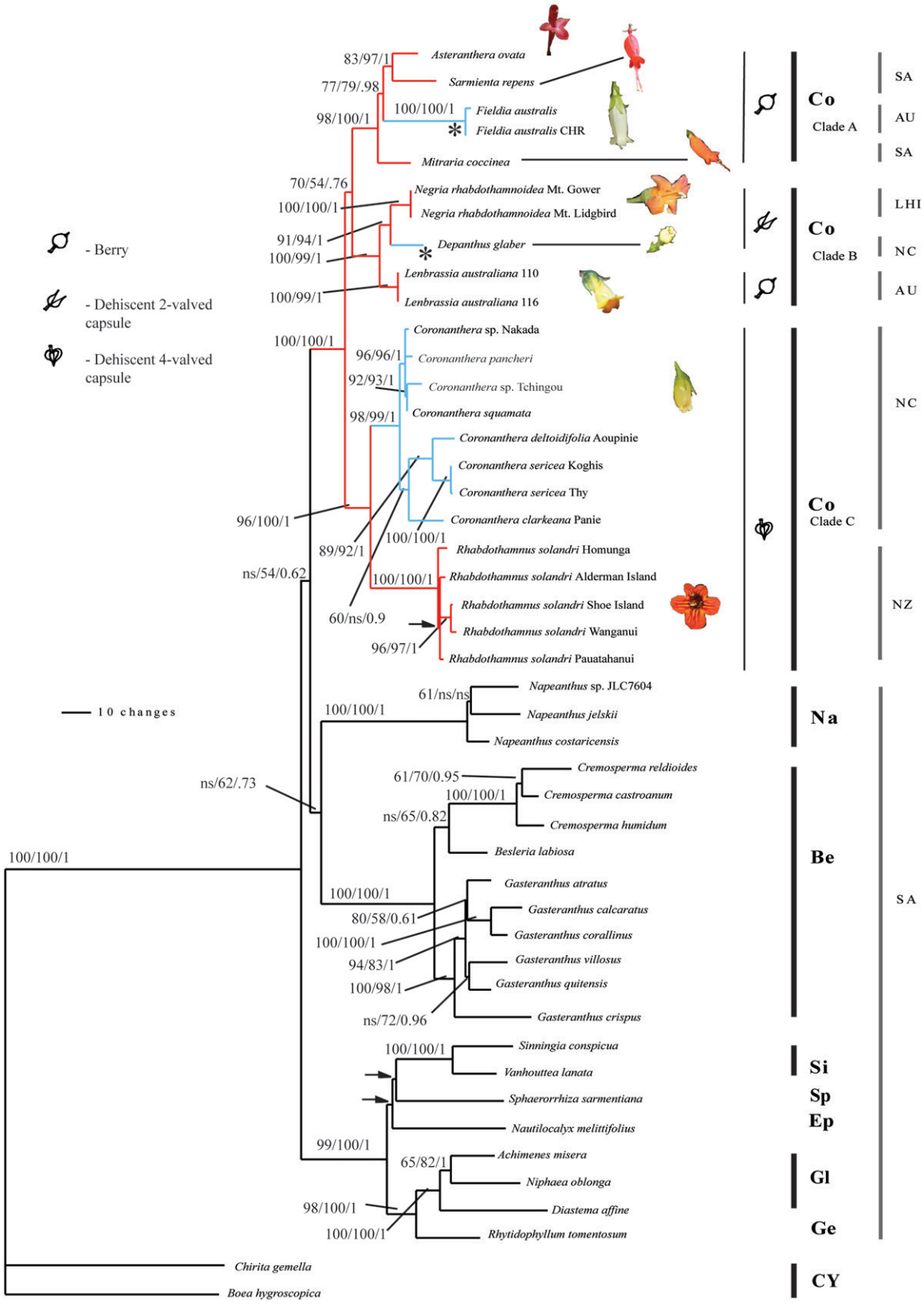

Fig. 2 Phylogram of the maximum likelihood (ML) tree ($-\ln = 15,416.339$) for the full analysis. Maximum parsimony (MP) bootstrap/ML bootstrap/Bayesian (BI) posterior probability values are shown for each branch; *ns* indicates that the node was not supported in that

termined by comparison with published sequences in GenBank. The 5.8S sequences were subsequently excluded in the analyses because they provided little phylogenetic signal.

Phylogenetic trees were estimated with MP, ML, and BI. MP analyses were performed with PAUP*4.0b10 (Swofford 2002). The full-analysis data set included 47 taxa. The data were analyzed with the stepwise method of detecting multiple islands of trees (Olmstead and Palmer 1994; Smith et al. 2004*a*), with indels treated as missing data. One thousand random stepwise addition replicates were performed five times with nearest-neighbor interchange and MulTrees off, and the shortest trees from each search were saved. Those trees together were used as the starting point for an additional heuristic search with the tree bisection-reconnection (TBR) branch-swapping algorithm and MulTrees on and all shortest trees saved. Those shortest trees were used to generate a strict consensus tree. Bootstrap support (BS) for nodes (Felsenstein 1985) was estimated with 1000 heuristic simple taxon addition searches with TBR and MulTrees on. Descriptive statistics reflecting the amount of phylogenetic signal in the parsimony analysis were given by the consistency index (CI; Kluge and Farris 1969), the retention index (RI; Farris 1989), and the resulting rescaled consistency index (RC).

ML analyses were performed with optimal substitution models suggested by MODELTEST 3.6 (Posada and Crandall 1998). The Aikake Information Criterion (AIC), which allows nonnested models to be evaluated, was used as a selection criterion (Posada and Buckley 2004). The TIM+Γ+I model was chosen. Analyses of ML were completed in GARLI v0.96 (Zwickl 2006) with 100 bootstrap replicates.

BI analyses were completed in MRBAYES 3.1.1 (Huelsenbeck and Ronquist 2003) with the TIM+Γ+I model and were run with 4 : 1 heated chains for 10 million generations. Convergence was determined by viewing in Tracer v1.3 (Rambaut and Drummond 2005), and burn-in of 50,000 generations was discarded before the posterior distribution was sampled. The analyses were repeated twice to ensure that parameter estimates converged to similar values. The separate runs were compared using the online version of AWTY (http://king2.scs.fsu.edu/CEBProjects/awty/awty.php?fromStart=1&sessionDir=tmp18595; Nylander et al. 2008) as a means of determining whether the separate chains approximated the same target distribution. We report the 50% majority-rule consensus tree sampled from the posterior probability distribution.

Phylogenetic Analyses: Reduced Analysis

Identical analyses for MP, ML, and BI were run with the reduced-sampling data set, with the exception that BI used a unique model for each DNA region based on AIC results of MODELTEST. The following models were employed: for *ndhF*, GTR+I+Γ ($I = 0.2543$, $\Gamma = 0.5653$); for the *trnL* intron, GTR+Γ ($\Gamma = 1.1119$); for the *trnL-trnF* spacer, TVM+Γ ($\Gamma = 1.5514$); for the *rpl20-rps12* spacer, TIM+Γ ($\Gamma = 0.9287$); for the ITS, GTR+I+Γ ($I = 0.0495$, $\Gamma = 2.8547$); for GCYC1E, TrN+I ($I = 0.0947$); and for GCYC1F, TVM+I ($I = 0.1739$). The phylogenetic trees and data sets used in the full and reduced analyses have been submitted to TreeBASE (study S2500).

Comparison of Full and Reduced Topologies

The full and reduced analyses resulted in several conflicting relationships. Shimodaira-Hasegawa (SH) tests (Shimodaira and Hasegawa 1999; Goldman et al. 2000) were employed to determine whether the unique clades recovered from one analysis were significantly different from those recovered from the other. Constraint trees were created in MacClade (Maddison and Maddison 2003) by altering the topology of the optimal tree recovered from each (full or reduced) analyses. Topologies were altered to test each set of alternate relationships separately while the remainder of the tree retained the topology recovered from that analysis (table 1). To determine whether these constrained trees had significantly poorer fit to the data than the unconstrained tree, they were examined with the SH test as implemented in PAUP*, with full optimization and 1000 bootstrap replicates (one-tailed test).

Estimation of Divergence Times

Molecular dating for Gesneriaceae is difficult because of the lack of a macrofossil record. The relatively unsculptured tricolp(or)ate pollen characteristics of the New World taxa are too generic to reliably assign fossil pollen to Gesneriaceae, although one report of gesneriaceous pollen has been attributed to a New Zealand sample of Quaternary age (Mildenhall 1980). Ideally, a molecular clock would allow us to use a single global substitution rate (Richardson et al. 2001; Bramley et al. 2004; Bartish et al. 2005; Rutschmann 2006). However, a likelihood ratio test indicated that our data are not evolving at a clocklike rate ($P < 0.005$); therefore, we could not rely on this method.

Alternatively, geological events can be used to place a maximum age on a clade. This approach has already been executed successfully for other Gesneriaceae (Clark et al. 2008, 2009; Roalson et al. 2008). Unfortunately, this provides only a single calibration point for Coronanthereae, with the presence of the oldest emergent seamounts of the Lord Howe Ridge dated to

analysis. Ornithophily (within Coronanthereae only) is designated with red lines, and shifts away from ornithophily are designated with blue branches. Floral images adjacent to generic names are examples of flowers for that genus. Asterisks indicate where there have been transitions to radial symmetry. Thin black vertical lines to the right of the tree designate fruit types, thick black lines represent tribal classifications and clades of Coronanthereae discussed in the text, and gray lines represent geographic regions. Nodes that collapse in the strict consensus of the MP, ML, and BI trees are indicated with arrows. Abbreviations for tribes within subfamily Gesnerioideae: Co = Coronanthereae, Na = Napeantheae, Be = Beslerieae, Si = Sinningieae, Sp = Sphaerorrhizeae, Ep = Episcieae, Gl = Gloxinieae, Ge = Gesnerieae, CY = Cyrtandroideae; Abbreviations for geographic regions: SA = South America, AU = Australia, LHI = Lord Howe Island, NC = New Caledonia, NZ = New Zealand. Photographs by Serge Aubert (*Asteranthera*), Hugh Nicholson (*Fieldia*, *Lenbrassia*), Vincent Woo (*Coronanthera*, *Depanthus*, *Mitraria*, *Rhabdothamnus*), and Robert Stewart (*Negria*, *Sarmienta*).

Table 1

Results of Shimodaira-Hasegawa Tests with Constrained Topologies Tested against the Full and Reduced Data Sets

Topology	Full–data set *P*	Reduced–data set *P*
(((*Asteranthera*, *Sarmienta*) *Fieldia*) *Mitraria*)	NA	<.001[a]
(((*Negria*, *Depanthus*) *Lenbrassia*) (*Coronanthera*, *Rhabdothamnus*))	NA	.001[a]
(((*Negria*, *Depanthus*) *Lenbrassia*) (((*Asteranthera*, *Sarmienta*) *Fieldia*) *Mitraria*))	NA	.001[a]
((((*Lenbrassia*, *Depanthus*) *Negria*) ((*Asteranthera*, *Fieldia*) (*Sarmienta*, *Mitraria*)))	NA*	.069
((*Asteranthera*, *Fieldia*) (*Sarmienta*, *Mitraria*))	.052	NA
((*Depanthus*, *Lenbrassia*), *Negria*) (((*Asteranthera*, *Sarmienta*) *Fieldia*) *Mitraria*))	.084	NA
((*Negria*, *Depanthus*) *Lenbrassia*) (*Coronanthera*, *Rhabdothamnus*))	.062	NA
((*Depanthus*, *Negria*), *Lenbrassia*) (((*Asteranthera*, *Sarmienta*) *Fieldia*) *Mitraria*)	.152	NA*
(Coronanthereae) (Gesnerioideae less Napeantheae and Beslerieae)	.178	NA
Coronanthereae (Napeantheae, Beslerieae)	NA	<.001[a]

Note. See "Species Sampling" for definition of the data sets. NA indicates that the topology was recovered in the analyses from that data set. NA* indicates clades where the topology differed from that of the other data set only in the placement of *Negria*, *Depanthus*, and *Lenbrassia*.

[a] Significant differences were recovered.

23 million years ago (Ma; McDougall et al. 1981; McDougall and Duncan 1988). All other regions are older than estimates for the age of Gesneriaceae itself (Bremer et al. 2004).

A final option is to rely on other analyses that have used fossils to calibrate a point in our tree. There are arguments against the use of such secondary calibration points (Shaul and Graur 2002; Graur and Martin 2004), but other authors have argued that the inclusion of secondary calibration dates for clades that lack fossils can be a means of improving calibration (Kumar and Hedges 1998; Wang et al. 1999; Hedges and Kumar 2004; Hedges et al. 2004). Recent analyses of the age of asterids can be used to place the origin of Gesneriaceae between a stem age of 78 Ma and a crown age of 71 Ma (Bremer et al. 2004).

Our molecular dating analysis was calibrated with the age of the seamounts of the Lord Howe Ridge (23 Ma) for the maximum age of clade B (fig. 3) because *Negria* is endemic to Lord Howe Island. A second calibration dated the root (fig. 3) with a minimum age of 78 Ma (Bremer et al. 2004). Roalson et al. (2008) determined ages for several clades of Gesnerioideae that were also sampled in our analysis. These dates could also serve as secondary calibrations, but taxon sampling differed between analyses. For example, in our analysis, the tribe Episcieae was sampled with *Columnea* and *Glossoloma*, two genera that are known to have diverged more recently in the tribe (Clark et al. 2006), whereas Roalson et al. (2008) include both *Lembocarpus* and *Paradrymonia*, genera from clades that are sister to the remainder of the tribe (Clark et al. 2006). Rather than introduce potential errors in calibrations (Hedges and Kumar 2004) by including these dates, we compared the ages recovered from the analyses here to those of Roalson et al. (2008).

Age estimates were calculated for the reduced analysis data set with BEAST v. 1.4.8 (Drummond and Rambaut 2005), which provides Bayesian credibility values. For these analyses, we assumed a TVM+I+G substitution model, which was indicated as optimal under an AIC criterion in MODELTEST (Posada and Crandall 1998), a Yule speciation model (a birth-death speciation model gave the same results), and an uncorrelated relaxed lognormal clock as recommended by Drummond and Rambaut (2005). Clade B (fig. 3), consisting of *Lenbrassia*, *Negria*, and *Depanthus*, was calibrated via lognormal calibration and a zero offset (essentially the age constraint) of 23.0 million years, and the second calibration included the entire tree and was likewise calibrated with a zero offset of 78.0 million years. Penalized likelihood (Sanderson 2002) was also used to estimate the ages by means of the branch lengths and topology of figure 3. Cross-validation was conducted to obtain the optimal smoothing value. Increments were set at 0.5, with 14 steps. To examine the effect of smoothing values on our data, we ran several separate analyses with smoothing values ranging from 2 to 100.

Ancestral-Area Reconstruction

Distribution areas for the taxa were coded according to figure 2 as Old World (not South Pacific), New World, Australia, New Zealand, New Caledonia, and Lord Howe Island. *Coronanthera grandis* is known from the Solomon Islands but was not sampled as part of our analysis. Therefore, the Solomon Islands were not coded here. Following the example of Clark et al. (2008), we estimated ancestral area with four different methods: (1) standard Fitch parsimony optimization (FPO; Fitch 1971) using Mesquite v. 2 (Maddison and Maddison 2006); (2) dispersal-vicariance analysis either with no constraints or limiting the number of ancestral areas to two (DIVA; Ronquist 1996, 1997); (3) stochastic mapping (SM) with SIMMAP v. 1.0 (Bollback 2005); and (4) dispersal-extinction-cladogenesis (DEC) analysis with lagrange (Ree et al. 2005; Ree and Smith 2008). Lagrange requires an ultrametric tree and priors on the connections between geographic regions that can vary over time. Priors were based on the inverse of the linear distance between areas and were normalized by dividing all values by the largest inverse (minimum) distance. Distances between large continental regions were based on the current distribution of Coronantheae in southern South America and Australia and the closest linear distance from these to other regions. For the Old World, the shortest distance between geographic areas was used (regardless of whether this was to Africa or to Asia). Since vicariance for the Southern Hemisphere is considered unlikely after 35 Ma, we opted to split our priors into two time-related sets. One was based on current distances from the present to 35

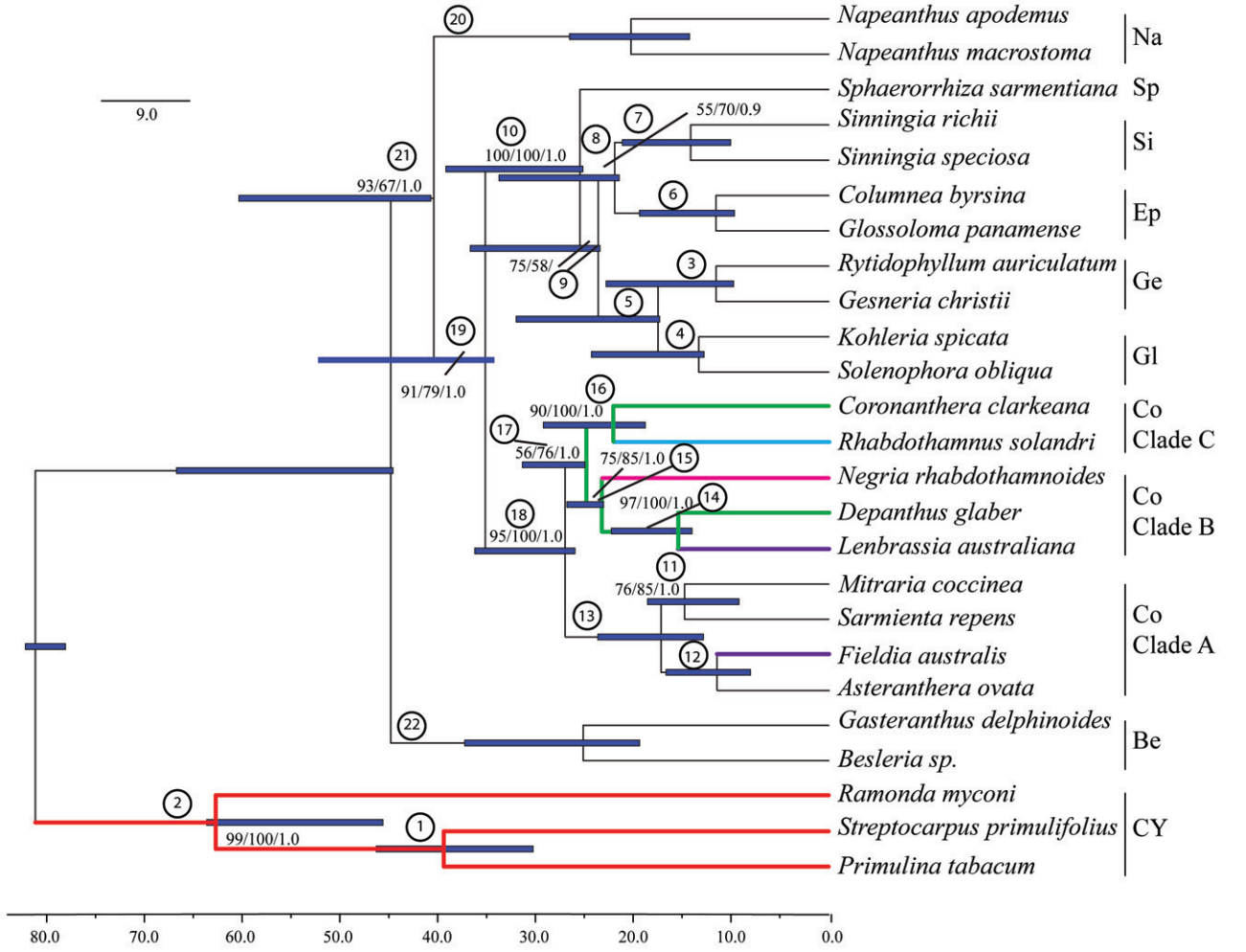

Fig. 3 Maximum parsimony (MP), maximum likelihood (ML), and Bayesian analyses of the reduced analysis. MP bootstrap/ML bootstrap/Bayesian posterior probability values are indicated above branches. Note that all branches have values of 100/100/1.0 unless otherwise shown. A time line is presented at the bottom, and branch lengths are proportioned according to divergence times. Blue boxes on branches represent 95% Bayesian credibility limits as determined from BEAST (Drummond and Rambaut 2005). Numbers in circles above branches mark clades referred to in table 6. Branches are colored according to geographic distribution and ancestral-area reconstructions as described in the text (note that alternative ancestral-area reconstructions were recovered with unconstrained DIVA and dispersal-extinction-cladogenesis analyses for nodes 12 and 15 [table 6]): red for Old World, black for New World, green for New Caledonia, purple for Australia, pink for Lord Howe Island, and blue for New Zealand. Abbreviations for tribes within subfamily Gesnerioideae: Na = Napeantheae, Sp = Sphaerorrhizeae, Si = Sinningieae, Ep = Episcieae, Ge = Gesnerieae, Gl = Gloxinieae, Co = Coronanthereae, Be = Beslerieae, CY = Cyrtandroideae.

Ma, and the other was based on older distributions of continents and covered the time frame for the origin of Gesneriaceae (35–80 Ma). For these latter regions, a map from the late Cretaceous was used to determine distances (http://australianmuseum.net.au/image/Map-of-world-late-Cretaceous). Lord Howe Island was not emergent before 23 Ma, so all priors to this region were set to 0 for the earlier time period. Clearly, factors other than linear distance determine likelihood of dispersal. However, linear distance does provide a justifiable means for setting priors. The priors for both time periods are presented in table 2. The ultrametric tree from figure 3 was used. The python script for the analysis was generated with the online configurator (http://www.reelab.net/lagrange/configurator/index) and run with the lagrange software.

Character State Evolution

Morphological character states of importance and interest for Coronanthereae (table 3) were scored on the basis of the literature, examination of specimens, or in the case of pollen, direct examination for this study (V. L. Woo, unpublished results). Floral and fruit characters for members of Coronanthereae were mapped onto figure 2 by use of both FPO in Mesquite v. 2.0 (Maddison and Maddison 2006) and SM with SIMMAP v. 1.0 (Bollback 2005). These characters were selected because fruit characters have been important in determining classification within Coronanthereae and floral characters have been considered important in the evolution and radiation of this group in the South Pacific.

Table 2

Priors Used for Connections between Geographic Regions in the Dispersal-Extinction-Cladogenesis (DEC) Analysis to Resolve Ancestral Distribution Areas of Coronanthereae

Geographic region	Prior for 35–80 Ma	Prior for present to 35 Ma
New World/Old World (1/2)	.23	.16
New World/Australia (1/3)	.08	.05
New World/New Caledonia (1/4)	.06	.05
New World/New Zealand (1/5)	.06	.06
New World/Lord Howe Island (1/6)	0	.05
Old World/Australia (2/3)	.19	.1
Old World/New Caledonia (2/4)	.2	.07
Old World/New Zealand (2/5)	.13	.06
Old World/Lord Howe Island (2/6)	0	.06
Australia/New Caledonia (3/4)	.5	.46
Australia/New Zealand (3/5)	.63	.24
Australia/Lord Howe Island (3/6)	0	.33
New Caledonia/New Zealand (4/5)	.4	.33
New Caledonia/Lord Howe Island (4/6)	0	.33
New Zealand/Lord Howe Island (5/6)	0	1.0

Note. Values were estimated by using the inverse of the linear distance between the areas based on their current (present to 35 Ma) and earlier (35–80 Ma) distributions and by scaling such that the maximum value (minimum distance) was 1.0. Numbers in parentheses after the geographic regions match the numerical values used in table 6. See "Material and Methods" for more details.

Results

The sequence characteristics for each DNA region are given in table 4.

Test of Incongruence

The partition homogeneity test (full analysis: $P = 0.0558$; reduced analysis: $P = 0.150$) did not find significant differences between any partitions. Likewise, BS analyses of each of the partitions did not detect any discrepancies that received BS >65 for either the full or the reduced analysis (trees not shown). Therefore, a combined analysis of the DNA regions was performed for both full and reduced analyses and is the basis for all results and discussion. We were unable to obtain amplifications for all cpDNA and ITS regions for all species in the full analysis. Phylogenetic analyses of each region separately did not indicate any discrepancies among trees; therefore, we present here the full analyses, including only the species for which we obtained sequences for all regions.

Maximum Parsimony Analysis

MP analysis resulted in 84 trees of 2106 steps (CI = 0.52, RI = 0.77, RC = 0.44) for the full analysis (fig. 2) and one tree of 5081 steps (CI = 0.5422, RI = 0.5933, RC = 0.3965; fig. 3) for the reduced analysis.

Maximum Likelihood and Bayesian Inference

The ML analyses used the TIM+Γ+I model, as suggested by MODELTEST 3.6, for the full analysis. The analysis produced one tree ($-\ln = 15,416.330$; fig. 2). The BI analyses recovered trees and strongly supported clades similar to those from the ML analyses (fig. 2). For the reduced analysis, ML and BI produced identical trees (fig. 3) that also matched the MP tree. The output from AWTY indicated that the separate chains approximated the same target distribution for both the full and reduced analyses (fig. 4).

Monophyly and Relationships of Coronanthereae within Gesnerioideae

The nine genera of Coronanthereae form a well-supported clade in our results (MPBS = 100, MLBS = 100, BI = 1.0; fig. 2; MPBS = 95, MLBS = 100, BI = 1.0; fig. 3). The position of Coronanthereae within Gesnerioideae was somewhat problematic in our full analysis because support for relationships among Coronanthereae, Beslerieae, Napeantheae, and a clade of the remaining Gesnerioideae was low (fig. 2). However, the reduced analysis provided solid support for the placement of Coronanthereae as sister to a clade comprising Sphaerorrhizeae, Gloxinieae, Gesnerieae, Episcieae, and Sinningieae (MPBS = 91, MLBS = 79, BI = 1.0; fig. 3).

Relationships within Coronanthereae

Three distinct and well-supported lineages are found within Coronanthereae. In all instances where more than a single individual per species or species per genus (*Coronanthera* only) were sampled, the species and genera were recovered as monophyletic (fig. 2), including separate analyses of each cpDNA region and ITS (results not shown) that included species lacking one or more of the other regions.

Clade A includes four monospecific genera (*Asteranthera*, *Sarmienta*, and *Mitraria* from South America and *Fieldia* from

Table 3

Morphological Comparison of Tribe Coronanthereae

	Clade A				Clade B			Clade C	
	Asteranthera	*Sarmienta*	*Mitraria*	*Fieldia*	*Depanthus*	*Negria*	*Lenbrassia*	*Rhabdothamnus*	*Coronanthera*
Habit	Facultative epiphyte creeper	Facultative epiphyte creeper	Epiphyte subshrub	Facultative epiphyte shrub	Tree	Tree	Tree	Shrub	Shrub tree
Leaf arrangement	Opposite	Opposite	Opposite	Opposite	Opposite	Whorled	Opposite	Opposite	Opposite
Flower shape	Zygomorphic	Zygomorphic	Zygomorphic	Actinomorphic	Actinomorphic	Zygomorphic	Zygomorphic	Zygomorphic	Zygomorphic
Flower color	Red	Red	Red	White-yellow	White	Orange	Yellow	Orange-red	White, green, yellow, pink, purple-brown
Inflorescence	Single axillary	Single axillary	Single axillary	Single axillary	Axillary cyme 1–3-flowered	Axillary cyme 1–3-flowered	Axillary cyme 1–3-flowered	Single axillary	Axillary cyme 1–8-flowered
Stamens	4	2	4	4	5	4	4	4	4
Anthers	Coherent	Free	Coherent	Free	Free	Free	Coherent	Coherent	Coherent
Pollen shape	Prolate	Perprolate	Perprolate	Prolate	Spheroidal	Spheroidal	Prolate	Spheroidal	Spheroidal
Pollen size (polar/equatorial lengths; μM)	18/12	31/14	38/19	25/15	12/10	21/20	22/18	26/14	10/9
Fruit type	Berry	Berry	Berry	Berry	Dry capsule	Dry capsule	Berry	Dry capsule	Dry capsule
Fruit dehiscence	Indehiscent	Indehiscent	Indehiscent	Indehiscent	2 valves	2 valves	Indehiscent	4 valves	4 valves
Seeds	Flattened cell crests; edges smooth	Flattened cell crests; edges smooth	Flattened cell crests; edges smooth	Flattened cell crests; edges smooth	Discrete cell crests; edges undulate	Discrete cell crests; edges smooth	Cell crests not flattened; edges undulate	Discrete cell crests; edges undulate	Discrete cell crests; edges undulate
Chromosome number (n)	Unknown	37	37	40	Unknown	45	Unknown	37	Unknown

Note. Chromosome numbers from Ratter (1963). Seed cell characters from Beaufort-Murphy (1983). Pollen characters from V. L. Woo (unpublished results).

Table 4

Nucleotide Sequence Characteristics of Regions Used for the Current Study

Parameter	ITS	*trnL-trnF* spacer	*trnE-trnT* spacer[a]	*psbA-trnK*[a]	GCYC1E	GCYC1F	*trnL* intron	*ndhF*	*rpl20-rps12* spacer
No. sequences	87	47	47	47	7	25	25	25	25
Length range (bp)	382–469	840–894	646–794	174–242	615–621	542–606	481–505	2015–2044	690–779
Length mean (bp)	425	878	757	221	617	548	486	2035	731
Aligned length (bp)	574	991	884	255	621	704	534	2071	817
G/C content range (%)	49.5–59.5	34.4–36.2	29.9–31.4	28.1–31.7	37.6–40.8	38.2–45.7	34.6–38.4	32.0–33.5	33.7–36.1
G/C content mean (%)	55.1	35.5	30.9	29.6	40.0	40.3	35.7	33.0	34.5
No. indels	24	19	17	6	3	35	13	2	11
Size of indels (bp)	2–10	2–24	2–78	2–11	6	3–54	2–17	6–9	2–9
Constant sites (%)	16.2	77.5	71.2	67.8	85.5	43.3	66.5	61.3	62.4
Autapomorphic sites (%)	15.3	10.2	15.7	13.3	12.1	24.0	19.5	21.1	22.5
Informative sites (%)	68.5	12.3	13.1	18.8	2.4	32.7	14.0	17.6	15.1
Sequence divergence (%)	.0–49.5	.0–8.6	.0–10.8	.0–15.3	2.1–4.7	2.4–41.2	.0–11.8	1.6–13.7	2.4–14.2

[a] Sequences used only for the full taxon sampling analyses (fig. 2).

Australia), all with indehiscent fleshy fruits (table 3), and we recognize this as subtrib. Mitrariinae J. Hanst. in appendix B. *Fieldia* is sister to the *Asteranthera* + *Sarmienta* pair (MPBS = 77, MLBS = 79, BI = 0.98; fig. 2). Additional data (albeit with fewer individuals) provide alternative relationships of *Asteranthera* as sister to *Fieldia*, with maximum support (MPBS = 100, MLBS = 100, BI = 1.0; fig. 3), and of *Mitraria* as sister to *Sarmienta* (MPBS = 76, MLBS = 85, BI = 1.0).

Clade B includes three monospecific genera, *Lenbrassia*, *Negria*, and *Depanthus*, that share an arborescent growth form (fig. 1; table 3); for this clade we formalize the name subtrib. Negriinae V.L.Woo, J.F.Smith, & Garn.-Jones in appendix B. This clade is strongly supported in the full analysis (MPBS = 100, MLBS = 99, BI = 1.0; fig. 2) and in the reduced analysis (MPBS = 75, MLBS = 85, BI = 1.0; fig. 3). The Australian *Lenbrassia* is sister to the southwest Pacific *Negria* + *Depanthus* pair (MPBS = 91, MLBS = 94, BI = 1.0) in the full analysis, but *Lenbrassia* is sister to *Depanthus* in the reduced analysis (MPBS = 97, MLBS = 100, BI = 1.0; fig. 3), with *Negria* sister to these two genera (MPBS = 75, MLBS = 85, BI = 1.0; fig. 3).

Clade C, comprising the monospecific New Zealand *Rhabdothamnus* (fig. 1) as sister to *Coronanthera* of New Caledonia, is strongly supported (MPBS = 100, MLBS = 100, BI = 1.0; fig. 2; MPBS = 90, MLBS = 100, BI = 1.0; fig. 3). The two genera have vegetative similarities in their leaf indumentum, although many *Coronanthera* are glabrous, and they share similar fruits (table 3). We recognize this clade as subtrib. Coronantherinae, with an emended circumscription (app. B). Monophyly of *Coronanthera* is also well supported (MPBS = 98, MLBS = 99, BI = 1.0; fig. 2), and there is moderate support for two sister clades within the genus, one comprising plants with glabrous leaves and the other plants with mostly scabrid leaves.

Comparison of Full and Reduced Analyses

Results of the SH tests are presented in table 1. These tests indicate that none of the constraints based on the topology of the reduced analysis could be rejected when that analysis was compared to the full analysis and its data set. However, one of these (constraining the topology of *Sarmienta*, *Mitraria*, *Asteranthera*, and *Fieldia*) was nearly significant, with $P = 0.052$. In contrast, only one constraint from the full analysis could not be rejected when that analysis was compared to the reduced analysis and its corresponding data set. This was the relationship of clade B as sister to clade A ($P = 0.069$) when the relationships among genera within clade B were retained as those in the reduced analysis.

Estimated Ages of Lineages

Ages for nodes and 95% Bayesian credibility values as determined from BEAST and r8s are presented in table 5 and figure 3. Coronanthereae were estimated to originate 26.9 Ma (range 36.0–25.0) or 27.1 Ma, on the basis of results from BEAST (with 95% credibility values) and r8s, respectively. Likewise, ages were 17.2 (23.0–13.6) or 16.7 Ma for the origins of Mitrariinae (clade A), 23.1 (26.0–23.1) or 19.2 Ma for Negriinae (clade B; note that this node was a constrained age), and 22.0 (29.5–18.0) or 17.9 Ma for Coronantherineae (clade C). Cross-validation in r8s gave an optimal smoothing value of 16 that was used for the dates presented here. Varying the smoothing value did not substantially change the dates obtained for nodes on the tree. Ages for tribes within Gesnerioideae determined here were within the 95% confidence intervals obtained by Roalson et al. (2008), who used geological events to calibrate their estimates (table 5; fig. 3). The one exception was the Episcieae clade and was largely due to taxon sampling differences, as mentioned in "Estimation of Divergence Times."

Ancestral-Area Reconstructions

Four analyses (FPO, DIVA limited to two ancestral areas [cDIVA], SM, and DEC) gave nearly identical optimal patterns of ancestral-area reconstruction, depicted in figures 3 and 5. Unconstrained DIVA (ucDIVA) analysis produced alternative scenarios with either the ancestral area shown in figure 3 or a widespread ancestor for Coronanthereae distrib-

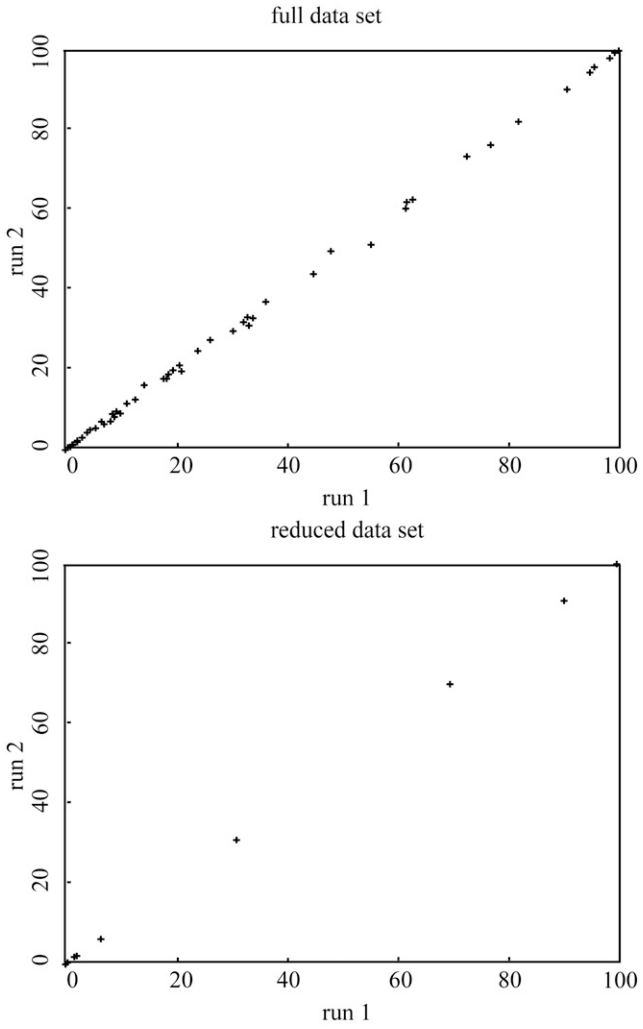

Fig. 4 Bivariate plots of split frequencies in the first and second runs of Bayesian analyses for the full (top) and reduced (bottom) analyses as produced by AWTY software (Nylander et al. 2008).

uted over all coded geographic regions (table 6). Lagrange also produced an optimal distribution that differed from those of other analyses for nodes 12 and 15 (fig. 3; table 6). For node 12 (*Fieldia* and *Asteranthera*), most analyses indicated the New World alone as the ancestral area, but both ucDIVA and DEC indicated that the New World and Australia were both ancestral areas (table 6). Although DEC selected these two areas as optimal with a relative probability of 0.683, the next most likely ancestral-area reconstruction for node 12 was the New World alone (relative probability of 0.2939; table 6), which matches the optimal ancestral area recovered from other methods. For node 15 (clade B), FPO, SM, and cDIVA selected an ancestral area of New Caledonia alone, whereas ucDIVA and DEC had an optimal distribution for this clade that encompassed both New Caledonia and Lord Howe Island (relative probability of 0.2694; table 6). However, the next alternative distribution from DEC was New Caledonia alone, with a relative probability of 0.2222 (table 6).

Regardless of any minor alternative scenarios, Coronanthereae have a South American origin, with two migrations to the South Pacific. One of these was that of the ancestor of *Fieldia australis* directly to Australia or the ancestor of *Fieldia* and *Asteranthera* directly to Australia (DEC; table 6). The second involved migration to New Caledonia (or New Caledonia and Lord Howe Island), with migration events to Australia, New Zealand, and Lord Howe Island (if the latter was not already part of the ancestral distribution, as optimized by DEC; table 6). Although *Coronanthera grandis* from the Solomon Islands was not sampled, we assume monophyly of *Coronanthera* on the basis of morphological characters and postulate another migration from New Caledonia to these islands (fig. 5).

Character State Evolution

Morphological character states are summarized in table 3. Both FPO and SM gave identical results regarding fruit and floral character state transitions, and these are presented in figure 2. On this tree, the berry fruit found in all South American and Australian species is interpreted to have a single origin, with a switch to the dehiscent two-valved capsule and a separate switch from the baccate to the dehiscent four-valved capsule. There are three independent shifts from ornithophily to insect pollination, one each in *Fieldia*, *Depanthus*, and *Coronanthera*, and two shifts from bilateral toward radial symmetry, once each in *Fieldia* and *Depanthus*.

Discussion

Monophyly and Relationships of Coronanthereae

The circumscription of Coronanthereae is clearly monophyletic in both the full (fig. 2) and reduced analyses (fig. 3). Likewise, where more than a single population was sampled, all species and genera were recovered as monophyletic (fig. 2).

Table 5

Divergence Date Estimates (Ma) Based on Results from BEAST (Drummond and Rambaut 2005) and Penalized Likelihood (Sanderson 2002) from r8s

Group	BEAST	r8s
Gesnerioideae	(66.0) 44.8 (44.81)	47.9
Beslerieae	(37.5) 25.1 (21.0)	23.8
Napeantheae	(33.5) 20.2 (14.5)	18.31
Coronanthereae + remainder of Gesnerioideae	(52.0) 35.1 (35.2)	34.6
Coronanthereae	(36.0) 26.9 (26.0)	27.2
Mitrariinae	(23.0) 17.2 (13.5)	16.7
Negriinae	(26.0) 23.1 (23.1)[a]	19.2[a]
Coronantherineae	(29.5) 22.0 (18.0)	17.9
Negriinae + Coronantherineae	(31.0) 24.7 (24.7)	23.9
Remainder of Gesnerioideae	(39.0) 25.4 (25.0)	23.5

Note. Calibration points were the origin of Gesneriaceae at 78 Ma (Bremer et al. 2004) and, for Negriinae, 23 Ma. Parenthetical values for BEAST represent 95% Bayesian credibility values.

[a] Dates were constrained in the analyses.

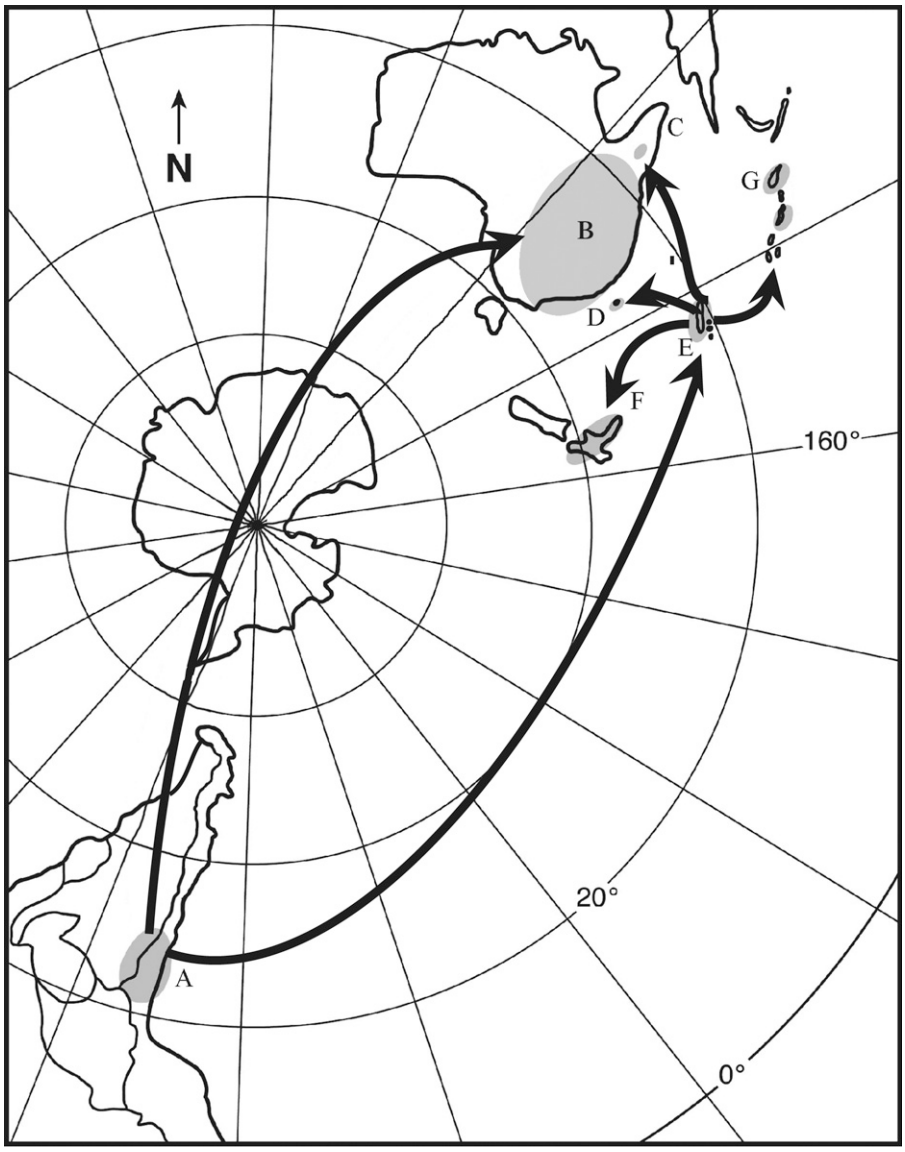

Fig. 5 Proposed path of long-distance dispersal of tribe Coronanthereae with two separate dispersal events from South America (adapted from Meudt and Simpson 2006): *A*, Chile and Argentina (*Asteranthera*, *Mitraria*, *Sarmienta*); *B*, Australia (*Fieldia*); *C*, Queensland, Australia (*Lenbrassia*); *D*, Lord Howe Island (*Negria*); *E*, New Caledonia (*Coronanthera*, *Depanthus*); *F*, New Zealand (*Rhabdothamnus*); *G*, Solomon Islands (*Coronanthera*). Note that *Coronanthera grandis* from the Solomon Islands was not included in our phylogenetic analysis. It is placed here on the basis of morphology shared with the remainder of the genus, which is found entirely on New Caledonia, and the migration from New Caledonia to the Solomon Islands, as depicted here, remains untested. Note that alternative ancestral areas reconstructions were recovered using unconstrained DIVA and dispersal-extinction-cladogenesis analyses for nodes 12 and 15 (table 6).

The placement of this clade, in either the full or reduced analyses, does not support its classification as a third subfamily, as proposed by Wiehler (1983), and our results are more in line with recent findings based on molecular phylogenetics. Smith et al. (1997) and Smith (2000*c*), using *ndhF*, *rbcL*, and morphology, found Coronanthereae to be sister to the remainder of Gesnerioideae, but this relationship was not strongly supported, nor was taxon sampling extensive within any tribe. Mayer et al. (2003) found that the Coronanthereae were a distinct lineage related to Gesnerioideae but did not fully resolve this relationship on the basis of cpDNA alone. To retain Gesnerioideae as monophyletic, the Coronanthereae clade should be recognized at the tribal (Fritsch 1893–1894) rather than the subfamilial (Wiehler 1983) rank. Demotion of subfamily Coronantheroideae to a single tribe Coronanthereae requires recircumscription of the tribe to (1) include the Mitrarieae of Burtt (1963), (2) form a single entity, Coronanthereae, and (3) place this one tribe within Gesnerioideae. Although our results suggest that geography and nectary structure are no longer considered evidence that justifies subfamily status, they are certainly useful in distinguishing this group from other members of the New World subfamily Gesnerioideae.

The placement of Coronanthereae as sister to Beslerieae/Napeantheae (fig. 2) is similar to results suggested by other molecular studies of Gesneriaceae (Smith et al. 2004*b*; Wang et al. 2004) that used fewer representatives of Coronanthereae. Likewise, the placement of Coronanthereae as sister to a clade of all Gesnerioideae except Beslerieae/Napeantheae (fig. 3) has been seen previously (Smith et al. 2006). Comparison between the two topologies indicates that neither the relationships among Coronanthereae that were unique to the reduced analysis nor the placement of the tribe as sister to Gesnerioideae except Napeantheae + Beslerieae can be rejected in a comparison between the full and reduced analyses and their data sets (table 1). In contrast, nearly all relationships within Coronanthereae recovered as unique in the full analysis and the placement of the tribe as sister to Napeantheae + Beslerieae can be rejected when compared against the reduced-analysis topology and its corresponding data set. The one topology that cannot be rejected by either data set is the position of clade B as sister to either clade A or clade C. This is the most weakly supported clade in the entirety of the reduced analysis (fig. 3). The differences between the analyses and the fact that the full analysis could not reject the topologies of the reduced analysis (and not vice versa) are likely due to the greater number of characters that were included in the reduced analysis.

Relationships within Coronanthereae

The presence of three distinct lineages (figs. 2, 3) was surprising, given that previous taxonomic treatments recognized at most two subgroups (Fritsch 1893–1894; Burtt 1963). However, a closer examination of morphological characters in each of these clades provides additional support, beyond the molecular data, for their monophyly.

Clade A: Mitrariinae. This predominantly South American clade is strongly supported (MPBS = 98, MLBS = 100, BI = 1.0; fig. 2; MPBS = 100, MLBS = 100, BI = 1.0; fig. 3) and contains facultative and obligate epiphytes (Fernanda Salinas et al. 2010; fig. 1) with indehiscent berry fruits (table 3; fig. 2). These plants occupy similar understory habitats in moist forests (Weber 2004; Fernanda Salinas et al. 2010). This grouping has previously been recognized (as Mitrariinae Fritsch and Mitrarieae Burtt) on the basis of its fleshy fruits (table 3), but its circumscription did not include *Fieldia*. Fleshy, indehiscent fruits also are seen in tribes Beslerieae and Episcieae, but these are anatomically distinct from the fruits of Coronanthereae (Wiehler 1983). Seeds of the four species in this clade are characterized by distinctively broad and flattened cell crests seen in only one other genus, *Neomortonia*, in Episcieae (Beaufort-Murphy 1983).

Relationships among genera in Mitrariinae differed between the full and reduced analyses (figs. 2 and 3, respectively). Although none of the relationships from the reduced analysis could be rejected by the full analysis on the basis of SH tests (table 1), the relationship recovered in the reduced analysis is close to being rejected by the full analysis ($P = 0.52$). This is likely due to the strong support for relationships among taxa in both analyses (figs. 2, 3). The discrepant relationships are thus difficult to explain.

Clade B: Negriinae. This clade of three species from Australia, Lord Howe Island, and New Caledonia is well supported as monophyletic (MPBS = 100, MLBS = 99, BI = 1.0; fig. 2; MPBS = 75, MLBS = 85, BI = 1.0; fig. 3). Although the fleshy fruit of *Lenbrassia* has suggested a close affinity to members of clade A, closer examination of the fruit from herbarium specimens points to a beaked shape and a structure similar to those of the septicidally dehiscent and lignacious fruits of both *Negria* and *Depanthus* (table 3). Vegetative characters of the two latter genera are grossly similar (table 3). *Lenbrassia* either is sister to *Negria* + *Depanthus* (fig. 2) and suggests a single reversion from fleshy to dehiscent capsular fruit or, alternatively, is sister to *Depanthus* (fig. 3) and implies a reversion to the berry fruit from a two-valved, dehiscent capsule. The SH tests indicated that the latter topology cannot be rejected by the full analysis, whereas the position of *Lenbrassia* as sister to *Depanthus* + *Negria* can be rejected by the reduced analysis.

The woody habit (fig. 1) of the three species within this clade might indicate a woody ancestor or reflect common ecological pressures acting independently in each species. The development of woodiness as a derived character, often seen on islands, highlights the lability of this character (Carlquist 1974). Gesneriaceae, a predominantly herbaceous family, does have some tree species, many of which occur in Coronanthereae (Wiehler 1994). Insular woodiness may be an adaptation for longevity in low-pollinator habitats, although other hypotheses for this phenomenon are also plausible (Francisco-Ortega et al. 2000). Alternatively, the placement of clade B as sister to clade C in figure 3 would indicate a single origin of woodiness. Unfortunately, neither of these relationships is strongly supported in either the full or the reduced analysis, and neither topology can be rejected by the other on the basis of SH tests (table 1).

Clade C: Coronantherineae. This clade of two genera is also well supported in our analyses (MPBS = 96, MLBS = 100, BI = 1.0; fig. 2; MPBS = 90, MLBS = 100, BI = 1.0; fig. 3) and is supported morphologically by the presence of four-valved, dry capsules (fig. 2; table 3). This clade also includes only woody plants (fig. 1), which supports the sister-group relationship to clade B recovered in the reduced-sampling analysis (MPBS = 56, MLBS = 76, BI = 1.0; fig. 3). However, see the discussion of clade B for alternative interpretations regarding the phylogenetic relationships of clades B and C.

Generic Circumscriptions

Most genera in the tribe are monospecific; the notable exception is *Coronanthera*, with ~20 species (V. L. Woo and P. J. Garnock-Jones, unpublished data). However, previous workers have proposed reducing *Fieldia* to synonymy of *Lenbrassia* and reducing *Depanthus* to synonymy of *Coronanthera* (Burtt 1998, 1999). Our findings support Weber (2004) in rejecting these changes. First, facultatively epiphytic *Fieldia* is shown to be related to South American epiphytes and are placed by us in Mitrariinae. Its similarity with *Lenbrassia*, indehiscent fruits, is likely to be a symplesiomorphy. Second, *Coronanthera* and *Depanthus* include shrubs and trees with small, often pale, flowers that approach actinomorphy of the corolla limb, but we found them not to be closely re-

Table 6

Results from Four Ancestral-Area Reconstruction Methods

Clade	FPO	SM	Posterior probability	ucDIVA	cDIVA	Lagrange	−LnL/relative probability
1	010000	010000	1.0	010000	010000	010000	36.64/.9837
2:							
	010000	010000	1.0	010000	010000	010000	36.84/.7639
	NA	NA	NA	NA	NA	110000	38.77/.1116
	NA	NA	NA	NA	NA	100000	39.96/.03384
3	100000	100000	1.0	100000	100000	100000	36.57/.9996
4	100000	100000	1.0	100000	100000	100000	36.57/.9996
5	100000	100000	1.0	100000	100000	100000	36.57/.9998
6	100000	100000	1.0	100000	100000	100000	36.57/.9998
7	100000	100000	1.0	100000	100000	100000	36.57/.9998
8	100000	100000	1.0	100000	100000	100000	36.57/.9998
9	100000	100000	1.0	100000	100000	100000	36.58/.9977
10	100000	100000	1.0	100000	100000	100000	37.35/.4614
11	100000	100000	1.0	100000	100000	100000	36.96/.683
12:[a]							
	100000	100000	.8	101000	100000	101000	36.96/.683
	NA	NA	NA	NA	NA	100000	37.8/.2939
13:							
	100000	100000	1.0	100000	100000	100000	37.35/.4619
	NA	NA	NA	NA	NA	101000	38.09/.2194
	NA	NA	NA	NA	NA	001000	40.26/.02518
	NA	NA	NA	NA	NA	100100	40.56/.01852
14:							
	000100	000100	.8	000110	000100	000100	37.49/.402
	NA	NA	NA	NA	NA	001000	39.23/.07048
	NA	NA	NA	NA	NA	001100	39.29/.06607
	NA	NA	NA	NA	NA	000001	41.15/.01034
15:[a]							
	000100	000100	.8	000101	000100	000101	37.89/.2694
	NA	001000	.2	000011	NA	000100	38.08/.2222
	NA	NA	NA	000111	NA	001100	38.52/.1433
	NA	NA	NA	NA	NA	001000	39.7/.0438
	NA	NA	NA	NA	NA	100100	40.42/.02134
	NA	NA	NA	NA	NA	001001	40.67/.01665
	NA	NA	NA	NA	NA	001010	41.15/.01032
16:							
	000100	000100	.8	001100	000100	000100	37.89/.2694
	NA	NA	NA	NA	NA	000110	38.08/.2222
	NA	NA	NA	NA	NA	000010	40.41/.0216
	NA	NA	NA	NA	NA	100100	40.57/.01846
	NA	NA	NA	NA	NA	000001	40.67/.01665
	NA	NA	NA	NA	NA	000010	41.15/.01032
17:							
	100000	100000	.8	000100, 001111	100000	100000	37.35/.4619
	NA	NA	NA	NA	NA	001000	38.09/.2194
	NA	NA	NA	NA	NA	000100	38.61/.1313
	NA	NA	NA	NA	NA	000001	39.52/.05251
	NA	NA	NA	NA	NA	000010	39.57/.05021
18:							
	100000	100000	.8	100100, 101111	100000	100000	37.35/.4614
	NA	NA	NA	NA	NA	101000	38.04/.2306
	NA	NA	NA	NA	NA	100100	38.42/.1577
	NA	NA	NA	NA	NA	100001	39.37/.06106
	NA	NA	NA	NA	NA	100010	39.43/.05766
19:							
	100000	100000	1.0	100100, 101111	100000	100000	36.79/.8031
	NA	NA	NA	NA	NA	101000	38.99/.08971
	NA	NA	NA	NA	NA	100100	39.46/.05595
	NA	NA	NA	NA	NA	100001	40.41/.0215
20	100000	100000	1.0	100000, 101111	100000	100000	36.79/.8031
21	100000	100000	1.0	100000	100000	100000	36.65/.9302

Table 6

(*Continued*)

Clade	FPO	SM	Posterior probability	ucDIVA	cDIVA	Lagrange	−LnL/relative probability
21	NA	NA	NA	NA	NA	101000	40.46/.02049
22	100000	100000	1.0	100000, 101111	100000	100000	36.65/.9302

Note. The clade numbers are from figure 3. FPO = Fitch Parsimony Optimization; SM = SIMMAP; ucDIVA = unconstrained DIVA; cDIVA = DIVA with the maximum number of ancestral areas constrained to 2; Lagrange = lagrange analysis with the maximum number of ancestral areas set to 2. The −LnL/relative probability scores are for the optimal reconstructions in lagrange. There was only a single optimal reconstruction for 13 of the splits. Alternative reconstructions are presented with their −LnL/relative probability values, with the smallest negative value listed first. In cases where alternative reconstructions were present for one split but only a single reconstruction for the other, only the highest probability value for that split is presented. NA indicates that no alternative ancestral area reconstructions were recovered for this analysis. Reconstructions are presented in binary format in the order New World, Old World, Australia, New Caledonia, New Zealand, and Lord Howe Island.

[a] Optimal ancestral areas conflicted between analyses (other than ucDIVA).

lated and place them in Coronantherineae and Negriinae, respectively. Their similarities are likely to be convergent.

Pollination, Seed Dispersal, and Flower and Fruit Morphology

Within flowers of Coronanthereae, we observed transitions from bird-pollinated flowers with red, zygomorphic, tubular, wide-throated corollas to insect- or self-pollinated flowers with white or yellow, actinomorphic, campanulate or gibbous, narrow-throated corollas (fig. 2). Our results, based on FPO and SM, suggest three changes from a baseline of ornithophily to pale or white flowers (fig. 2; once each in clades A, B, and C) and two instances of conversion to radial symmetry in (a) white-flowered Australian *Fieldia australis* nested in the red-flowered South American clade Mitrariinae and (b) white-flowered New Caledonian *Depanthus* nested within the yellow-orange bilaterally symmetric clade Negriinae. These shifts from morphologically ornithophilous syndromes to insect- or self-pollinated syndromes and from bilateral to radial symmetry are likely the result of pollinator selection. Lloyd (1985) noted that many New Zealand plants have small, pale flowers that he considered despecialized in relation to overseas relatives; he considered low pollinator numbers and unique pollinator assemblages (particularly a lack of long-tongued bees) as the basis for selection of the generalized pollination syndrome seen in many New Zealand flowers (but see Newstrom and Robertson 2005). Carpenter et al. (2003) found a dominance of small, actinomorphic (often dishlike), white or pale-colored flowers in a study of 123 tropical tree species in New Caledonia and considered that the limited availability of specialist pollinators was a major factor in the selection for generalist flowers there. The similar flower structures seen in New Caledonian *Depanthus* and *Coronanthera* indicate similar ecological pressures, because these genera are not closely related (figs. 2, 3), as Burtt (1998, 1999) had previously suggested.

Biogeography of Coronanthereae

The hypothesis of a Gondwanan origin for Gesneriaceae (Burtt 1998) is based on Coronanthereae having a distribution that bridges the Old and New World subfamilies Cyrtandroideae and Gesnerioideae. Burtt (1998) speculated that Coronanthereae represented a relict group that survived on the Australian plate and invaded the Americas via Antarctica to give rise to Gesnerioideae while the Australasian coronantheroid Gesneriaceae moved northward and gave rise to Cyrtandroideae. For this hypothesis to be supported, Coronanthereae would have to be recovered as a grade of taxa basal to all other Gesneriaceae or at least as a single clade sister to the remainder of the family. Previous molecular studies have placed Coronanthereae in a clade with Gesnerioideae, either as sister to the rest of that subfamily (Smith 2000*c*) or nested within it in a position higher in the tree than the attachment node of tribes Napeantheae and Beslerieae (Smith et al. 2004*b*; Wang et al. 2004). With wider taxon and area sampling than previous studies, our analyses place Coronanthereae as sister to a subclade within Gesnerioideae that does not include Napeantheae and Beslerieae (fig. 3). These findings are consistent with earlier molecular analyses and refute the hypothesis that Coronanthereae represents a basal grade in the family and that its geographic distribution is an ancestral area for Gesneriaceae.

Additional refutation for the Gondwanan origin of Gesneriaceae comes from the results of our molecular dating. The estimates for the time of divergence of the three clades of tribe Coronanthereae suggest a more recent emergence than a vicariance model can allow, since age estimates for these nodes (fig. 3; table 5) indicate divergence times subsequent to the times of separation of Southern Hemisphere landmasses (fig. 3; table 5). Our tree topology also suggests two independent migration events from South America to the southwest Pacific. These findings are best explained by more recent dispersal events (figs. 2, 5).

The pattern we have recovered indicates direction of dispersal but not routes or mechanisms. Two dispersal routes seem worth consideration: direct (trans-Pacific) or via Antarctica. A trans-Pacific route involves long distances, even for island hopping, and is against current prevailing winds, and Gesneriaceae is absent from the southeast Pacific. However, such a pattern is not unique to Gesneriaceae. Motley et al. (2005) postulated one or two long-distance dispersal events from the Caribbean to the western Pacific among *Bikkia* and its relatives (Rubiaceae), with no evidence of island hopping.

As unlikely as trans-Pacific dispersal may seem, migration via Antarctica seems less likely for Coronanthereae. Trans-

Antarctic overland migration between South America and Australia might have been possible until perhaps 35 Ma, but such an age is older than our estimates for the entire tribe (fig. 3; table 5). Even more recently, the sea distances were quite small, and groups such as *Fuchsia*, *Ourisia*, Coronanthereae, and Stylidiaceae might have used this route. This pathway has also been proposed in Asteraceae (Wagstaff et al. 2007). However, subtropical Coronanthereae might have been unsuited for the cool climate and extreme seasonality of Antarctica, which finally became inhospitable to woody plants ~15 Ma (Hill and Scriven 1995).

The findings in numerous molecular studies now support the hypothesis that current biotic patterns in the southern Pacific are influenced by dispersal (Swenson and Bremer 1997; Hurr et al. 1999; Wagstaff et al. 2000, 2002; Mummenhoff et al. 2001; Gemmill et al. 2002; Winkworth et al. 2002*b*; Howarth et al. 2003; Nepokroeff et al. 2003; Smissen et al. 2003; Berry et al. 2004; Clement et al. 2004; Mummenhoff 2004; Albach et al. 2005; Bartish et al. 2005; Cronk et al. 2005; Motley et al. 2005; Meudt and Simpson 2006; Clark et al. 2008, 2009; Pfeil and Crisp 2008; Smith et al. 2008; Tay et al. 2010). The inference of dispersal has been most obvious for species on oceanic islands of recent origin but less so for those on continental islands. Dispersal across vast distances may be difficult to envisage, but island hopping across shorter distances has been postulated for areas where the presence of oceanic islands could have facilitated this process (Pole 1994). Many such dispersal cases involve angiosperms not known to be particularly good dispersers, and they have challenged the notion of how species disperse, whether by animal mediation or more passive forces such as wind or water.

Enhanced dispersal ability is often linked to propagule type and method of dispersal, and several different mechanisms have been suggested for Gesneriaceae as a whole. However, there are no dispersal data within this family, so the proposed mechanisms, all of which may be applied to Coronanthereae, are speculative. Some authors have suggested that the minute seeds, characteristic within the family, are dispersed either by animals or by water splatter (Wiehler 1983; Burtt 1998). However, minute seeds may also be wind dispersed (Wiehler 1983), and plants of *Kohleria*, a genus within Gesnerioideae, have been found on islands 500 km from source populations (Kvist and Skog 1992). As a whole, the presence of wind dispersal is high in the New Caledonian flora (Carpenter et al. 2003), and the four-valved dry capsules and tiny seeds of *Coronanthera* may represent adaptations for this mechanism. It also has been argued that distributional patterns, if wind based, may demonstrate some directionality (Cook and Crisp 2005), and analyses of floristic similarities in comparisons of wind connectivity and geographic proximities do show this (Muñoz et al. 2004). Fruit type may also be a factor in dispersal success, with fleshy fruits attractive to frugivorous birds or more resilient to transoceanic dispersal (Cronk et al. 2005). A review of dispersibility across the Tasman Sea (Jordan 2001) examined a number of factors contributing to transoceanic dispersal success but recognized that success was often specific to the plant group in question and that generalities could not be made. Additional ecological studies will be essential to determining how fruits and seeds of Coronanthereae have managed transoceanic dispersal.

On the basis of our ancestral-range-reconstruction analyses, we postulate two independent dispersals from South America to explain the distribution of Coronanthereae in the South Pacific (figs. 3, 5). First, for Mitrariineae, the presence of an Australian species nested within this South American group suggests dispersal from South America to Australia (fig. 5). Second, subtribes Negriinae and Coronantherinae appear to have arisen from a South American ancestor that migrated to New Caledonia (or possibly New Caledonia and Lord Howe Island; table 6), with subsequent migrations from there to New Zealand, Australia, and Lord Howe Island (figs. 3, 5). We assume another dispersal event from New Caledonia to account for the presence of the only species of *Coronanthera* that is not found on New Caledonia, the Solomon Islands' *Coronanthera grandis*. However, this hypothesis has not been tested with molecular data.

Secondary dispersal events are proposed for members of both Negriineae and Coronantherinae. Within Negriineae, r8s shows a divergence of ~20 Myr between *Negria* of Lord Howe Island and both *Depanthus* of New Caledonia and *Lenbrassia* of Queensland, and BEAST shows a divergence of 23 Ma (note that 23 Ma was a constrained date for this clade in both analyses; fig. 3; table 5). Lord Howe Island itself has been emergent only since 7 Ma (Lee et al. 2001; McLoughlin 2001), but the continental shelf on which it sits has been in existence for >50 Myr and has had a long association with both New Caledonia and New Zealand (Raven and Axelrod 1972). The oldest estimates for the age of the now-submerged seamounts are 23 Myr; they are part of a northward-lying chain of volcanic islands, each of which was produced in a relatively short burst of activity (<1 Myr; McDougall et al. 1981; McDougall and Duncan 1988). The Lord Howe ridge has been much larger at times in its history, but it has stayed at its present-day latitude, thus allowing for long periods of mild, subtropical climate. Geological evidence is somewhat sparse for this area, but old submerged volcanic rocks recovered from this shelf provide the possibility of emergent arc islands, allowing for continuous vegetation for many millions of years before the existence of the current Lord Howe Island. Island hopping from older to younger volcanic islands with extinction of the original source populations has been postulated for other taxa where the island is younger than the clade in question. The discovery that the Hawaiian endemic *Hillebrandia* is sister to all other Begoniaceae illustrates the possibility of this relict scenario occurring in other groups (Clement et al. 2004).

Botanists have long considered the flora of Lord Howe Island to be more closely allied to those of New Caledonia and New Zealand than to that of Australia (Savolainen et al. 2006). Our scenario agrees with this close affinity between these islands because the ancestor of *Negria* may have dispersed from New Caledonia (figs. 3, 5; table 6).

Within Coronantherineae, the sister relationship between the New Zealand endemic *Rhabdothamnus solandri* and New Caledonian *Coronanthera* is well supported (MPBS = 96, MLBS = 100, BI = 1.0; fig. 2; MPBS = 90, MLBS = 100, BI = 1.0; fig. 3), and it provides more evidence for the floristic affinities between these two continental islands. Bartish et al. (2005) provided evidence that Sapotaceae have dispersed to New Caledonia multiple times from Australia and that the long-distance-dispersal component of New Caledonia's flora is significant, even though the flora there has traditionally been

regarded as relictual. Unique geologic factors on New Caledonia may be the driving factor behind rapid speciation on the island. Cretaceous submersion, laying on a peridotite layer up to 2000 m thick that covered large portions of the island 38 Ma, and the island's isolation from other landmasses since the Permian (Morat et al. 1986) have provided the beginnings for highly inhospitable habitats. The patchy distribution of ultramafic soils with high metal contents has likely driven the local specialization of founder species. The estimate of 17.9–22.0 Ma (table 5; fig. 3) for the origin of this subtribe indicates a long-distance dispersal event to account for its presence on New Caledonia. The identification of a single species of *Coronanthera* on Bougainville Island of the Solomons (Gillett 1967; fig. 5) provides further evidence of the dispersal potential of this group.

Floristic affinities between New Caledonia and New Zealand have been explained on the basis of geologic evidence in the area. Interpretation of that evidence has variously proposed the existence of different land connections, from direct land bridges persisting up to 30 Myr (Herzer et al. 1997) to the close proximity of larger emergent landmasses of the Lord Howe Ridge, providing a series of volcanic islands that would have reduced significantly the distances for dispersal events between the two areas (McDougall et al. 1981; Pole 1994). Certainly, the existence of sister taxa of small genera found only on New Zealand and New Caledonia (e.g., *Xeronema*) has suggested this association of the two floras previously (Morat et al. 1986; Lowry 1998).

The presence of the monospecific *Rhabdothamnus* on New Zealand contrasts with the 20 species in its New Caledonian sister genus *Coronanthera*, which probably reflects the differing environments and histories of the islands. Both floras may represent a mixture of ancient and recent immigrants that complicates the understanding of these assemblages (Carpenter et al. 2003). *Coronanthera* has experienced a radiation of species that may be due to unique ultramafic soils, which seem to have driven speciation in some of the other groups present in New Caledonia (Morat et al. 1986; Lowry 1998; Murienne et al. 2005). *Rhabdothamnus* might have experienced a long period of stasis in New Zealand, or it might have suffered recent extinctions, resulting in just a single species. New Zealand's forests underwent severe range restrictions during the Oligocene (the "Oligocene-drowning" hypothesis of Cooper and Cooper 1995; Stöckler et al. 2002; Biffin et al. 2010) and during the Pleistocene glaciations, when forest plants such as *Rhabdothamnus* were mostly confined to a small area in the far north of the country as recently as 14,000 yr ago (McGlone 1985). Either of these events (or a combination of both) may explain the lower number of species on New Zealand compared to New Caledonia.

Conclusions

The monophyly of Coronanthereae, based on combined nuclear and cpDNA data set analyses, is now well supported, and we present evidence that it is a distinct lineage clearly nested within Gesnerioideae and sister to a subclade of Gesnerioideae that does not include tribes Beslerieae and Napeantheae. This is consistent with the isocotyly seen in all members of this diverse group. Our estimated dates do not support Gondwanan vicariance; rather, they suggest that multiple long-distance dispersal events in the Miocene explain the tribe's current distribution in South America and the southwest Pacific regions.

The structure within tribe Coronanthereae is of three major lineages: (1) Mitrariinae, epiphytic plants that produce indehiscent berries; (2) Negriinae, trees; and (3) Coronantherinae, wind-dispersed shrubs and trees. Burtt's (1998) proposed reductions to synonymy of two genera of Coronanthereae (*Lenbrassia* into *Fieldia* and *Depanthus* into *Coronanthera*) are not supported here.

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Appendix A

Taxa Used in This Study, Vouchers, Native Distributions, and GenBank Accession Numbers

For each taxon, the following information is provided: voucher or herbarium collection number, herbarium, distribution, and GenBank numbers in the order ITS, *trnL-trnF*, *trnE-trnT*, *psbA-trnK*, *ndhF*, *trnL* intron, GCYC1E/GCYC1F, *rpl20-rps12* spacer. "NA" indicates not applicable because the taxon-sequence combination was not included in the analyses. Herbarium abbreviations follow the Index Herbariorum (http://sciweb.nybg.org/science2/IndexHerbariorum.asp). Superscripts refer to the following publications: 1, Möller and Cronk (1997); 2, Smith et al. (2004*b*); 3, Smith et al. (1997); 4, Smith et al. (1998); 5, Mayer et al. (2003); 6, Smith et al. (2006); 7, Smith et al. (2004*a*); 8, Zimmer et al. (2002).

Ingroup: Coronanthereae Wiehler

Asteranthera ovata Hanst., RBGE 19980608 Universidad de Chile 362, E, Chile, EF445669, EF445726, EF445777, EF445817, NA, NA, NA, NA; *A. ovata* Hanst., *Stewart 12234*, SRP, Chile, cultivated, GQ497203, GQ497197, NA, NA, U62204,[3] GQ497191, AY363949/AY363950,[6] GQ497182;

Coronanthera aspera C. B. Clarke, *Munzinger 1032*, NOU, New Caledonia, EF445670, NA, NA, NA, NA, NA, NA, NA; *Coronanthera clarkeana* Schltr., *McPherson & Werff 17771*, NOU, New Caledonia, EF445671, NA, NA, NA, NA, NA, NA, NA; *C. clarkeana* Schltr. (Panié), *Woo 05–015, Dawson, Dawson & Burns*, WELTU, New Caledonia, EF445672, EF445728, EF445778, EF445820, NA, NA, NA, NA; *C. clarkeana* Schltr., *Motley 2191*, NY, New Caledonia, GQ497204, GQ497196, NA, NA, GQ497212, GQ497192, AY363952/DQ406720,[6] GQ497180; *Coronanthera deltoidifolia* Vieill. ex C. B. Clarke, *Suprin 2636*, NOU, New Caledonia, EF445673, EF445729, EF445779, EF445821, NA, NA, NA, NA; *Coronanthera pancheri* C. B. Clarke, *Woo 02–029, Garnock-Jones & Dawson*, WELTU, New Caledonia, EF445674, EF445730, EF445780, EF445822, NA, NA, NA, NA; *Coronanthera pedunculosa* C. B. Clarke, *MacKee 3746*, E, New Caledonia, EF445675, NA, NA, NA, NA, NA, NA, NA; *Coronanthera sericea* C. B. Clarke (Koghis), *Woo 02–008, Garnock-Jones & Dawson*, WELTU, New Caledonia, EF445676, EF445731, EF445781, EF445823, NA, NA, NA, NA; *C. sericea* C. B. Clarke, *MacKee 46088*, E, New Caledonia, EF445677, EF445732, EF445782, EF445824, NA, NA, NA, NA; *C. sericea* C. B. Clarke (Yahoué), *Woo 02–026, Garnock-Jones & Dawson*, WELTU, New Caledonia, EF445678, NA, NA, NA, NA, NA, NA, NA; *Coronanthera squamata* Virot, *Munzinger 1204*, NOU, New Caledonia, EF445679, EF445733, EF445783, EF445826, NA, NA, NA, NA; *Coronanthera* sp. Koniambo, CHR 442982, CHR, NOU, P, S, New Caledonia, EF445680, NA, NA, NA, NA, NA, NA, NA; *Coronanthera* sp. Nakada, *Munzinger 784*, MO, NOU, P, New Caledonia, EF445681, EF445734, EF445784, EF445828, NA, NA, NA, NA; *Coronanthera* sp. Tchingou, *Munzinger 527*, MO, NOU, P, New Caledonia, EF445682, EF445735, EF445785, EF445829, NA, NA, NA, NA; *Depanthus glaber* (C. B. Clarke) S. Moore, *Woo 03–010, Garnock-Jones & Dawson*, WELTU, New Caledonia, EF445683, EF445736, EF445786, EF445830, NA, EF445736, NA, NA; *D. glaber* (C. B. Clarke) S. Moore, *Woo 05–008 & Dawson*, WELTU, New Caledonia, EF445684, NA, NA, NA, NA, NA, NA, NA; *D. glaber* (C. B. Clarke) S. Moore, *Woo 05–010*, WELTU, New Caledonia, EF445685, NA, NA, NA, GQ497210, NA, DQ406723/DQ406727,[6] GQ497186; *Fieldia australis* A. Cunn., *Woo 03–027*, WELTU, Australia, cultivated, EF445686, EF445738, EF445787, EF445832, NA, NA, NA, NA; *F. australis* A. Cunn., CHR, CHR, NSW, Australia, EF445687, EF445739, EF445788, EF445833, NA, NA, NA, NA; *F. australis* A. Cunn., *Stewart s. n.*, SRP, Australia, cultivated, GQ497205, GQ497194, NA, NA, U62196,[3] GQ497190, AY363954/DQ406721,[6] NA; *Lenbrassia australiana* (C. T. White) G. W. Gillett, *Telford & Rudd 11314*, E, Queensland, Australia, EF445688, EF445740, EF445789, EF445834, GQ497211, EF445740, NA/DQ406726,[6] GQ497185; *L. australiana* (C. T. White) G. W. Gillett, *Telford & Rudd 11299*, E, Queensland, Australia, EF445689, EF445741, EF445790, EF445835, NA, NA, NA, NA; *L. australiana* (C. T. White) G. W. Gillett var. *glabrescens* B. D. Morley, AD 99846103, AD, Queensland, Australia, EF445690, NA, NA, NA, NA, NA, NA, NA; *Mitraria coccinea* Cav., RBGE, E, Argentina, EF445691, EF445743, EF445791, EF445837, NA, NA, NA, NA; *M. coccinea* Cav., *Woo 03–028*, WELTU, Chile, cultivated, EF445692, NA, NA, NA, NA, NA, NA, NA; *M. coccinea* Cav., *Smith 3936*, SRP, Chile, Argentina, cultivated, AY372321/AY372340,[2] AY364287,[1] NA, NA, U62193,[3] AY364265,[2] AY423153/AY363953,[6] GQ497183; *Negria rhabdothamnoides* F. Mueller, *Stewart s. n.*, US, Lord Howe Island, cultivated, EF445693, EF445744, EF445792, EF445839, NA, NA, NA, NA; *N. rhabdothamnoides* F. Mueller, *E. A. Brown 2003/33-LHB* NSW 606588, S, Lord Howe Island, EF445694, EF445745, EF445793, EF445840, NA, NA, NA, NA; *N. rhabdothamnoides* F. Mueller, *E. A. Brown 2003/33-LHD* NSW 606590, S, Lord Howe Island, cultivated, EF445695, NA, NA, NA, NA, NA, NA, NA; *N. rhabdothamnoides* F. Mueller, *Nordenstam 8608*, S, Lord Howe Island, cultivated, GQ497206, GQ497195, NA, NA, U62195,[3] GQ497189, DQ406724/DQ406725,[6] GQ497178; *Rhabdothamnus solandri* A. Cunn., *Woo 03–322*, WELTU, Alderman Island, New Zealand, EF445696, EF445747, EF445794, EF445841, NA, NA, NA, NA; *R. solandri* A. Cunn., *Woo 03–012, Miller & Miller*, WELTU, Homunga, New Zealand, EF445697, EF445748, EF445795, EF445842, NA, NA, NA, NA; *R. solandri* A. Cunn., *Woo 03–101 & Teo*, WELTU, Pauatahanui, New Zealand, EF445698, EF445749, EF445796, EF445843, NA, NA, NA, NA; *R. solandri* A. Cunn., AK 133215, AK, Shoe Island, New Zealand, EF445699, EF445750, EF445797, EF445844, NA, NA, NA, NA; *R. solandri* A. Cunn., *Woo 03–131, Miller & Miller*, WELTU, Anganui, New Zealand, EF445700, EF445751, EF445798, EF445845, NA, NA, NA, NA; *R. solandri* A. Cunn., *Smith 4393*, SRP, New Zealand, cultivated, GQ497207, GQ497198, NA, NA, GQ497209, GQ497188, AY363955/AY363956,[6] GQ497179; *Sarmienta repens* Ruiz &. Pav., *Gardner & Knees 4033*, E, K, Chile, EF445701, EF445752, EF445799, EF445846, NA, NA, NA, NA; *S. repens* Ruiz &. Pav., *Smith 3933*, SRP, Chile, cultivated, AY372320/AY372339,[2] AY364264,[1] NA, NA, U62194,[3] AY364264,[2] NA/AY363951,[6] GQ497181.

Outgroup: Gesnerioideae

Achimenes misera Lindl., *Skog 8222*, US, South America, AY047067,[8] AY047126,[8] AY047185,[8] EF445847, NA, NA, NA, NA; *Besleria angustiflora* Fritsch, *John L. Clark 4574*, US, Ecuador, EF445702, NA, NA, NA, NA, NA, NA, NA; *Besleria divaricata* Poepp. & Endl., *John L. Clark 5629*, US, Ecuador, Peru, EF445703, NA, NA, NA, NA, NA, NA, NA; *Besleria filipes* Urban., *John L. Clark 6559*, US, Dominica, EF445704, NA, NA, NA, NA, NA, NA, NA; *Besleria formicaria* Nowicke, *John L. Clark 8611*, US, Panama, EF445705, NA, NA, NA, NA, NA, NA, NA; *Besleria labiosa* Hanst., *Skog & Brothers 7631*, US, cultivated, AY047041,[8] AY047100,[8] AY047159,[8] EF445852, NA, NA, NA, NA; *Besleria* sp., *Amaya & Smith 525*, COL, Colombia, AY372330/AY372348,[2] AY364296,[1] NA, NA, AF176626,[2] AY364274,[2] NA/AY363943,[6] GQ497177; *Columnea byrsina* (Wiehler) Kvist & L. Skog, *Smith 3408*, SRP, Ecuador, AF272176/AF272177,[2] AY364304,[1] NA, NA, AY364308,[2] AY364282,[2] NA/AY363931,[6] AY623365;[7] *Columnea gloriosa* Sprague, *Woo 03–098*, WELTU, Costa Rica, EF445706, NA, NA, NA, NA, NA, NA, NA; *Columnea sanguinea* (Pers.) Hanst.,

Woo 03–097, WELTU, South America, EF445707, NA, NA, NA, NA, NA, NA, NA; *Cremosperma castroanum* C. V. Morton, *ROH 03–52*, WELTU, Ecuador, EF445708, EF445759, EF445800, EF445855, NA, NA, NA, NA; *Cremosperma humidum* Kvist & Skog, *ROH 03–09*, WELTU, Ecuador, EF445709, EF445760, EF445801, EF445856, NA, NA, NA, NA; *Cremosperma reldioides* Kvist & Skog, *ROH 03–11*, WELTU, Ecuador, EF445710, EF445761, EF445802, EF445857, NA, NA, NA, NA; *Diastema affine* Fritsch, *Woo 04–006*, WELTU, Ecuador, EF445711, EF445762, EF445803, EF445858, NA, NA, NA, NA; *Gasteranthus atratus* Wiehler, USBRG 06–013, US, Ecuador, EF445712, EF445763, EF445804, EF445859, NA, NA, NA, NA; *Gasteranthus calcaratus* ssp. *calcaratus* (Kunth.) Wiehler, USBRG 02–008, US, Ecuador, EF445713, EF445764, EF445805, EF445860, NA, NA, NA, NA; *Gasteranthus corallinus* (Fritsch) Wiehler, *Woo 04–037*, WELTU, Ecuador, EF445714, EF445765, EF445806, EF445861, NA, NA, NA, NA; *Gasteranthus crispus* (Mansf.) Wiehler, *John L. Clark 7370*, US, Ecuador, EF445715, EF445766, EF445807, EF445862, NA, NA, NA, NA; *Gasteranthus quitensis* Benth., *John L. Clark 6197*, US, Ecuador, EF445716, EF445767, EF445808, EF445863, NA, NA, NA, NA; *Gasteranthus villosus* Skog & Kvist, USBRG 06–004, US, Ecuador, EF445717, EF445768, EF445809, EF445864, NA, NA, NA, NA; *Gasteranthus delphinioides* (Seem.) Wiehler, *Amaya & Smith s. n.*, COL, Colombia, AY372331,[2] AY364297,[1] NA, NA, AF176629,[2] AY364275,[2] NA/AY363946,[6] GQ497176; *Gesneria christii* Urban, USBRG 94–507, US, Hispaniola, cultivated, AY372336/AY372353,[2] AY364302,[1] NA, NA, U62191,[3] AY364280,[2] NA/AY363923,[6] AY623341;[7] *Glossoloma panamense* (C. V. Morton) J. L. Clark, *Skog et al. 7641*, US, South America, AF206202, AY364305,[1] NA, NA, AF013685,[2] AY364283,[2] NA/AY363933,[6] AY623366;[7] *Kohleria spicata* (Kunth) Oerst., *Skog 7701*, US, South America, AY372327/AY372345,[2] AY364293,[1] NA, NA, U62181,[3] AY364271,[2] NA/AY363919,[6] AY623334;[7] *Napeanthus apodemus* J. D. Smith, *Amaya & Smith 605*, COL, Colombia, AY372332/AY372349,[2] AY364298,[1] NA, NA, AF176623,[2] AY364276,[2] NA/AY363947,[6] GQ497174; *Napeanthus costaricensis* Wiehler, *Woo 04–013*, WELTU, Costa Rica, EF445718, EF445769, EF445810, EF445865, NA, NA, NA, NA; *Napeanthus jelskii* Fritsch, *Skog 7697*, US, French Guiana, AY047044,[8] AY047103,[8] AY047162,[8] EF445866, NA, NA, NA, NA; *Napeanthus macrostoma* Leeuwenberg, *Feuillet s. n.*, US, French Guiana, cultivated, AY372333/AY372350,[2] AY364299,[1] NA, NA, U62161,[3] AY364277,[2] NA/AY363948,[6] GQ497175; *Napeanthus* sp., *John L. Clark 7604*, US, Ecuador, EF445719, EF445770, EF445811, EF445867, NA, NA, NA, NA; *Nautilocalyx melittifolius* (L.) Wiehler, *Skog & Brothers 8096*, US, South America, AY047086,[8] AY047145,[8] AY047204,[8] EF445868, NA, NA, NA, NA; *Niphaea oblonga* Lindl., *Woo 04–008*, WELTU, Guatemala, EF445720, EF445771, F445812, EF445869, NA, NA, NA, NA; *Rhytidophyllum auriculatum* Hook., USBRG 94–524, US, Hispaniola, cultivated, AY372335/AY372352,[2] AY36430,[1] NA, NA, U62199,[3] AY364279,[2] NA/AY363927,[6] AY623358;[7] *Rhytidophyllum tomentosum* (L.) Mart., USBRG 2002–156, US, Puerto Rico, AY047056,[8] AY047115,[8] AY047174,[8] EF445870, NA, NA, NA, NA; *Sinningia conspicua* (Seem.) Nichols., *Woo 04–038*, WELTU, Brazil, EF445721, EF445772, EF445813, EF445871, NA, NA, NA, NA; *Sinningia guttata* Lindl., *Woo 04–010*, WELTU, Brazil, EF445722, NA, NA, NA, NA, NA, NA, NA; *Sinningia richii* Clayb., USBRG 94–554, US, Brazil, cultivated, AY372338/AY372355,[2] AY364307,[1] NA, NA, U62186,[3] AY364285,[2] NA/AY363935,[6] AY623370;[7] *Sinningia speciosa* Hiern. (peloric mutant), *Smith 4512*, SRP, Brazil, cultivated, AY372337/AY372354,[2] AY364306,[1] NA, NA, AY364309,[2] AY364284,[2] NA/AY363942,[6] AY623369;[7] *Solenophora oblique* D. L. Denham & D. N. Gibson, *Breedlove 71542*, CAS, Mexico, AY372328/AY372346,[2] AY364294,[1] NA, NA, U62202,[3] AY364272,[2] NA/AY363921,[6] AY62333;[7] *Sphaerorrhiza sarmentiana* (Gardn. ex Hook.) Roalson & Boggan, *Skog 8220*, US, Brazil, AY047079,[8] AY047138,[8] AY047197,[8] EF445873, GQ497213, GQ497193, NA/GQ497208, GQ497173; *Vanhouttea lanata* Fritsch, *Skog & Dunn 7712*, US, Brazil, AY047080,[8] AY047139,[8] AY047198,[8] EF445874, NA, NA, NA, NA; *Sanango racemosum* (Ruiz & Pav.) K. Barringer, USBRG cultivated, US, Ecuador, Peru, EF445725, EF445776, EF445816, EF445877, NA, NA, NA, NA.

Outgroup: Cyrtandroideae

Boea hygroscopica F. Mueller, *Woo 04–029*, WELTU, Australia, EF445723, EF445774, EF445814, EF445875, NA, NA, NA, NA; *Chirita gemella* D. Wood, *Skog 8048*, US, Vietnam, EF445724, EF445775, EF445815, EF445876, NA, NA, NA, NA; *Primulina tabacum* Hance, *Smith 4032*, SRP, China, cultivated, GQ497202, GQ497200, NA, NA, U62167[3], AJ492300[5], NA/AF208320[6], GQ497172; *Ramonda myconi*, *Katzenstein s. n.*, SRP, Spain, cultivated, NA, GQ497199, NA, NA, U62185,[3] AJ492301,[5] AF208318 (=GCYC2)/AF208323,[6] GQ497171; *Streptocarpus primulifolius* Gandoger, USBRG 94–0096, US, South Africa, cultivated, AF316984,[1] GQ497201, NA, NA, AF012847,[4] GQ497187, AF208336 (=GCYC1B)/AF208340 (=GCYC1A), NA.

Appendix B

Subtribal Classification of Coronanthereae

Trib. Coronanthereae. Fritsch in Engl. & Prantl, *Nat. Pflanzenfam. IV, 3b*: 143. (1893).

Subtrib. Coronantherinae. An autonym that came into being when Fritsch (1893–1894) transferred subtr. Mitrarinae from Beslerieae to Coronanthereae (Holotype: *Coronanthera*).

Trees and shrubs, 2–15 m tall; leaves small to large, 2–25 cm, pubescent, or bristly, or scabrid, or glabrous, toothed or weakly toothed; inflorescence an axillary cyme, peduncle short, generally 3–8-flowered, or flower solitary; flowers zygomorphic, small; corolla tube 0.5–2 cm, urceolate or gullet-shaped, white, green, yellow, pink, purple, brown or orange, orange-red; stamens 4, didynamous, staminode 1, anthers coherent, in coronal formation; fruit an ovoid dry capsule,

four-valved, valves apically coherent, dehiscing by basal slits, septicidally then loculicidally; seeds subglobose to ellipsoid, striated, minute, 0.2–0.4 mm long, numerous; pollen spheroidal to prolate in shape, small (10 μm) to medium-sized (26 μm).

Genera included: *Coronanthera*, *Rhabdothamnus*.

Subtrib. Mitrariinae. J. Hanst., *Linnaea 26*: 198, 199 (1854, as Beslerieae subtr. Mitrarieae, Holotype: *Mitraria* Cavan.) = Sarmientinae J. Hanst., *Linnaea 26*: 198, 199. Apr 1854 (as Beslerieae subtr. Sarmienteae, Holotype: *Sarmienta* Ruiz & Pavon).

Epiphytic creepers and subshrubs to 1 m tall, weak-stemmed, straggling; leaves small 0.5–4 cm, ovate to lanceolate, pubescent or glabrous, toothed or weakly toothed, may be fleshy; inflorescence axillary, solitary; flowers zygomorphic or actinomorphic, large; corolla tube 2–4 cm long, white-yellow or red; stamens 2–4, didynamous or free; fruits baccate, glabrous or pubescent, indehiscent; seeds with broad and flattened cell crests; pollen prolate to perprolate in shape, medium (21 μm) to large-sized (38 μm).

Genera included: *Mitraria*, *Sarmienta*, *Asteranthera*, *Fieldia*.

Subtrib. Negriinae. V. L. Woo, J. F. Smith, & Garn.-Jones, subtr. nov. (Holotype: *Negria*).

Coronantherinae similis foliis grandis et habitu arborescente, differt fructibus rostratis carnosisque aut siccis nunc valvis 2 non cohaerenibus ad apicem dehiscentibus, seminibus majoribus, 0.7–0.9 mm longis; Mitrariinae habitu arborescente, foliis grandis integris vel grosse dentatis differt.

Trees, 6–13 m tall; leaves glabrous or pubescent, entire or toothed, lanceolate to ovate, large, 2.5–11 cm × 5–20 cm long; inflorescence an axillary cyme, peduncle short to long, 1–3-flowered; flowers zygomorphic or actinomorphic, white, yellow, orange; stamens 4–5, free or coherent; fruits beaked, fleshy, and indehiscent, or dry, woody, and two-valved, apically septicidally dehiscent. Seeds subglobose to elliptic, striated, minute, 0.7–0.9 mm long, numerous; pollen spheroidal to mildly prolate in shape, small (12 μm) to medium-sized (22 μm).

Genera included: *Negria*, *Lenbrassia*, *Depanthus*.

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