ORIGIN, DIVERSIFICATION, AND CLASSIFICATION OF THE AUSTRALASIAN GENUS *DRACOPHYLLUM* (RICHEEAE, ERICACEAE)[1]

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ABSTRACT

The genus *Dracophyllum* Labill. (Ericaceae) has a fragmented distribution in Australasia, but reaches the greatest level of species richness and morphological diversity in New Zealand. We investigated evolutionary processes that contribute to this disparity in species richness by comparing DNA sequences from members of *Dracophyllum*, its close relatives *Richea* Labill. and *Sphenotoma* R. Br. ex Sweet (together constituting tribe Richeeae Crayn & Quinn), along with more distant relatives in the Ericaceae. We created complementary data sets for the chloroplast-encoded genes *matK* and *rbcL*. Parsimony, Bayesian, and maximum likelihood analyses were conducted to assess the robustness of our phylogenetic inferences. The results were largely congruent and, when analyzed in combination, provided greater resolution. In our analyses, tribe Richeeae formed a monophyletic group that diverged during the Eocene (at least 33.3 million years ago [Ma]) with a crown radiation during the Early Miocene (at least 16.5 Ma) that resulted in two disjunct lineages. This date corresponds roughly to the onset of aridification in central Australia. The southern Western Australian genus *Sphenotoma* formed an isolated evolutionary lineage, while *Dracophyllum* and *Richea* together formed a second lineage restricted to eastern Australia, Lord Howe Island, New Caledonia, and New Zealand. The relationships of the Tasmanian endemic, *D. milliganii* Hook. f., remain an enigma. It was ambiguously placed as sister to *Sphenotoma* or to the *Dracophyllum–Richea* clade. We recovered two distinct lineages, traditionally recognized as *Richea* sect. *Cystanthe* (R. Br.) Benth. and *Richea* sect. *Dracophylloides* Benth., which were nested within *Dracophyllum*. The Lord Howe Island endemic, *D. fitzgeraldii* F. Muell., emerged as sister to an eastern Australian clade of *Dracophyllum*. Our evidence suggests that the New Caledonian and New Zealand species of *Dracophyllum* dispersed from Australia; we document two independent episodes of long-distance dispersal in the Late Miocene to Early Pliocene. Low levels of sequence divergence suggest a rapid and recent species radiation in these two island archipelagos largely within the last three to six million years. This radiation accompanied Pliocene uplift of the New Zealand Southern Alps and episodes of glaciation during the Pleistocene. Because *Dracophyllum* is paraphyletic and *Richea* is polyphyletic, the taxonomic circumscription of these genera requires revision.

Key words: Adaptive radiation, angiosperm, Australia, biogeography, classification, diversification, *Dracophyllum*, Epacridaceae, epacrids, Ericaceae, island floras, Lord Howe Island, *matK*, molecular clock, molecular phylogenetics, molecular sequence data, molecular systematics, New Caledonia, New Zealand, phylogeny, plant evolution, *rbcL*, *Richea*, speciation, species richness, *Sphenotoma*, Tasmania.

Due to a combination of geographic isolation, diverse climate, and varied topography, oceanic islands host some of the world's unique floras and hence are often considered to be hot spots of biodiversity (Myers et al., 2000; Emerson, 2002; Warne, 2002; Leigh et al., 2007). Darwin (1859)

observed that a high proportion of the species on islands were endemics, and some of the groups that had colonized isolated islands had diversified in spectacular adaptive radiations that exceeded those in mainland settings. He proposed that large remote islands allowed more effective evolutionary innovation, and the competition driving natural selection was more severe. Physical factors, such as the age of these island archipelagos, their geographic area, and topographic diversity, would have also contributed to promote diversification. MacArthur and Wilson (1967) proposed that species diversity on islands reflects a delicate interaction between immigration, speciation, and extinction. Here, we reconstruct phylogenetic patterns and use this as a framework to investigate evolutionary processes that contribute to a disparity in species richness between continental and island species of *Dracophyllum* Labill. (Ericaceae).

The genus *Dracophyllum* reaches its greatest level of species richness and morphological diversity in the island archipelagos of New Zealand and to a lesser extent in New Caledonia, but has close relatives on mainland Australia and Tasmania (Oliver, 1929, 1952; Venter, 2008) (Fig. 1). About 51 species of *Dracophyllum* are currently recognized, and these vary from low-growing cushion plants to trees up to 14 m tall (Fig. 2A–H). They are characteristic shrubs of upland forests and heathlands in mainland Australia (e.g., Powell, 1992; Brown & Streiber, 1999; Streiber et al., 1999), Tasmania (e.g., Rodway, 1903; Curtis, 1963; Buchanan et al., 1989), Lord Howe Island (Oliver, 1917), New Caledonia (Virot, 1975; Venter, 2004), and New Zealand (Allan, 1961; Venter, 2002) and are commonly known as dragon-leaf or grass tree because of their distinctive spiky growth form.

Three subgenera of *Dracophyllum* were recognized by Oliver (1929, 1952) (Fig. 2A–H). Twenty-nine species have been recognized in *Dracophyllum* subg. *Oreothamnus* (F. Muell.) W. R. B. Oliv. (Fig. 2F–H); all are endemic to New Zealand with the exception of *D. minimum* F. Muell. of Tasmania (Fig. 2H). About 21 species are placed in *Dracophyllum* subg. *Dracophyllum* (Fig. 2A–D); of these, seven are endemic to New Zealand, eight to New Caledonia, four to mainland Australia, one to Tasmania, and one to Lord Howe Island. A third subgenus, *Cordophyllum* W. R. B. Oliv., comprises a single species, *D. involucratum* Brongn. & Gris, which is endemic to New Caledonia (Fig. 2E).

Systematists have long recognized a close relationship between *Dracophyllum* and two morphologically similar Australian genera, *Richea* Labill. and *Sphenotoma* R. Br. ex Sweet, and, in recognition of this close relationship, place these three genera in the Australasian tribe Richeeae. The genus *Richea* (Fig. 2I–M) includes 11 species from southeastern Australia and Tasmania (Menadue & Crowden, 2000), while *Sphenotoma* (Fig. 2N–P) includes six described species that are restricted to Western Australia (Powell et al., 1996, 1997; Paczkowska & Chapman, 2000). Unique morphological (Powell et al., 1996) and molecular traits (Crayn & Quinn, 2000; Kron et al., 2002) shared by these three genera indicate that they once shared a common ancestor whose descendants form a single lineage. While tribe Richeeae forms a well-defined monophyletic group (Powell et al., 1996; Crayn & Quinn, 2000; Kron et al., 2002), the phylogenetic relationships among *Dracophyllum*, *Richea*, and *Sphenotoma* are less clear due to the sparse sampling in previous studies.

The Australasian epacrids were formerly placed in the family Epacridaceae. However, recent phylogenetic studies (Powell et al., 1996; Stace et al., 1997; Crayn & Quinn, 2000; Kron et al., 2002) revealed that the epacrids form a well-supported monophyletic group nested within the Ericaceae. As a consequence, they have all been transferred to the family Ericaceae, and the epacrids are now recognized as a distinct subfamily, the Styphelioideae Sweet. The Styphelioideae include about 35 genera and 420 species found throughout the Australasian region, but are most diverse and abundant in southwestern and southeastern regions of mainland Australia and Tasmania. Outliers extend the range to Tierra del Fuego, Argentina (*Lebetanthus* Endl.), Hawaii (*Styphelia* Sm. s.l.), and Southeast Asia (*Leucopogon* R. Br.) (Kron et al., 2002).

The Ericaceae have an ancient evolutionary history (Collinson & Crane, 1978; Nixon & Crepet, 1993; Jordan & Hill, 1996; Zetter & Hesse, 1996; Jordan et al., 2007, 2010). Remarkably well-preserved fossilized flowers related to the extant genus *Enkianthus* Lour. are reported from North American deposits dating from the Late Cretaceous some 90 million years ago (Ma), and these exhibit characteristics associated with specialized insect pollination (Nixon & Crepet, 1993). Fossil seeds and pollen resembling those of extant species of *Rhododendron* L. are described from Early Tertiary deposits in Europe (Collinson & Crane, 1978; Zetter & Hesse, 1996). The appearance of two pollen types in the epacrids suggests that the group had diversified by the mid-Eocene, at which time fossil pollen is observed in both southeastern Australia and New Zealand (Mildenhall, 1980; Jordan & Hill, 1996; Jordan et al., 2007). Fossil leaves and fragments of Styphelioideae, including fragments attributed to Richeeae, are reported from Early Oligocene sediments in Tasmania, which provides additional evidence for a mid-Tertiary diversification of the family (Jordan & Hill, 1996). The distinctive
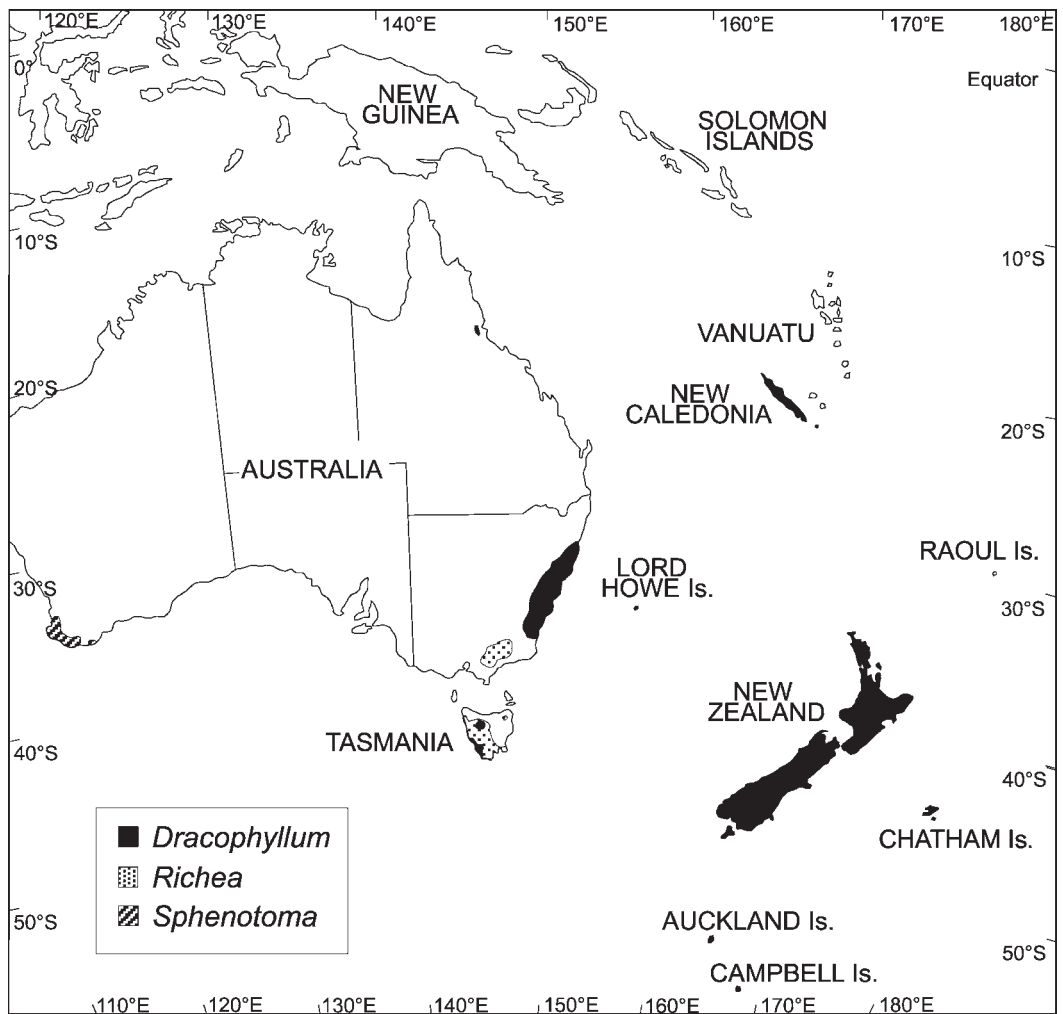
Figure 1.   Extant distribution of tribe Richeeae. As presently circumscribed, *Dracophyllum* subg. *Dracophyllum* (21 spp.) occurs in New Zealand, New Caledonia, and Australia (including Tasmania and Lord Howe Island); *Dracophyllum* subg. *Oreothamnus* (29 spp.) is restricted to New Zealand (except for *D. minimum* of Tasmania); *Dracophyllum* subg. *Cordophyllum* (one sp., *D. verticillatum*) is endemic to New Caledonia; *Richea* (11 spp.) is restricted to southeastern Australia (including Tasmania); *Sphenotoma* (six spp.) is restricted to southern Western Australia.

pollen tetrads characteristic of *Richea procera* (F. Muell.) F. Muell. and *R. sprengelioides* (R. Br.) F. Muell. appear in Late Pliocene deposits (Jordan & Hill, 1996). Small-leaved sclerophyllous ericads, similar to many of the fossils, are presently found in a wide range of habitats including cool temperate rainforest, dry woodlands, heathlands, and alpine environments, so it is difficult to trace the diversification of the group based on fossil evidence alone.

The evolutionary history of *Dracophyllum* undoubtedly reflects vicariance, dispersal, adaptive radiation, and extinction. Here, we attempt to unravel the evolutionary history of *Dracophyllum* and its relatives

in tribe Richeeae by examining the DNA sequence data in conjunction with evidence from the fossil record. We aim to address the following questions:

1. Is the genus *Dracophyllum* monophyletic, and how is it related to *Richea* and *Sphenotoma*?
2. Does the current classification reflect the phylogeny?
3. Where did these lineages originate and when did they diverge?
4. Are the extant species of *Dracophyllum* ancient relics that have survived since the breakup of Gondwana, or are they the descendants of more
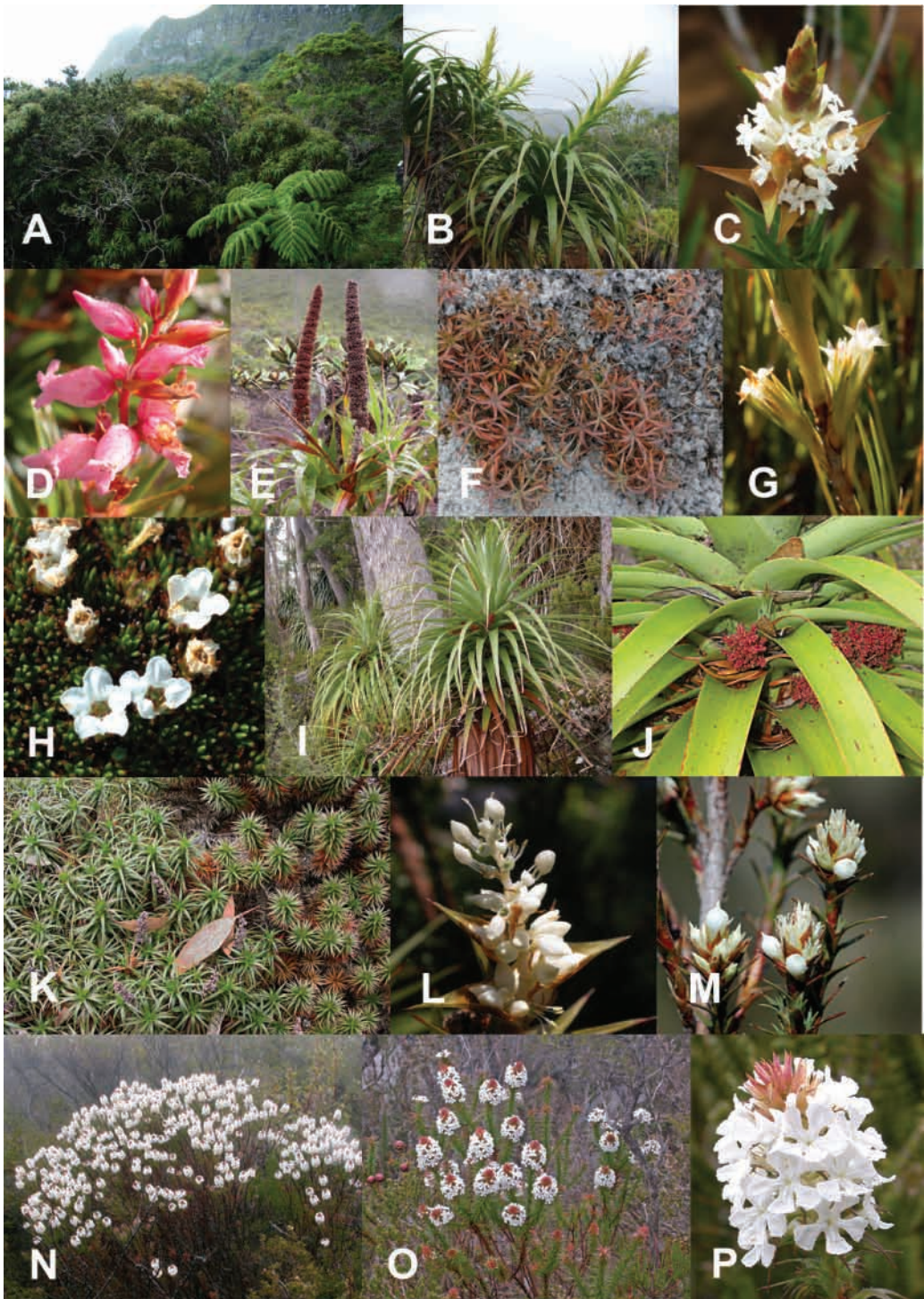
Figure 2. Morphological variation in *Dracophyllum*, *Richea*, and *Sphenotoma* (tribe Richeeae). —A. *Dracophyllum fitzgeraldii* is endemic to Lord Howe Island. It is quite common near the summit of Mt. Lidgbird and Mt. Gower where it occupies light gaps or grows on forest margins. In this photo it is associated with *Cyathea* sp. —B. Habit of *D. verticillatum* (subg. *Dracophyllum*), New Caledonia. —C. Close-up of the flowers of *D. mackeeanum* (subg. *Dracophyllum*), New Caledonia. —D. Close-up of the flowers of *D. ouaiemense* (subg. *Dracophyllum*), New Caledonia. —E. Infructescence of *D. involucratum*

recent founder populations that radiated following long-distance dispersal, as has been observed in many other New Zealand taxa?

5. What are the underlying reasons for differences in species richness between continental Australia, Tasmania, Lord Howe Island, New Caledonia, and New Zealand?

METHODS

STUDY GROUP

During the 2005 and 2006 field seasons, we conducted four collecting expeditions and obtained material of *Dracophyllum*, *Richea*, and *Sphenotoma* from throughout their range. Further material was obtained from other collectors and herbarium specimens. The study group included 78 DNA samples that represented the range of morphological variation and the majority of species within tribe Richeeae (*Dracophyllum*, 36/51 spp.; *Richea*, 10/11 spp.; *Sphenotoma*, four/six spp.). Twenty-eight outgroups were selected to provide a diverse representation of Australasian epacrids, as well as more distant members of the Ericaceae. We sequenced *Cosmelia rubra* R. Br. and *Sprengelia incarnata* Sm. Sequences for the remainder of the outgroups were obtained from GenBank (<http://www.ncbi.nlm.nih.gov>).

The study group is listed in Appendix 1, along with collection details, herbarium voucher information, and GenBank accession numbers. The complete data sets are available on request from the first author and were deposited in TreeBASE (<http://www.treebase.org>; study accession number = S2437, matrix accession numbers = M4629 to M4631).

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

Total DNA was extracted from fresh leaves, leaves dried using silica gel, or from herbarium specimens, using a Qiagen DNeasy extraction kit (Qiagen Pty Ltd, Clifton Hill, Victoria, Australia) and following the manufacturer's recommended protocols. Most extractions were performed at Landcare Research, Lincoln, New Zealand, although a few DNA samples were prepared at the National Herbarium of New South Wales, and aliquots were sent to Lincoln for subsequent amplification and sequencing. These amplification and sequencing techniques generally followed those of Crayn and Quinn (2000) and Kron et al. (2002).

The chloroplast-encoded genes *rbcL* and *matK* were amplified by polymerase chain reaction (PCR). These gene regions were chosen to provide informative data at different taxonomic levels; the *rbcL* gene evolves at a relatively slow rate, which allows comparisons of more distantly related taxa at higher taxonomic levels, whereas the *matK* gene evolves more rapidly than *rbcL* and is more suitable for comparisons within and among related genera. Standard *rbcL* primers (Olmstead et al., 1992) were used as listed in Table 1; 1351R was sometimes also used with difficult material. The majority of the *matK* primers (Table 1) were designed specifically for this project. One primer, which we labeled Aus50F, was designed (by D.M.C.) for earlier projects in the Ericaceae (Cherry et al., 2001; Quinn et al., 2003). The selection of *matK* primers that we developed for tribe Richeeae (Table 1) gave us better results than some of the others that we trialed (those reported by previous workers as successful for epacrids).

Following amplification, the excess primers and unincorporated nucleotides were removed from the PCR products using a shrimp alkaline phosphatase and exonuclease (SAP/EXO) enzyme digest. The purified DNA samples were labeled with fluorescent dyes (BigDye Chemistry, Applied Biosystems, Foster City, California, U.S.A.) and then sequenced at the Waikato and Massey universities' DNA sequencing facilities. In all instances, both the forward and reverse DNA strands were sequenced.

PHYLOGENETIC ANALYSES

The sequences were initially aligned using ClustalX (Thompson et al., 1997) and gaps were inserted in the data matrix. The resulting alignments were visually inspected and minor changes were made manually to ensure positional homology prior to the phylogenetic analyses. The aligned data sets were subjected to phylogenetic analysis using parsimony, Bayesian inference, and maximum likelihood as

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(subg. *Cordophyllum*), New Caledonia. —F. Habit of *D. recurvum* (subg. *Oreothamnus*), New Zealand. —G. Close-up of the flowers of *D. longifolium* (subg. *Oreothamnus*), New Zealand. —H. Habit of *D. minimum* (subg. *Oreothamnus*), Tasmania. —I. Habit of *Richea pandanifolia* (sect. *Dracophylloides*), Tasmania. —J. Infructescence of *R. pandanifolia* (sect. *Dracophylloides*). —K. Habit of *R. scoparia* (sect. *Dracophylloides*), Tasmania. —L. Close-up of the flowers of *R. victoriana* (sect. *Dracophylloides*), Victoria, Australia. —M. Close-up of the flowers of *R. acerosa* (sect. *Cystanthe*), Tasmania. —N. Habit of *Sphenotoma* sp., Stirling Range, Western Australia. —O. Inflorescences of *Sphenotoma* sp., Stirling Range. —P. Close-up of the flowers of *Sphenotoma* sp., Stirling Range.

Table 1. PCR and sequencing primers used for *Dracophyllum* and related genera.

Primers	Bases	Reference
rbcL		Olmstead et al. (1992)
5′	GGC CGT CGA CAT GTC ACC ACA AAC AGA RAC TAA AGC	
346F	ATA TTT ACT TCC ATT GTG GGT AAC GTA TTT	
895F	GCA GTT ATT GAT AGA CAG AAA AAT CAT GGT	
1204F	TTT GGT GGA GGA ACT TTA GGA CAC CCT TGG GG	
346R	AAA TAC GTT ACC CAC AAT GGA AGT AAA TAT	
895R	ACC ATG ATT CTT CTG TCT ATC AAT AAC TGC	
1351R	TTC ACA AGC TGC GGC TAG TTC AGG ACT CCA	
3′	CTC GGA GCT CCT TTA GTA AAA GAT TGG GCC GAG	
matK		Cherry et al. (2001), Quinn et al. (2003)
Aus50F	TAG AAC TAG ATA GAT CTC AGC	
DracMatK1	ATG GAG GAA TTC AAA AGA TAT	This paper
496F	ACT CTT CGC TAC TGG GTA AAA	This paper
888F	TGA TGA ATA AAT GGA AAT ATT	This paper
496R	TTT TAC CCA GTA GCG AAG AGT	This paper
888R	AAT ATT TCC ATT TAT TCA TCA	This paper
2R	AAC TAG TCG GAT GGA GTA G	This paper

optimality criteria (Huelsenbeck & Ronquist, 2001; Swofford, 2002; Ronquist & Huelsenbeck, 2003).

The parsimony analysis was conducted using PAUP* with tree bisection-reconnection (TBR) branch-swapping, MULPARS, and random addition with 1000 replicates. Duplicate trees were eliminated using the condense trees option that collapsed branches with a maximum length of zero. The characters were unordered and equally weighted, and gaps were treated as missing data. Indels (insertions or deletions) were coded separately as binary characters and included in the parsimony, but not the maximum likelihood and Bayesian analyses. Following the method of Simmons and Ochoterena (2000), gaps in the same position were treated as homologous binary characters. Gaps that differed in length, sequence, or position were treated as different characters. We assessed the amount of phylogenetic signal in the data by generating one million random trees and calculating the g1 statistic (Hillis, 1991). Congruence of the data matrices was assessed by the incongruence length difference (ILD) test of Farris et al. (1994, 1995) with 100 data partition replicates. In the event that the phylogenetic relationships recovered by our analyses did not correspond to the current classification, we used the topological constrain option to assess the costs associated with these differences. Support for clades was estimated by bootstrap analyses (Felsenstein, 1985), with 1000 replications excluding uninformative sites; starting trees were obtained by random addition with one replication for each bootstrap replication, TBR branch-swapping, MULPARS in effect, and a MAX-TREE limit of 1000. Clades with > 90% bootstrap

support (BS) or > 95% posterior probability (PP) were considered well supported.

The most appropriate maximum likelihood model and parameter estimates for the Bayesian inference and maximum likelihood analyses were determined by the Akaike Information Criterion (AIC) and Bayesian Inference Criterion (BIC) with model averaging (Posada & Buckley, 2004). These approaches are implemented in Modeltest version 3.06 (Posada & Crandall, 1998).

DIVERGENCE TIME ESTIMATES

The likelihood ratio (LR) test (test statistic = −2 log LR, where LR is the difference between the unconstrained and the −ln likelihood value constrained by a molecular clock, distributed as the χ^2 distribution, with n − 2 *df*, and n = the number of taxa) was used to determine whether the data satisfied the assumptions of a molecular clock (Felsenstein, 1988). In the absence of a molecular clock, we used a penalized likelihood with the truncated Newton algorithm to accommodate rate heterogeneity across lineages (Sanderson, 1997, 2002a). This procedure is implemented in the program r8s (Sanderson, 2002b) and uses a likelihood model combined with a smoothing parameter estimated by cross-validation to estimate divergence times.

We calculated bootstrap confidence limits associated with the divergence dates using a bootstrapping procedure (Sanderson, 2003). The initial maximum likelihood tree was used as a constraint during a bootstrap search, and 100 rooted bootstrap trees with maximum likelihood branch lengths were saved using

the ALNEXUS format (without a translation table). This saves trees with branch lengths and taxon labels as an integral part of the tree description. We then used the profile command to summarize confidence intervals to the divergence estimates at designated nodes in the maximum likelihood tree.

A fossil-based cross-validation procedure was used to assess the magnitude of the violations to minimum and maximum age constraints (Sanderson, 2003). We used four calibration points that were based on the fossil record and geological events (e.g., the formation of Lord Howe Island). We placed a fixed age of 90 Ma at the node separating *Enkianthus* from all other Ericaceae. A minimum age constraint of 40.5 Ma was placed on the node separating *Rhododendron* and *Cassiope* D. Don, and a minimum age constraint of 37.8 Ma was placed on the node separating the Styphelioideae from all other Ericaceae. Finally, a maximum age constraint of 7.5 Ma was placed on the node separating the Lord Howe endemic *Dracophyllum fitzgeraldii* F. Muell. from the eastern Australian species *D. oceanicum* E. A. Br. & N. Streiber. This maximum age constraint corresponds to the emergence of Lord Howe Island around 7.5 Ma, while the minimum age constraints were based on first appearances in the fossil record. The cross-validation approach initially removes each of the minimum or maximum age constraints and then completes a full estimation of divergence times and rates across the tree. If the estimated age is younger than a minimum age or older than a maximum age constraint, then the magnitude of the violation is determined and a running total of these is recorded across the tree. The analysis is repeated across a range of smoothing values using the penalized likelihood method. Two kinds of errors are reported, a fractional value node per constrained node, and a raw value in terms of absolute time (Sanderson, 2003).

We conducted two independent Markov chain Monte Carlo (MCMC) searches using BEAST version 1.4.8 (Yang & Rannala, 1997; Rambaut, 2006–2008; Drummond & Rambaut, 2007; Rambaut & Drummond, 2007) with a relaxed uncorrelated log-normal molecular clock model with the AIC settings as priors. The tree prior was set to a Yule speciation process with log-normal calibration times and 95% confidence intervals.

BEAST version 1.4.8 allows the incorporation of more uncertainty when assigning calibration points than r8s. We set log-normal priors of 90.0 with 95% confidence intervals of 97.7 Ma and 82.9 Ma for the most recent common ancestor (MRCA) of *Enkianthus*; 40.4 (43.9–37.2 Ma) for the MRCA of *Rhododendron*; 37.7 (40.9–34.7 Ma) for the MRCA of subfamily Styphelioideae; and 7.5 (8.1–6.9 Ma) for the MRCA of *Dracophyllum fitzgeraldii*. The log files were examined

using Tracer version 1.4 to optimize priors and to assess effective sample sizes. The Tracer log files are available upon request from the first author. LogCombiner and TreeAnnotator (Drummond & Rambaut, 2007) were used to combine and summarize the information in the tree output files; a summary tree with 95% highest posterior density (HPD) confidence intervals on the branch divergence estimates was drawn using FigTree (Rambaut, 2006–2008; Drummond & Rambaut, 2007; Rambaut & Drummond, 2007).

LINEAGE THROUGH TIME PLOT

We used GENIE version 3.0 (Pybus & Rambaut, 2002a, b) to construct a lineage through time plot to study diversification rates. Under the simplest model (constant speciation rate), the probability of a speciation event occurring at a given time is constant both over time and among species, and a straight line with a slope equal to the per lineage diversification rate is expected (Barraclough & Nee, 2001). However, several evolutionary processes can cause departures from the expectations of a constant diversification rate. An increase in the slope could reflect an increase in the net diversification rate (speciation minus the extinction rate), whereas a slowdown in the diversification rate, a flattening of the slope, can be caused by a decrease in the speciation rate or an increase in the extinction rate. Sampling artifacts can also influence the pattern that is observed. Incomplete sampling tends to underestimate the number of nodes toward the present, which gives the illusion of a slowdown in the diversification rate (Barraclough & Nee, 2001).

RESULTS

The aligned *rbcL* data set included 1402 characters (Table 2). Of these, 1042 characters were constant, 188 variable characters were parsimony uninformative, and 172 were informative. A parsimony analysis recovered 11,177 trees in 97 islands of 700 steps (consistency index [CI] = 0.513 [excluding uninformative characters], retention index [RI] = 0.755). A strict consensus tree is shown in Figure 3.

The aligned *matK* sequence data set included 1523 characters (Table 2). Ten indels were inferred, and gaps were created to maintain positional homology in the *matK* data set. These were always in multiples of three nucleotides and varied in length from six to 12 nucleotides. The gaps were positioned so as not to disrupt the reading frame of the gene. Of the 1533 sequence and gap characters, 840 were constant, 385 variable characters were parsimony uninformative, and 308 were informative. The relationships inferred

Table 2. Summary statistics for the *rbcL* and *matK* data partitions. Uninformative characters were excluded from the consistency index calculation. The g1 statistic was calculated from one million randomly generated trees using PAUP*.

Data partition	Total characters	Informative characters	MPTs	Tree length	CI	RI	g1	ILD test
rbcL	1402	172	11177	700	0.513	0.755	−0.618	—
matK	1533	308	432	1452	0.526	0.772	−0.502	—
Combined	2935	557	36	2166	0.512	0.775	−0.537	0.11

CI, consistency index; ILD, incongruence length difference; MPTs, maximum parsimony trees; RI, retention index.

by the *matK* sequences were more resolved than the *rbcL* results. The parsimony analysis recovered 432 trees in a single island of 1452 steps (CI = 0.526 [excluding uninformative characters], RI = 0.772). The *rbcL* and *matK* strict consensus trees are compared in Figure 3. Significant g1 values (−0.618 and −0.502, respectively; *P* = 0.01) indicated that the random distribution of tree lengths was significantly left skewed, which suggested the *rbcL* and *matK* data sets were converging on a small subset of the possible parsimony trees (Table 2). Furthermore, the data sets were congruent (ILD *P* = 0.11), and so were converging on a subset of trees with a similar topology (Fig. 3).

Because of the lack of conflict, we combined the data sets and conducted parsimony, maximum likelihood, and Bayesian analyses to assess the robustness of our results to the different assumptions associated with these approaches to phylogenetic inference. However, the phylogenetic position of three taxa seemed anomalous and required confirmation. We sequenced a second accession of *Dracophyllum milliganii* Hook. f., *D. minimum*, and *D. strictum* Hook. f. to check for possible misidentification, incorrect labeling, or contamination, and the new sequences obtained for each taxon matched the original data.

The combined *rbcL*, *matK*, and gap data set included 2935 total characters. Of these, 1882 characters were constant, 496 variable characters were parsimony uninformative, and 557 were informative. The combined parsimony analysis provided greater resolution and support for relationships. A heuristic search of the combined data recovered 36 trees in two islands of 2166 steps (CI = 0.512 [excluding uninformative characters], RI = 0.775); a strict consensus tree is shown in Figure 4.

We identified 10 clades that were supported by the combined data set labeled clades A–J in Figure 4. Monophyly of *Dracophyllum* subg. *Oreothamnus* (with the exception of *D. minimum*) was supported (86% BS) with *D. strictum* (subgenus *Dracophyllum*) emerging as sister (100% BS); together, these taxa comprise clade A. The five New Zealand species of *Dracophyllum* subg. *Dracophyllum* (*D. fiordense* W. R. B. Oliv., *D. menziesii* Hook. f., *D. latifolium* A. Cunn.,

D. townsonii Cheeseman, and *D. traversii* Hook. f.) formed a second well-supported clade (clade B) with a 96% BS value. The nine species of *Dracophyllum* from New Caledonia (clade C) (subgenus *Dracophyllum* and subgenus *Cordophyllum*) were at best weakly supported (53% BS). However, two subclades, one comprising *D. alticola* Däniker, *D. balansae* Virot, *D. cosmelioides* Pancher ex Brongn. & Gris, *D. mackeeanum* S. Venter, and *D. ramosum* Pancher ex Brongn. & Gris (88% BS), and a second comprising *D. involucratum* and *D. verticillatum* Labill. (91% BS), were supported. *Richea* sect. *Cystanthe* (R. Br.) Benth. (clade D) formed a fourth well-supported clade (100% BS) in the combined analysis, but emerged in a different part of the tree from the members of *Richea* sect. *Dracophylloides* Benth. (clade F). Three Australian members of subgenus *Dracophyllum*, *D. oceanicum*, *D. secundum* R. Br., and *D. macranthum* E. A. Br. & N. Streiber, formed a fifth clade (clade E) (100%), with the Lord Howe Island endemic, *D. fitzgeraldii*, emerging as sister, but with weak BS (Fig. 4). A sixth clade, *Richea* sect. *Dracophylloides* (clade F), was well supported with a 96% BS value with two subclades within *Richea* sect. *Dracophylloides* also supported. *Richea alpina* Menadue, *R. continentis* B. L. Burtt, *R. pandanifolia* Hook. f., and *R. scoparia* Hook. f. received 99% BS, and *R. gunnii* Hook. f. and *R. victoriana* Menadue received 100% BS. The Tasmanian endemic *Dracophyllum minimum* was also included in clade F, but its relationships to the two subclades of *Richea* sect. *Dracophylloides* were not resolved.

Dracophyllum sayeri F. Muell. emerged as sister to a large clade (100% BS) composed of most species of *Dracophyllum* (except *D. milliganii*) and all of the species of *Richea*, together forming clade G (100% BS) (Fig. 4). Clade G is united by a unique 6 bp duplication in their *matK* sequences at nucleotide positions 543–548. This duplication is not present in *D. milliganii*, *Sphenotoma*, or any of the other members of the Ericaceae in our survey. The sister to this large clade is not clear; *D. milliganii*, the four species of *Sphenotoma* (clade H) (100% BS), and the *Dracophyllum–Richea* clade (clade G) form a trichotomy. These three clades comprise tribe Richeeae and form a monophyletic group (clade I) with 95% BS.
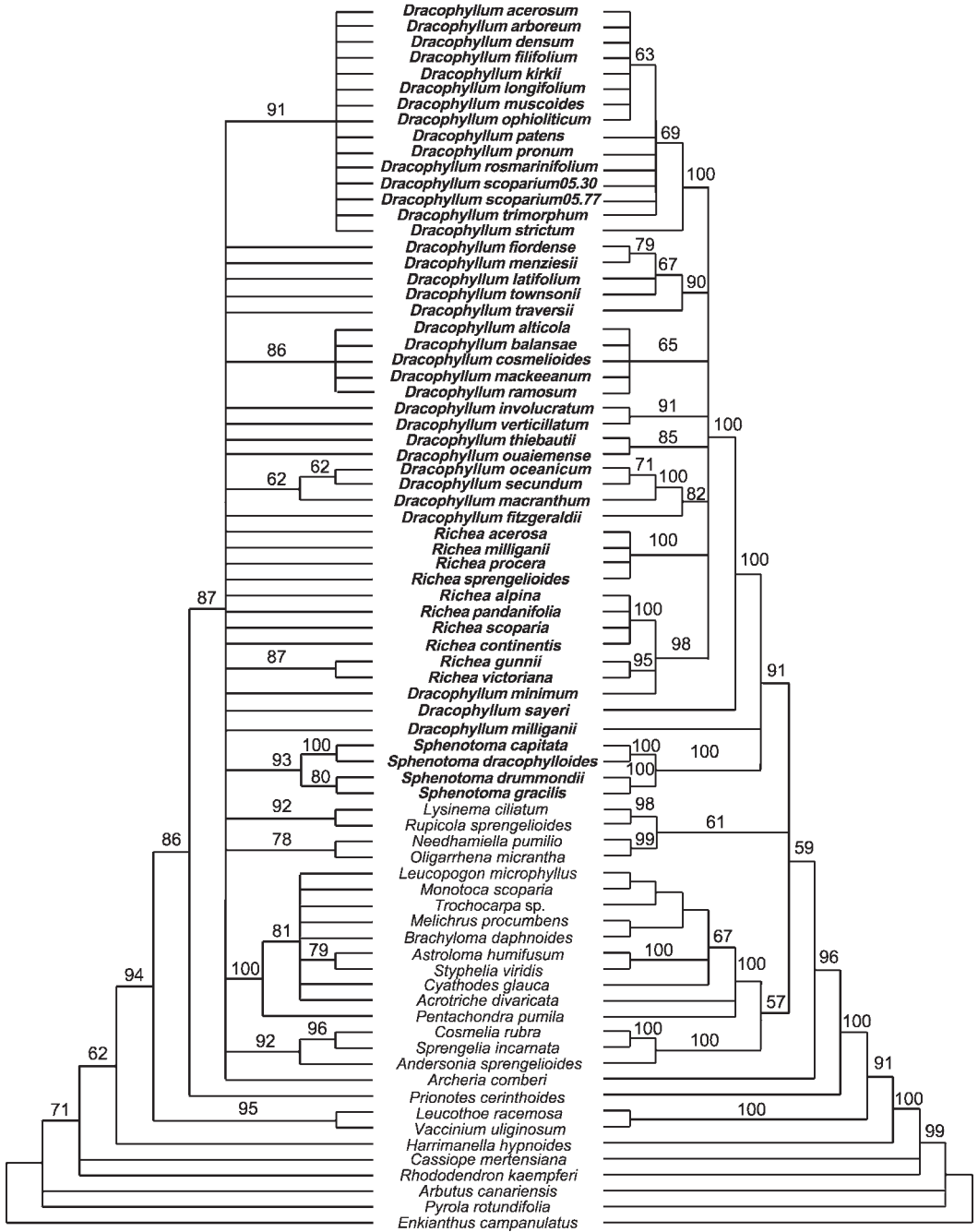
Figure 3.   Comparison strict consensus trees of Australasian Ericaceae from parsimony analysis of *rbcL* and *matK* sequences. The relationships inferred by the *matK* sequences were more resolved than the *rbcL* sequences. Members of tribe Richeeae are highlighted in bold, and bootstrap values > 50% are presented above the branches.

Figure 4. Strict consensus tree from parsimony analysis of the combined *rbcL* and *matK* data sets. A heuristic search of the combined data recovered 28 trees in two islands of 2151 steps (CI = 0.512 [excluding uninformative characters], RI = 0.775; Table 2). Bootstrap values > 50% are presented above the branches. The combined parsimony analysis provided greater resolution and support for relationships than the independent analysis of either *rbcL* or *matK*. Well-supported clades labeled A–J are discussed in the text. Tribe Richeeae, the subgenera of *Dracophyllum*, and sections of *Richea* are shown at right.

Tribe Richeeae is nested within the Southern Hemisphere epacrids (clade J), which receive 100% BS in our analysis (Fig. 4).

We used topological constraints to assess the differences between the current classification and the results inferred from the combined analysis of *rbcL* and *matK* sequences. Enforcing a topological constraint so *Richea* formed a monophyletic group

recovered 272 trees of 2176 steps; these were 10 steps longer than the maximum parsimony trees of 2166 steps. However, this clade was still nested within *Dracophyllum*. Constraining the analysis so that *Richea* and *Dracophyllum* emerged as monophyletic sisters were 25 steps longer than the maximum parsimony trees. Constraining the analysis so that *Dracophyllum* and *Richea* were each monophyletic as

well as the three subgenera of *Dracophyllum* required an additional 51 steps.

AIC and BIC selected the general time reversible model (GTR + G + I) with an assumed proportion of invariable sites = 0.3008 and a rate distribution of variable sites following a gamma approximation with a shape parameter = 0.8861 as the best-fit substitution model for the combined analysis of the *rbcL* and *matK* sequences. Nucleotide frequencies determined by the AIC test were set as: A = 0.3074, C = 0.1654, G = 0.1871, and T = 0.3401. These settings were used in the maximum likelihood and Bayesian inference analyses.

A heuristic search using maximum likelihood as the optimality criterion with these AIC settings resulted in a single tree ($-$Ln = 16709.592; shown in Fig. 5). This tree is also largely congruent with the parsimony and Bayesian trees (Figs. 4, 6). There appears to be considerable rate variation across lineages (Fig. 5), which is apparent, for example, in *Oligarrhena micrantha* R. Br. and *Lysinema ciliatum* R. Br. with relatively long branches and *Arbutus canariensis* Duhamel and *Cassiope mertensiana* (Bong.) G. Don with comparatively short branches. Most of the branches leading to species of *Dracophyllum* and *Richea* are approximately the same length (Fig. 5), which suggests the substitution rates in this part of the tree are approaching clocklike behavior. Nonetheless, the substitution rates across the entire maximum likelihood tree violated a molecular clock assumption, exhibiting significant rate heterogeneity across lineages (LR test = 2 [16709.592–16959.605] = 500.026, df = 75, $P \leq 0.001$). Therefore, we used the penalized likelihood approach of Sanderson (2002a, b) to estimate substitution rates and divergence times in the absence of a molecular clock.

The minimum and maximum age constraints placed on the maximum likelihood tree (Fig. 5) were assessed across five smoothing values to evaluate the quality of the penalized likelihood model and the parameters that were selected for the r8s analysis. The fractional and raw errors were relatively low across all five smoothing values. Only one violation of the minimum age constraint placed on the Styphelioideae was noted; the estimated age of 37.65 Ma was 0.15 Ma younger than the fossil-based constraint of 37.80 Ma. However, the maximum age constraint of 7.5 Ma was exceeded across four of the five smoothing values. The violations ranged in magnitude from 0.3–4.5 Ma; these violations would suggest the split between *Dracophyllum fitzgeraldii* and *D. oceanicum* was older, conceivably up to 4.5 million years older than the emergence of Lord Howe Island.

Assuming the fixed age and minimum/maximum age constraints created realistic boundaries for the r8s divergence estimates, we inferred a minimum stem age for tribe Richeeae of approximately 33.4 ± 3.5 Ma (range, 12.2–44.1 Ma) (sample statistics derived from 100 BS trees presented as mean ± SD and range) (Table 3). The minimum age for the crown radiation in tribe Richeeae was Early Miocene, about 20.6 ± 2.9 Ma (range, 7.2–35.9 Ma). The New Zealand *Dracophyllum* lineage was slightly older than the New Caledonian lineage with a minimum stem age of 6.2 ± 1.0 Ma (range, 2.6–8.8 Ma compared with 5.6 ± 0.7 Ma; range, 3.9–7.0 Ma), which dates the origin of both lineages to the Late Miocene. The crown radiation occurred at approximately the same time in New Zealand and New Caledonia—3.0 ± 1.2 Ma (range, 1.1–7.7 Ma and 3.5 ± 1.1 Ma; range, 0.7–6.5 Ma), respectively, whereas the crown age of *Dracophyllum* subg. *Oreothamnus* is more recent. The stem age for *Dracophyllum* subg. *Oreothamnus* in New Zealand was 1.1 ± 1.1 Ma (range, 0.0–7.1 Ma). Zero-length branches were collapsed in the r8s analysis, and in some of the bootstrap trees the profiled node was not present, so divergence estimates could not be calculated. This was most evident in shallow divergences, e.g., those with short branches such as the New Caledonian node, which was only present in 47 of the 100 bootstrap trees. In general, the divergence estimates derived from the r8s estimates were younger than those derived from the Bayesian analysis. However, with one exception the means were still within the 95% confidence intervals of the HPD. The estimated stem age of the New Zealand radiation, 6.2 Ma, was slightly younger than the 95% confidence interval of the HPD of 6.9–11.2 Ma.

We ran two MCMC chains, each for five million generations, logging parameters every 1000 generations; 500,000 states were excluded as burn-in. The mean states for the first and second MCMC runs were $-$Ln = 16750.0 ± SD of the means, which were 0.374 and 0.511, respectively. Five thousand trees were saved during each run; 5% (250 trees) were excluded as burn-in from each, and the tree files were combined. Figure 6 shows the combined tree files with bars representing the 95% HPD intervals for the divergence estimates. Well-supported clades are identified with PP > 95% provided above each node. The Bayesian tree was more resolved than parsimony trees, with the PP values consistently higher than the bootstrap support values (Figs. 3, 4, 6).

The New Zealand species of *Dracophyllum* formed a monophyletic group in the Bayesian tree, but there was little PP support for this relationship (Fig. 6). However, two subclades within New Zealand *Dracophyllum* are well supported (100% PP); these correspond to *Dracophyllum* subg. *Oreothamnus* (plus *D. strictum*) (clade A) and *Dracophyllum* subg.

Figure 5.   Maximum likelihood tree (−Ln = 16709.592) that is largely congruent with the parsimony and Bayesian trees (compare Figs. 4, 6). Branches of unequal length indicate considerable rate variation across lineages. Four calibration points were used to estimate divergence times using a penalized likelihood rate smoothing procedure implemented in r8s (Sanderson, 2002b). The ages (given as million years ago [Ma]) and nodes upon which the calibration points were applied are indicated with an arrow.

Dracophyllum (clade B). Within subgenus *Oreotham-nus* (clade A) is a clade composed of *D. ophioliticum* S. Venter, *D. filifolium* Hook. f., *D. kirkii* Berggr., *D. densum* W. R. B. Oliv., *D. trimorphum* W. R. B. Oliv.,

D. patens W. R. B. Oliv., *D. rosmarinifolium* (G. Forst.) R. Br., and *D. acerosum* Berggr., which received 100% PP support. Relationships among the New Zealand species of subgenus *Dracophyllum*
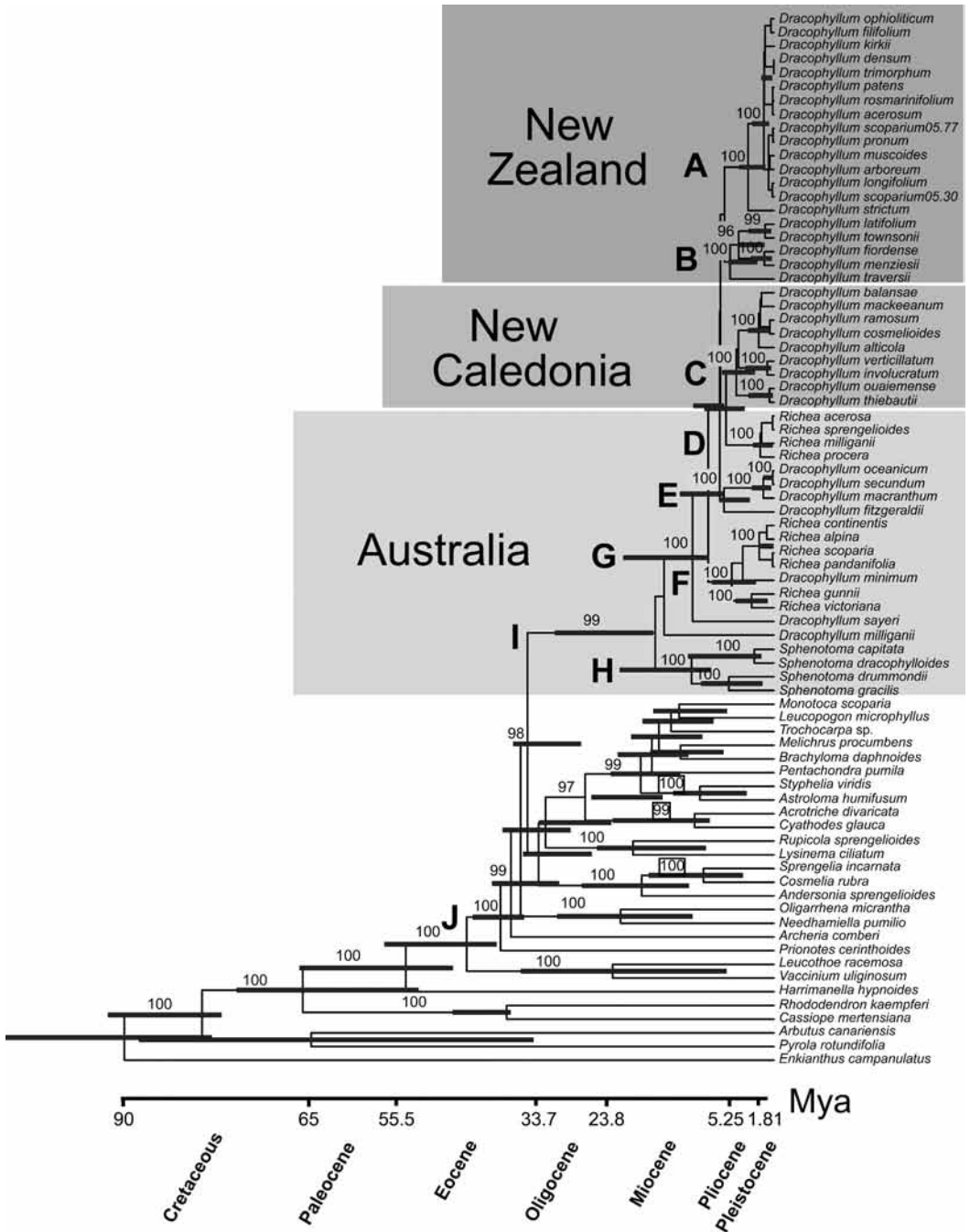
Figure 6.   Bayesian consensus of 9500 trees MCMC analysis. Well-supported clades labeled A–J are discussed in the text. Log-normal priors of 90.0 with 95% confidence intervals of 97.7 million years and 82.9 were set for the MRCA of *Enkianthus*; 40.4 (43.9–37.2 Ma) for the MRCA of *Rhododendron*; 37.7 (40.9–34.7 Ma) for the MRCA of subfamily Styphelioideae; and 7.5 (8.1–6.9 Ma) for the MRCA of *Dracophyllum fitzgeraldii*. This latter prior is a maximum age corresponding to the emergence of Lord Howe Island around 7.5 Ma. Posterior probability values > 95% are presented above each node, and an evolutionary timescale is shown at the bottom. The bars represent 95% confidence intervals of the HPD.

Table 3.   Divergence estimates given as Ma. Zero-length branches were collapsed in the r8s analysis. In some of the bootstrap trees, the profiled node was not present so divergence estimates could not be calculated. The estimates derived from maximum likelihood are presented as means ± SD with the range in parentheses, while the Bayesian estimates are presented as means with 95% confidence intervals of the HPD.

Node	No. of bootstrap trees in r8s profile	Maximum likelihood (Ma)	Bayesian (Ma)
Stem age for tribe Richeeae	100	33.4 ± 3.5 (12.2–44.1)	34.3 (26.9–36.3)
Crown radiation in tribe Richeeae	100	20.6 ± 2.9 (7.2–35.9)	16.5 (8.7–21.4)
Stem age of New Caledonian radiation	47	5.6 ± 0.7 (3.9–7.0)	6.7 (4.0–9.7)
Crown age of New Caledonian radiation	92	3.5 ± 1.1 (0.7–6.5)	5.2 (2.6–7.2)
Stem age of New Zealand radiation	95	6.2 ± 1.0 (2.6–8.8)	7.4 (6.9–11.2)
Crown age of New Zealand radiation	100	3.0 ± 1.2 (1.1–7.7)	6.1 (2.3–6.3)
Stem age of *Dracophyllum* subg. *Oreothamnus* in New Zealand	100	1.1 ± 1.1 (0.0–7.1)	1.4 (0.7–3.0)

(clade B) are completely resolved by the Bayesian analysis. *Dracophyllum traversii* emerged as sister to a clade (96% PP) consisting of *D. latifolium*, *D. townsonii*, *D. fiordense*, and *D. menziesii*, with *D. latifolium* and *D. townsonii* (99% PP) and *D. fiordense* and *D. menziesii* (100% PP) each sisters.

The New Caledonian species of *Dracophyllum* (clade C) form a well-supported clade (100% PP) with three well-supported subclades (Fig. 6). *Dracophyllum verticillatum* and *D. involucratum* form a clade (100% PP). *Dracophyllum ouaiemense* Virot and *D. thiebautii* Brongn. & Gris form a second clade (100% PP) that is sister to a clade composed of *D. alticola*, *D. cosmelioides*, *D. ramosum*, *D. mackeeanum*, and *D. balansae* (100% PP). *Dracophyllum thiebautii* was previously considered as a synonym of *D. verticillatum* by Virot (1975), but is here recognized as a distinct species.

Most of the Australian species of *Dracophyllum* and *Richea* form a grade at the base of tribe Richeeae; two lineages emerge in succession as sisters to the New Caledonian species of *Dracophyllum* (Fig. 6). The four species of *Richea* sect. *Cystanthe* (clade D) (100% PP) are again well supported in the Bayesian tree. Similarly, *D. oceanicum*, *D. secundum*, and *D. macranthum* (100% PP) (clade E) and *Richea* sect. *Dracophylloides* (plus *D. minimum* nested within this clade) (100% PP) (clade F) are well supported by both analyses. *Richea gunnii* and *R. victoriana* form a clade (100% PP) that is sister to a clade composed of *R. pandanifolia*, *R. scoparia*, *R. alpina*, and *R. continentis*.

In the Bayesian tree, *Dracophyllum milliganii* emerged as sister to all of the other species of *Dracophyllum* and *Richea* (clade G), but there was low PP support for this relationship. The four species of *Sphenotoma* in our analysis form clade H (100% PP). Within clade H, *S. capitata* (R. Br.) Lindl. and *S.*

dracophylloides Sond. form a clade (100% PP) that is sister to a clade comprised of *S. drummondii* (Benth.) F. Muell. and *S. gracilis* (R. Br.) Sweet (100% PP). Tribe Richeeae received greater support (99% PP) in the Bayesian tree (clade I, Fig. 6) than in the parsimony tree (Fig. 4) and again was nested within the Southern Hemisphere epacrids (clade J) (100% PP).

The nodes separating the 77 terminals in the r8s analysis are plotted through time in Figure 7A–C. Our sample was fairly complete within tribe Richeeae, but most of the genera in subfamily Styphelioideae were only represented by single exemplars, and the relatively flat portion of the plot partly reflects this taxonomic bias (Fig. 7A). Within tribe Richeeae, we estimated that a new species lineage was formed approximately every 338,000 years. However, we observed two plateaus in the lineage through time plot, which suggested a departure from this average diversification rate. The earliest punctuation was observed among the 20 Australian members of tribe Richeeae (e.g., *Sphenotoma*, *Richea*, and five species of *Dracophyllum*) beginning approximately 20.6 Ma and lasting for 13.5 million years (Fig. 7B). This period was marked by a substantial slowdown in the diversification rate and/or an increase in the extinction rate. A second punctuation in the diversification rate beginning around 6.5 Ma and lasting for 3.3 million years was noted among the 30 species of *Dracophyllum* found in New Zealand and New Caledonia (Fig. 7C). This occurred shortly after these island archipelagos were colonized by *Dracophyllum* and may reflect a slowdown in the diversification rate during establishment. Most of the net diversification in tribe Richeeae has occurred within the last two million years, as indicated by the steep slope in the lineage through time plot during this time period (Fig. 7A–C).

DISCUSSION

We provide a robust inference of the phylogenetic relationships within tribe Richeeae. Our results indicated that only *Sphenotoma* is monophyletic, whereas *Dracophyllum* and *Richea* are polyphyletic. The differences in species richness between continental Australia, Tasmania, Lord Howe Island, New Caledonia, and New Zealand partly reflect a taxonomic bias in the manner that genera within the tribe have been circumscribed. The disparity would not be so great if the species of *Richea* were lumped in *Dracophyllum*. This taxonomic bias is superimposed on an evolutionary history of long-distance dispersal, diversification, and extinction. There appears to be a biogeographical basis to the patterns of diversification that we recovered. While the greatest levels of species richness and morphological diversity in *Dracophyllum* are found in New Zealand and New Caledonia, the phylogenetic diversity is greatest in Australia. The Australian species of *Dracophyllum* are remnants of older lineages, and their present distributions are fragmented and disjunct. In contrast, our results suggest that the New Caledonian and New Zealand species (especially *Dracophyllum* subg. *Oreothamnus*) have recently radiated following at least two unique instances of long-distance dispersal from eastern Australia.

PHYLOGENY AND CLASSIFICATION OF TRIBE RICHEEAE

On its own, the analysis of *rbcL* does not support monophyly of tribe Richeeae (comprising *Dracophyllum*, *Richea*, and *Sphenotoma*). However, it is not in conflict with the *matK* results, which provide better support for the tribe (Fig. 3). The combined analyses provide stronger support and resolution within the tribe (Figs. 4–6). Our findings confirm earlier molecular studies with an expanded sample of the tribe (Crayn & Quinn, 2000; Kron et al., 2002). Additional morphological characters that unite the members of tribe Richeeae include the presence of a single bract that subtends the sepals, sheathing leaves that leave a distinct annular scar, leaf nodes that are tri- or multilacunar, and the absence of platelet waxes on the adaxial surface of the leaves (Powell et al., 1996; Crayn et al., 1998; Kron et al., 2002; Venter, 2008). Our results also suggest the current generic circumscriptions do not form monophyletic groups (Fig. 4).

The molecular analyses supported monophyly of *Sphenotoma* (clade H, Fig. 4). The genus was originally erected by Sweet (1827), but for a time Bentham (1869) submerged it in *Dracophyllum*. *Sphenotoma gracilis* is the type for the genus. *Sphenotoma* differs from *Dracophyllum* in having a narrow corolla tube, with the throat almost closed by longitudinal folds at the base of the lobes and the filaments adnate to the corolla tube (Powell et al., 1996) (Fig. 2N–P). Six species are currently recognized, but there are probably one to two undescribed species (Paczkowska & Chapman, 2000).

Of the three subgenera of *Dracophyllum* recognized by Oliver (1929, 1952), only the New Zealand members of subgenus *Oreothamnus* form a clade in our analyses (clade A, Fig. 4). *Dracophyllum* subg. *Oreothamnus* has solitary flowers or a raceme, and the subtending bracts become differentiated according to their position, with the lowermost being the most leaflike (Fig. 2F, G). The type for subgenus *Oreothamnus*, *D. minimum* (Fig. 2H), is distinct from the New Zealand clade (Fig. 4), contradicting the phenetic and cladistic morphological analyses of Venter (2008) that supported the traditional placement of *D. minimum* as a member of subgenus *Oreothamnus*. The morphological similarities could be the product of convergence, as *D. minimum* (Fig. 2H) and the New Zealand cushion herbs within *Dracophyllum* subg. *Oreothamnus* (e.g., *D. muscoides* Hook. f.) are found in similar alpine habitats, and their distinct cushion morphology is an adaptation (by morphological reduction) to the harsh environments that they inhabit. Pollen evidence may also help resolve the correct placement of *D. minimum*, as McGlone (1972) demonstrated that pollen morphology of the New Zealand members of *Dracophyllum* subg. *Oreothamnus* differs from that of *Dracophyllum* subg. *Dracophyllum*, but unfortunately *D. minimum* was not included in his survey.

Dracophyllum strictum (*Dracophyllum* subg. *Dracophyllum*) emerges as sister to *Dracophyllum* subg. *Oreothamnus* (clade A, Fig. 4). It is distinguished from the other New Zealand members of subgenus *Dracophyllum* by its small, narrow panicle and included anthers and was instead allied by Oliver (1929, 1952) with the Australian and New Caledonian members of subgenus *Dracophyllum*. The adult leaves of *D. strictum* are (3.5)5.5–8.5 cm × 6–7 mm and the juvenile leaves are 10–11 cm × 11–13 mm (Oliver, 1929), approaching those of subgenus *Oreothamnus*, especially the heteroblastic juvenile forms.

Dracophyllum subg. *Dracophyllum* is the most widely distributed of the three subgenera and occurs across the full geographic range of the genus. However, the distribution is fragmented. Several members of *Dracophyllum* subg. *Dracophyllum* are narrow endemics. *Dracophyllum sayeri* emerged at the base of clade G. It is geographically isolated from the other Australian species of *Dracophyllum* and *Richea* and is restricted to a few isolated mountaintops in northeast Queensland. *Dracophyllum fitzgeraldii* is endemic to Lord Howe Island, and *D. ouaiemense* and
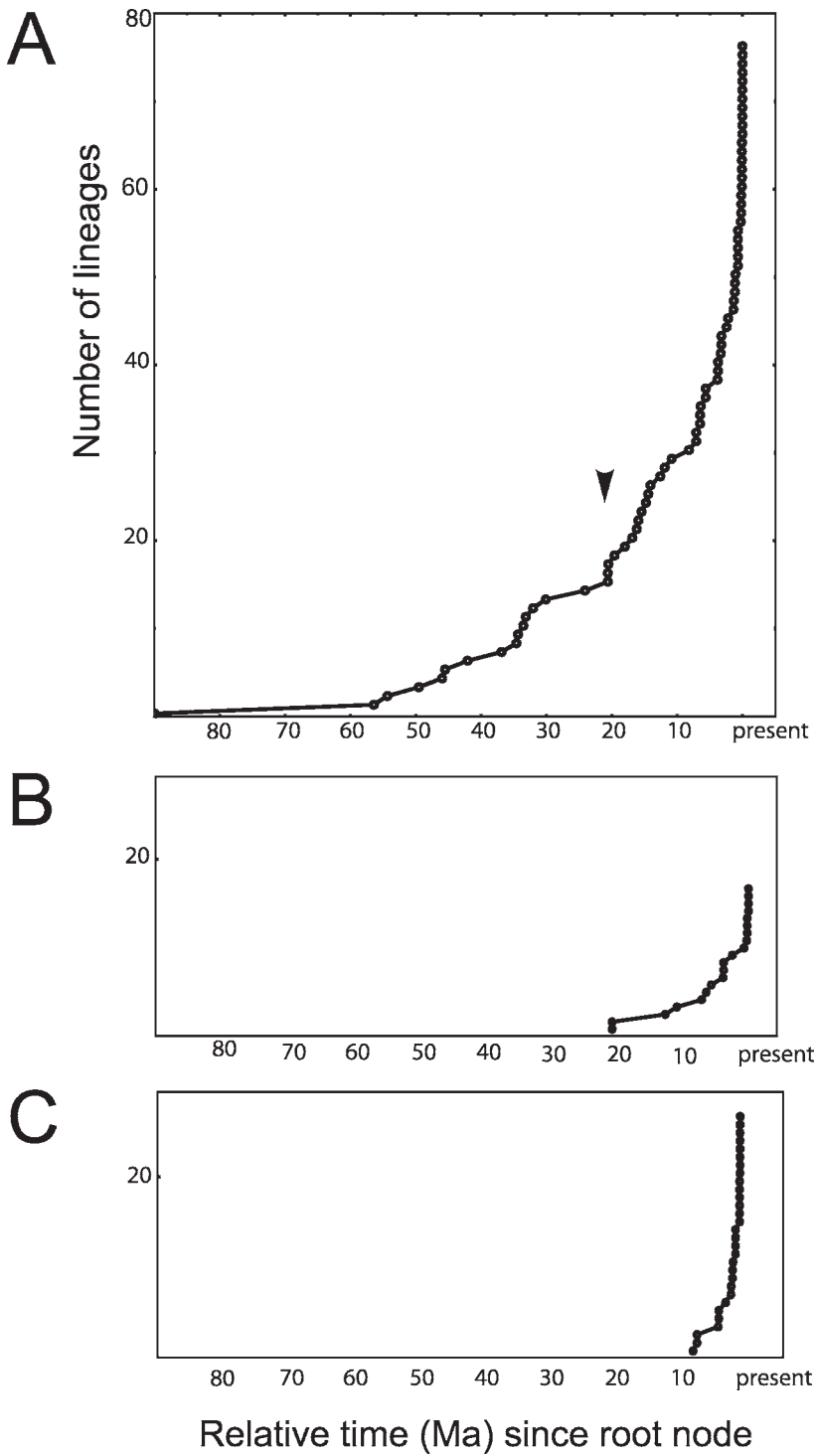
Figure 7. Lineage through time plot. —A. Seventy-seven lineages were plotted that corresponded to the terminals in our study. Our sample was fairly complete within tribe Richeeae, but most genera within subfamily Styphelioideae were represented by single exemplar. The relatively flat portion of the plot reflects this taxonomic bias. The arrow shows the stem lineage giving rise to tribe Richeeae. —B. Plot of the Australian species of *Dracophyllum*, *Richea*, and *Sphenotoma* shows a broad plateau from 20.6 Ma that may represent an increase in the extinction rate relative to the rate of speciation. —C. In

D. alticola to a few isolated mountain peaks in New Caledonia.

Our results suggest the subgenus is at best paraphyletic, and it is probably polyphyletic (Fig. 4; with representatives in clades A, B, E). Oliver (1929, 1952) recognized four groups based on the characteristics of the panicle, sepals, corolla, and anther position (Fig. 2A–D). A paniculate inflorescence is the only morphological character that unites the members of *Dracophyllum* subg. *Dracophyllum*, although it can be either terminal or lateral. The bracts can be short and broad as in *D. strictum* or greatly elongated as in *D. milliganii* and are generally deciduous. The corolla tube can be quite long with inserted stamens or short with the stamens far exserted.

The New Caledonian species, *Dracophyllum involucratum*, which alone forms *Dracophyllum* subg. *Cordophyllum*, is nested among the species of *Dracophyllum* subg. *Dracophyllum* from New Caledonia (clade B, Fig. 4). *Dracophyllum involucratum* is distinguished by a terminal spikelike raceme with the flowers in whorls (Fig. 2E), each on a separate pedicel subtended by small bracts (Oliver, 1929, 1952), but in most other respects it is quite similar to the other members of *Dracophyllum* subg. *Dracophyllum*. There is little sequence variation that distinguishes *D. involucratum* from the other New Caledonian species of *Dracophyllum*, so continued recognition as a distinct subgenus is unwarranted, and the homology of its inflorescence structure needs to be investigated in greater detail. It shares the large colorful deciduous bracts and paired bracteoles of the other members of subgenus *Dracophyllum*. Its unique inflorescence structure is undoubtedly an autapomorphy.

Both *Richea* lineages are well supported (clades D, F, Fig. 4) and correspond to the two sections (*Richea* sect. *Cystanthe* and *Richea* sect. *Dracophylloides*) recognized from morphological and flavonoid characters (Mueller, 1867–1868; Menadue & Crowden, 2000). Because we found *Richea* to be polyphyletic, each lineage could potentially be recognized as a distinct genus. Indeed, this approach was originally taken by Robert Brown (1810) when he described *Cystanthe* and *Richea* based on their unusual cap-shaped corolla (Fig. 2L, M) but distinguished by their

inflorescences. *Richea* sect. *Cystanthe* has a simple spike (Fig. 2M) and persistent bracts, whereas *Richea* sect. *Dracophylloides* has elongate spikes or compound panicles and deciduous bracts (Fig. 2I–L). The floral characters that were used by Brown (1810) to identify *Richea* are homoplasious and have apparently evolved independently in two different lineages.

To overcome the issue of polyphyly, either *Dracophyllum* could be enlarged to accommodate *Richea* (clade G, Fig. 4) or tribe Richeeae (clade I, Fig. 4) could be subdivided into further genera. For example, Venter (2008) advocated elevating *Dracophyllum* subg. *Oreothamnus* as a distinct genus. While this latter approach is enticing, the type, *D. minimum*, was distant from the other members of subgenus *Oreothamnus*, so it may be necessary to apply a different name to the New Zealand clade (clade A, Fig. 4). Nonetheless, we acknowledge that there may be merit in recognizing monophyletic groups restricted to New Caledonia and New Zealand as distinct genera, but this would require the circumscription of at least five new Australian genera to resolve the other issues of polyphyly in *Dracophyllum* and *Richea*. Unfortunately, the relationships among these genera are not well supported by our results, so it is possible that any newly circumscribed genus would not be monophyletic. One approach is to adopt a broad circumscription of *Dracophyllum* that includes *Richea*. If this approach is followed, tribe Richeeae would then be comprised of two well-supported lineages that have been reproductively isolated for millions of years and an infrageneric treatment could be used to account for some of the observed variation. *Sphenotoma* and *Dracophyllum* s.l. (including *Richea*) are geographically isolated and taxonomically distinct. The ambiguous placement of *D. milliganii* poses a conundrum for either approach. It could be recognized as a distinct genus or included in *Sphenotoma*, but because of its morphological similarity to the other species in *Dracophyllum* subg. *Dracophyllum*, we would recommend tentatively including it there, at least until additional evidence suggests otherwise. The presence of sclereid thickenings on the top and bottom of the cells and two bracteoles (with reversal in the members of *Dracophyllum* subg. *Dracophyllum*) is a putative synapomorphy for *Sphenotoma*, whereas possible synapomor-

←

contrast, the plot of the New Caledonia and New Zealand species of *Dracophyllum* is represented by a brief plateau beginning about 6.2 Ma that lasted for 3.8 Ma. This may represent a slower net diversification rate during the initial colonization of these island archipelagos. Most of the net diversification in tribe Richeeae has occurred within the last two million years as indicated by the steep slope in the lineage through time plot during this time period.

phies for *Dracophyllum* s.l. are leaves with a serrate margin (with reversal in *D. sayeri*, *D. alticola*, and some species of *Richea* sect. *Cystanthe*) (Venter, 2008).

Sources of error in divergence time estimation have recently received critical attention (Sanderson et al., 2004; Heads, 2005; Renner, 2005). Foremost is obtaining a well-supported inference of phylogenetic relationships and the proper integration of fossil evidence to calibrate a molecular clock. The issue is the choice of node to which a fossil applies. Moreover, the fossil record is scanty and incomplete. The first appearance in the fossil record implies only a minimum age, and it can be difficult to assess their affinities to extant taxa. Basing divergence time estimates on a single calibration point can be problematic. We applied both maximum likelihood and Bayesian approaches to estimate divergence times, using multiple fossil dates and the emergence of Lord Howe Island as calibration points and a fossil-based cross-validation procedure, but nonetheless we acknowledge there is substantial uncertainty associated with our estimates.

Members of the Ericaceae appear relatively early in the fossil record documented for angiosperms. We rooted our phylogeny on the long branch leading to *Enkianthus* and set the minimum age of this branch at 90 Ma, which reflects the first appearance of allied fossils during the Late Cretaceous (Nixon & Crepet, 1993). The environmental conditions that existed during the early evolution of the Ericaceae were dramatically different from those of the present day (Raven & Axelrod, 1972; McLoughlin, 2001; Hill, 2004; Hopper & Gioia, 2004; Gibbs, 2006; McGlone, 2006; Ladiges & Cantrill, 2007). The southern continents were united, forming the supercontinent Gondwana, but began to drift apart during the Late Cretaceous. Because of their position in high latitudes, there were three months of complete darkness in winter followed by nearly continuous daylight during the brief summer (Hill, 2004; McGlone, 2006). The forest vegetation was dominated by diverse angiosperms, podocarps, araucarias, and ferns. Warm temperate, moist climatic conditions prevailed as the continents continued to shift apart and migrate northward. The landmass that was to form New Zealand retained connections to New Caledonia, possibly until the end of the Eocene, and faced an almost continuous Gondwanan coastline consisting of South America, Antarctica, and Australia. Until the Oligocene to Early Miocene, southeastern Australia and New Zealand were clothed in diverse rainforest vegetation, resembling that

presently found in northeastern Australia, New Guinea, and New Caledonia (McLoughlin, 2001; Hill, 2004; Gibbs, 2006; McGlone, 2006).

The divergence estimates depicted in the Bayesian chronogram (Fig. 6) are generally older than those derived from the r8s analysis (Table 3); nonetheless, the mean estimates from both approaches fall within the confidence intervals surrounding the means. The branch leading to *Rhododendron* diverged during the Early Tertiary about 45.1 Ma. Both fossilized pollen and seeds of *Rhododendron* are reported from this time period (Collinson & Crane, 1978; Zetter & Hesse, 1996). Our results also suggest that Southern Hemisphere epacrids are nested among the Ericaceae at about 40.5 Ma, emerging as sister to subfamily Vaccinioideae (Kron et al., 2002). Tribes Oxydendreae, Lyonieae, and Andromedeae are basically Northern Hemisphere groups, whereas tribes Vaccinieae and Gaultherieae have expanded into both the Northern and Southern hemispheres. The maximum likelihood divergence estimates that we obtained were older than the minimum age constraints that we placed on these two lineages. This is roughly when the land connections from South America to Australia via Antarctica were broken. Perhaps this ancient geological event is related to the isolation of the Southern Hemisphere Styphelioideae from the predominately Northern Hemisphere vaccinioids.

Diversification in subfamily Styphelioideae (clade J, Fig. 6) was rapid, with lineages presently recognized as tribes diverging by the mid-Tertiary (Jordan & Hill, 1996; Jordan et al., 2007, 2010). Fossilized ericaceous pollen was present in New Zealand and Australia by the mid-Eocene. Our results suggest the members of tribe Richeeae (clade I, Fig. 6) diverged from the other epacrids at least 33.4 Ma (Table 3). This date is very close to the age of the earliest fossils of Richeeae—both pollen and macrofossils (Mildenhall, 1980; Jordan & Hill, 1996; Jordan et al., 2007, 2010)—and implies the stem lineage of tribe Richeeae had evolved diagnostic traits of the crown group virtually back to the split between tribe Richeeae and its sister, and the first appearance of the fossils closely followed the evolution of the clade. This is rather surprising given the rarity of the fossils (there are only about five leaves in all of Australia and perhaps 20 in New Zealand older than two million years) (Jordan & Hill, 1996; Jordan et al., 2007).

Our results suggest that the major splits within tribe Richeeae evolved by the Early Miocene at least 16.5 Ma (Table 3). The Western Australian genus *Sphenotoma* (clade H, Fig. 6) forms a distinct evolutionary lineage, and *Dracophyllum* and *Richea* together form a second lineage (except the ambiguous placement of *D. milliganii*) (clade G, Fig. 6).

Divergences between the Australian genera *Andersonia* R. Br., *Cosmelia* R. Br., and *Sprengelia* Sm. also occurred during the Miocene (Fig. 6). Today, *Andersonia* and *Cosmelia* are restricted to Western Australia, while *Sprengelia* is restricted to the eastern states including Tasmania. These disjunct lineages may have been geographically isolated by the onset of climatic changes that occurred during the Oligocene and progressed through the Miocene (Hill, 2004; Hopper & Gioia, 2004; Crisp et al., 2004; Crisp & Cook, 2007). The final separation of Australia from Antarctica initiated climatic changes that created the central Australian deserts. The gradual expansion of the deserts isolated the mesic high-rainfall forests of southwestern and southeastern Australia with a belt of semiarid vegetation. Increasing aridity during the Miocene saw the fragmentation of the rainforests and their replacement by drier scleromorphic and xeromorphic vegetation (Hill, 2004; Hopper & Gioia, 2004; Crisp et al., 2004; Crisp & Cook, 2007; Byrne et al., 2008). We document a substantial increase in the rate of extinction and/or a slowdown in the diversification rate in Australia beginning approximately 20 Ma (Fig. 7A).

DISPERSAL AND ESTABLISHMENT ON ISLAND ARCHIPELAGOS IN THE WEST PACIFIC

The divergence estimates suggest that lineages of *Dracophyllum* independently colonized the Western Pacific archipelagos of Lord Howe Island, New Caledonia, and New Zealand. The progenitor of the Lord Howe endemic species *D. fitzgeraldii* likely originated in eastern Australia and dispersed to Lord Howe Island (Fig. 6). These findings are similar to those reported for *Planchonella* Pierre by Swenson et al. (2007). Our results suggest this lineage diverged less than 7.5 Ma, so *D. fitzgeraldii* must have dispersed shortly after the emergence of the island. It may have existed on the mainland prior to this date, but subsequently went extinct. Lord Howe Island is the eroded remnant of a large shield volcano formed during the Late Miocene (Oliver, 1917; Paramonov, 1960; McDougall et al., 1981; McDougall & Duncan, 1988). The period of volcanic activity was relatively brief, lasting less than one million years. A line of reefs, guyots, and banks extends to approximately 1000 km north of Lord Howe Island, and these steep-sided seamounts have a volcanic origin as well. Lord Howe Island lies on the boundary of two major physiographic features, the Lord Howe Rise and the Tasman Basin. Despite its close proximity to mainland Australia, the flora of Lord Howe Island also share close affinities with Norfolk Island, New Zealand, and New Caledonia (Oliver, 1917; Green, 1994).

The New Zealand and New Caledonian species of *Dracophyllum* similarly trace their origins to eastern Australia, having diverged from eastern Australia species at least 7.4 Ma (see Table 3; Figs. 6, 7). The progenitors of these lineages most likely arrived by long-distance dispersal long after these lands had separated from Gondwana. New Caledonia and New Zealand were gradually inundated by rising sea levels beginning in the Late Cretaceous with only a fraction of the present land surface emergent during the Middle to Late Oligocene (Cooper & Cooper, 1995; Lee et al., 2001; Gibbs, 2006; Pelletier, 2006; Grandcolas et al., 2008); much of the extant flora and fauna must therefore have been introduced after the Late Oligocene. Nonetheless, there are a large number of ferns and conifers with a long, continuous fossil record in New Zealand (Cieraad & Lee, 2006), notably the New Zealand kauri, *Agathis australis* (D. Don) Lindl. (Knapp et al., 2007; Lee et al., 2007), suggesting many ancient lineages may have survived Oligocene drowning.

The recent discovery of a remarkable 20–25 Ma fossil allied to tribe Richeeae (Jordan et al., 2010) significantly predates our minimum age estimates of the extant lineages in New Zealand (Jordan et al., 2010). This fossil, *Richeaphyllum waimumuensis* G. J. Jord. & Bannister, exhibits anatomical synapomorphies characteristic of Richeeae, but its affinities within the tribe remain unresolved. This finding suggests the ancestors of *Dracophyllum* may have been present in New Zealand prior to Oligocene drowning. We evaluated the effect on our divergence estimates of using this 20 Ma fossil as a fixed calibration point for the stem age of *Dracophyllum* subg. *Dracophyllum* in New Zealand. The two minimum age constraints were still satisfied, but the maximum age constraint of 7.5 Ma was violated in our r8s analysis. Based on this calibration point, the estimated stem age for *Dracophyllum* subg. *Oreothamnus* in New Zealand was 4.2 Ma, the New Zealand and New Caledonian crown dates were 12.7 and 13.2 Ma, respectively, and the New Caledonian stem age was 18.1 Ma. While these dates seem within reason, the crown age for tribe Richeeae was pushed back to 317.2 Ma, the stem age to 402.3 Ma, the epacrids to 592.62 Ma, and the split between *Enkianthus* and all other Ericaceae to 1331.3 Ma. This latter value predates the origin of land plants. These older values seem unrealistic and are not supported by the fossil record. It is conceivable that the ancestor of *D. milliganii* was more widely distributed during the Miocene, and while its descendants are still found in Australia, they are extinct in New Zealand. This extinct *Dracophyllum* lineage may have been later replaced by progenitors of the extant New Zealand

lineages. This hypothesis would be consistent with the minimum age estimate presented here, but would involve two more recent dispersals to New Zealand and extinction of the earlier lineage.

Dispersal to and from New Caledonia and New Zealand has occurred in many plant groups (Pole, 1994; Macphail, 1997; Wagstaff & Dawson, 2000; Winkworth et al., 2002; Bartish et al., 2005; Swenson et al., 2007), but Ladiges and Cantrill (2007) suggested that vicariance cannot be justifiably dismissed in others. There is a correlation between plant distribution and wind patterns in the Southern Hemisphere, and wind has been proposed as one possible vehicle of long-distance dispersal (Muñoz et al., 2004). *Dracophyllum* has a capsular fruit and produces numerous small seeds within each capsule that could be dispersed by wind, birds, or water.

New Caledonia and New Zealand were independently colonized by species of *Dracophyllum* at least 5.6 and 6.2 Ma (Table 3; Figs. 6, 7). Because of their geographic isolation, the initial island founder populations were most likely small and may have consisted of only a single individual. Punctuation in the net diversification rate (Fig. 7C) may be correlated to these dispersal, colonization, and establishment phases. However, after an initial colonization and establishment phase, diversification in each archipelago was rapid and largely occurred during the Pliocene and Pleistocene some 3–6 Ma (Table 3; Figs. 6, 7). We suggest that inbreeding and strong selection in these small founding populations would have played an important role in the rapid evolution of *Dracophyllum*. The conspicuous contrast between levels of morphological and genetic diversity may partly be a reflection of the interplay between these dynamic evolutionary processes (Winkworth et al., 2005).

This disparity is particularly evident in New Zealand species of *Dracophyllum* subg. *Oreothamnus*. With 29 species, this subgenus is the most species rich in *Dracophyllum* and includes growth forms ranging from alpine cushion herbs to sizeable trees. However, they have virtually identical *matK* and *rbcL* sequences. This low level of sequence divergence suggests that a recent species radiation has occurred within *Dracophyllum* subg. *Oreothamnus*. We documented a brief punctuation in the net diversification rate beginning about 2.2 Ma, followed by a rapid radiation about 1.1 Ma (Table 3; Figs. 6, 7). This may have been spurred by geologic and climatic changes during the Late Tertiary. The uplift of the Southern Alps in New Zealand began during the Pliocene and was accompanied by cooler climates and expansion of subarid areas in the interior of the South Island. This was a time of severe disturbance; the onset of glaciation and erosion during the Pleistocene created a variety of new habitats such as extensive scree slopes, alluvial plains, river terraces, and glacial moraine.

MacArthur and Wilson (1967) stated that species diversity on islands reflects a delicate interaction between immigration, speciation, and extinction. The environmental heterogeneity and biotic diversity in oceanic islands such as New Caledonia and New Zealand may actually contribute to the processes of diversification through increased competition, predation, and the evolution of symbiosis. The impressive and relatively recent species radiation that *Dracophyllum* has undergone upon its arrival in these island archipelagos certainly supports Darwin's early observations, whereas the vagaries of a dramatically changing climate isolated their mainland ancestors in Australia. Extinction may have had a profound influence by diminishing the extant species diversity. The level of phylogenetic diversity within the Australian lineages far exceeds that found in their island cousins; the present species of *Sphenotoma* and *Dracophyllum* s.l. appear to be some of the remaining relics of a once more widely distributed forest flora in Australia. It remains a challenge to classify the members of tribe Richeeae in a manner that accurately conveys their complex evolutionary history. The data presented in this paper yield a chloroplast DNA (cpDNA) gene tree only. It is likely that relationships of *Dracophyllum* are further confounded by evolutionary reticulation, and nuclear data might be more congruent with morphology. This hypothesis could be tested by future research using nuclear genes.

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APPENDIX 1. A list of the DNA vouchers for this study. Information is presented in the following order: species, collection locality and details, herbarium accession number, GenBank number: *matK, rbcL*.

Acrotriche divaricata R. Br., Cherry et al. (2001), Crayn et al. (1998), AY005094, U80432. *Andersonia sprengelioides* R. Br., Kron et al. (1999a), Crayn et al. (1996), AF015631, U79742. *Arbutus canariensis* Duhamel, Kron (1997), Kron & Chase (1999), U61345, L12597. *Archeria comberi* Melville, Kron et al. (1999a), Crayn et al. (1996), AF015632, U79741. *Astroloma humifusum* (Cav.) R. Br., Cherry et al. (2001), Crayn et al. (1998), AY372602, U80433. *Brachyloma daphnoides* (Sm.) Benth., Kron et al. (1999a), Crayn et al. (1998), AF015633, U80428. *Cassiope mertensiana* (Bong.) G. Don, Kron (1997), Kron & Chase (1999), U61346, L12603. *Cosmelia rubra* R. Br., Australia, Western Australia, *D. M. Crayn 117*, 1 Oct. 1995, UNSW 23017, GQ392946, GQ392894. *Cyathodes glauca* Labill., Cherry et al. (2001), Crayn et al. (1998), AY005095, U80434. *Dracophyllum acerosum* Berggr., New Zealand, *M. I. Dawson s.n.*, 11 Sep. 2003, CHR 570437, GQ392947, GQ392895. *Dracophyllum alticola* Däniker, New Caledonia, Province Sud, Mt. Humboldt. *S. Venter 13855 & S. J. Wagstaff*, 17 May 2005, CHR 585693, GQ392948, GQ392896. *Dracophyllum arboreum* Cockayne, New Zealand, *M. I. Dawson s.n.*, 23 Sep. 2003, CHR 570439A&B, GQ392949, GQ392897. *Dracophyllum balansae* Virot, New Caledonia, Province Sud, *S. Venter 13848, S. J. Wagstaff & J. Munzinger*, 14 May 2005, CHR 585694, GQ392950, GQ392898. *Dracophyllum cosmelioides* Pancher ex Brongn. & Gris, New Caledonia, Province Sud, *P. J. Garnock-Jones 2481 & V. L. Woo*, 10 Dec. 2002, CHR 550299, GQ392951, GQ392899. *Dracophyllum densum* W. R.

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