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Evolution of exceptional species richness among lineages of fleshy-fruited Myrtaceae

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• *Background and Aims* The angiosperm family Myrtaceae comprises 17 tribes with more than half of the estimated 5500 species being referred to the fleshy-fruited and predominantly rainforest associated Syzygieae and Myrteae. Previous studies suggest that fleshy fruits have evolved separately in these lineages, whereas generally shifts in fruit morphology have been variously implicated in diversification rate shifts among angiosperms. A phylogenetic hypothesis and estimate divergence times for Myrtaceae is developed as a basis to explore the evidence for, and drivers of, elevated diversification rates among the fleshy-fruited tribes of Myrtaceae.
• *Methods* Bayesian phylogenetic analyses of plastid and nuclear DNA sequences were used to estimate intertribal relationships and lineage divergence times in Myrtaceae. Focusing on the fleshy-fruited tribes, a variety of statistical approaches were used to assess diversification rates and diversification rate shifts across the family.
• *Key Results* Analyses of the sequence data provide a strongly supported phylogenetic hypothesis for Myrtaceae. Relative to previous studies, substantially younger ages for many of the clades are reported, and it is argued that the use of flexible calibrations to incorporate fossil data provides more realistic divergence estimates than the use of errorless point calibrations. It is found that Syzygieae and Myrteae have experienced elevated diversification rates relative to other lineages of Myrtaceae. Positive shifts in diversification rate have occurred separately in each lineage, associated with a shift from dry to fleshy fruit.
• *Conclusions* Fleshy fruits have evolved independently in Syzygieae and Myrteae, and this is accompanied by exceptional diversification rate shifts in both instances, suggesting that the evolution of fleshy fruits is a key innovation for rainforest Myrtaceae. Noting the scale dependency of this hypothesis, more complex explanations may be required to explain diversification rate shifts occurring within the fleshy-fruited tribes, and the suggested phylogenetic hypothesis provides an appropriate framework for this undertaking.

Key words: Myrtaceae, Myrtoideae, Myrteae, Syzygieae, phylogeny, molecular dating, speciation, diversification rates.

INTRODUCTION

A central question in evolutionary biology is the nature of processes that lead to accelerated rates of speciation relative to extinction, and species-rich groups provide some of the clearest examples of this phenomenon. Such groups are often significant in terms of taxonomic diversity, relative abundance and contribution to total biomass over broad geographic regions and can provide good model systems for interpreting the origins and maintenance of biotic diversity at the biome scale (Richardson *et al.*, 2001; Ladiges *et al.*, 2003; Crisp *et al.*, 2004; Erkens *et al.*, 2007). Recent methodological developments (e.g. Sanderson, 2002; Drummond and Rambaut, 2007) have seen the increasing availability of time-calibrated molecular phylogenetic trees, which provide a framework for evaluating the timing of, and correlations with, phenomena that have impacted on rates of lineage accumulation among clades (Moore and Donoghue, 2007; Rabosky *et al.*, 2007). The recurrence of similar phenotypes in separate lineages provides an opportunity to assess the significance of the evolution of a trait, or traits, on diversification (Donoghue, 2005).

Myrtaceae are a moderate sized (approx. 5500 species in 140 genera), predominantly southern hemisphere family with a postulated origin in the Cretaceous (Briggs and Johnson, 1979; Wilson *et al.*, 2001; Ladiges *et al.*, 2003; Sytsma *et al.*, 2004). A remarkable aspect is the ubiquity of the family within Australasia, and groups such as *Eucalyptus s.l.* have been considered a model for understanding the radiation of the Australian sclerophyll flora in response to Miocene–Pliocene aridification (e.g. Crisp *et al.*, 2004; Ladiges *et al.*, 2003). Myrtaceae are also an important component of humid tropical forests, including the tribe Myrteae (*sensu* Wilson *et al.*, 2005; including approx. 2500 species), which is

pantropical, although particularly well developed in Central and South America (McVaugh, 1968; Landrum and Kawasaki, 1997; Lucas *et al.*, 2007), and Syzygieae (approx. 1000–1500 species; Parnell *et al.*, 2006), which is widely distributed in the humid Palaeotropics, but with species richness and lineage diversity centred on the Australasian region (Craven, 2001). Traditionally, Syzygieae and Myrteae were included in Myrtaceae subfamily Myrtoideae, due to the shared possession of a succulent pericarp. Evidence from morphology (Schmid, 1972; Johnson and Briggs, 1984) and molecular phylogenetic studies (Wilson *et al.*, 2001, 2005; Sytsma *et al.*, 2004) suggests that the fleshy fruit of Myrtaceae has multiple origins, arising separately within Syzygieae, Myrteae and elsewhere in the family.

The relationships in Myrtaceae have been the focus of several recent studies (e.g. Johnson and Briggs, 1984; Gadek *et al.*, 1996; Wilson *et al.*, 2001, 2005; Sytsma *et al.*, 2004). Wilson *et al.* (2001, 2005) presented an hypothesis, based upon plastid *trnK-matK* sequence data that forms the basis for the modern tribal classification of Myrtaceae (Wilson *et al.*, 2005) whereas Sytsma *et al.* (2004) analysed a comparable family-wide taxon sample but included plastid *matK* and *ndhF* sequences. A limitation of the existing molecular-based hypotheses is the generally poor resolution of relationships among the tribes. Sytsma *et al.* (2004) used three fossil constraints, and Penalised Likelihood rate smoothing (Sanderson, 2002) to estimate divergence times among the lineages of Myrtaceae. Their approach employed fossil dates as fixed points and does not consider uncertainty, whereas for the same calibrations, Rutschmann *et al.* (2007) noted potentially large errors in divergence time estimates associated with alternative nodal placements (i.e. crown versus stem node) for the fossil dates. Recently developed Bayesian relaxed clock (BRC) methods allow calibration information to be incorporated in the form of parametric prior probability distributions (Yang and Rannala, 2006; Drummond *et al.*, 2006) that, in contrast to point calibrations, can be designed to incorporate uncertainty associated with paleontological data (Yang and Rannala, 2006; Sanders and Lee, 2007).

Here, a reassessment of relationships within Myrtaceae are provided, based upon the Bayesian phylogenetic analysis of nuclear ribosomal internal transcribed spacer (ITS) sequences and plastid *matK* and *ndhF* sequences specifically aimed at improving resolution of relationships among the tribes. Using BRC methods and five fossil calibrations, lineage divergence times for the family were estimated. With this framework in place, the focus was on tribes Syzygieae and Myrteae. Using taxonomic and phylogenetic data, the hypothesis was tested that high species richness in either or both of these groups can be related to unusually high rates of lineage diversification and, specifically, that the recurrence of similar phenotypes in Syzygieae and Myrteae provides an opportunity to consider how shifts from dry to fleshy fruits has impacted on diversification rates among arborescent rainforest lineages.

METHODS

Sequence data

Sequences of the 18S–26S rDNA ITS and plastid regions *matK* and *ndhF* were assembled for 91, 96 and 84 taxa, respectively, Wherever possible, sequences for each of the three regions were sourced from a single accession, although in some cases the ITS data are from a different accession of the same taxon or a congeneric taxon (Appendix). Taxon sampling was designed to reflect the classification proposed by Wilson *et al.* (2005), including representatives of each of their 17 tribal groupings and a representative of the New Caledonian genus *Cloezia*, which was included but not placed by Wilson *et al.* (2005). The outgroup comprised representatives of Vochysiaceae, which in previous phylogenetic studies of both Myrtaceae and Myrtales, have been resolved (although with varying support) as sister to Myrtaceae *s.l.* (Gadek *et al.*, 1996; Conti *et al.*, 1997; Wilson *et al.*, 2001, 2005; Sytsma *et al.*, 2004; Rutschmann *et al.*, 2007) but due to difficulties aligning the ITS regions, only plastid data for Vochysiaceae were included in analyses. Sequences were sourced from GenBank, or, for novel sequences (Appendix), primers, PCR and sequencing conditions were as outlined in Biffin *et al.* (2006), Harrington and Gadek (2004) and Lucas *et al.* (2007). The ITS alignment was performed using the structural partitioning scheme described by Biffin *et al.* (2007), which divides the spacers into 'stem' and 'loop' partitions based upon Minimum Free Energy predictions of putative RNA secondary structures. The plastid data were manually aligned.

Phylogenetic analysis

First, the nuclear and plastid data were analysed separately using MrBayes v. 3·1·2 (Ronquist and Huelsenbeck, 2003). For the ITS, the 'doublet' nucleotide substitution model with an HKY85-like rate matrix and gamma-distributed rate variation with an estimated proportion of invariant sites was applied to the stem-paired data. For the ITS 'loop' partition, and the *matK* and *ndhF* data, a General Time Reversible (GTR) + I + Γ substitution model was used, and each of the concatenated ITS and plastid data sets was analysed with model parameters estimated separately for each data partition (for details of model selection, refer to Biffin *et al.*, 2007). All analyses were performed with uninformative priors on model parameters, and two independent runs (each with four chains, one cold, three heated) of 2×10^6 generations sampling every hundredth generation. Convergence between independent runs and the appropriate burn-in fraction were determined using the post-run 'sump' command in MrBayes and by analysing the output in Tracer v. 1·4 (Rambaut and Drummond, 2004).

A visual comparison of the topologies estimated for the ITS and plastid data was performed to identify strongly supported nodes [posterior probability (PP) ≥ 0·95] with conflicting resolutions amongst data sets. In subsequent analyses the separate data sets were concatenated and analysed in MrBayes with substitution model parameters estimated for each partition as above for the separate analyses of the nuclear and plastid data and analysis settings as previously described.

The concatenated data were also analysed using BRC methods as implemented in BEAST v. 1·4·7 (Drummond *et al.*, 2006; Drummond and Rambaut, 2007) using a four-way partitioning scheme comprising ITS 'stems', ITS 'loops', *matK* and *ndhF*. A GTR + I + Γ substitution model was assumed with the model parameters unlinked across data

partitions (note that BEAST v. 1·4·7 does not incorporate RNA-specific models). An uncorrelated log-normal model of rate variation among branches in the tree and a Yule prior on branching rates were used. Three independent MCMC runs were performed, each of 5×10^6 steps (sampling topology and parameter values every 250 steps) and Tracer was used to assess convergence between runs and estimate an appropriate burn-in proportion, estimate the mean and 95 % highest posterior density (HPD) of parameters sampled from the posterior distribution of the combined runs, and to ensure that the effective sample size was sufficient to provide reasonable estimates of model parameter variance (i.e. >200). After excluding an appropriate burn-in fraction (as described above), the topologies estimated from the three independent runs were combined and topology and parameter values were summarized (using TreeAnnotator; Drummond and Rambaut, 2007) on the 'maximum credibility' tree.

Molecular dating

Fossil dates were used to calibrate molecular evolutionary rates, including those derived from five myrtaceous fossils. In addition, the estimated age of the eudicots [approx. 121 million years ago (Ma) based upon the earliest appearance of tricolpate pollen in the fossil record; Drinnan *et al.*, 1994; Magallón *et al.*, 1999)] was used to constrain the upper age of the root. The Myrtaceae fossils include (*a*) the pollen taxon *Myrtaceidites lisamae*, which appears in the fossil record from the Cretaceous of Gabon (Santonian, 86 Ma; Herngreen, 1975; Boltenhagen, 1976; Muller, 1981), Borneo (Senonian, 89–83 Ma; Muller, 1968) and Colombia (Maastrichtian, 71–65 Ma; van der Hammen, 1954), and provides the earliest estimate for the radiation of Myrtaceae; (*b*) the eucalyptoid fruits from the Redbank Plains formation of eastern Australia, which are placed at 48 Ma (early Eocene; Rozenfelds, 1996), with postulated affinities to Eucalypteae; (*c*) *Paleomyrtinaea princetonensis*, from the Palaeocene (56 Ma; Crane *et al.*, 1990; Pigg *et al.*, 1993) to early Eocene (53 Ma; Manchester, 1999) of North America, comprising well-preserved fruits and seeds suggesting a relationship with guava (*Psidium*) and *Mosiera* (Pigg *et al.*, 1993), or, more broadly, Myrtaceae subtribe Myrtineae (i.e. Myrteae genera with a pimentoid/myrtoid embryo; McVaugh, 1968; Landrum and Kawasaki, 1997); (*d*) the fossil leaves and fruits of *Metrosideros* from the Early Miocene (approx. 20 Ma) of New Zealand, which are considered to show close affinity to extant *Metrosideros* and are the stratigraphically oldest evidence of that genus in New Zealand (Pole *et al.*, 2008); and (*e*) *Tristaniandra alleyii* from the Eocene of South Australia (41–46 Ma; Basinger *et al.*, 2007), comprising flowers and fruits with characters that do not closely match an extant genus although the combination of flowers and fruit structures suggest an affinity to tribe Kanieae (Greenwood and Christophel, 2005; Basinger *et al.*, 2007).

Lineage divergence times were estimated using BEAST v. 1·4·7, with model parameters and settings as outlined above. Where applicable, the fossils were used to provide a minimum age for the associated lineage by constraining the stem node (or the next deeper well-supported node) to be at least as old as the fossil-derived date. In these instances, the prior probability on the age of the node was assumed to follow a log-normal distribution with a 'hard' lower bound (i.e. there is a zero probability of dates much younger than the oldest known fossil assigned to that lineage) and a 'soft' upper bound (i.e. non-zero, but decreasing probability for dates that are older than the fossil constraint) on the age of the node (Sanders and Lee, 2007). Three fossils (*Myrtaceidites*, *Paleomyrtinaea* and the 'eucalyptoid' material) were used as minimum age constraints for the stem node of each corresponding lineage (Table 1 and Fig. 3). These calibrations were designed such that the 'hard' minimum node age (zero offset) was approx. 20 % younger than the age of the fossil, the lower limit of the 95 % confidence interval (CI) of the prior distribution approximates the fossil age, whereas for *Paleomyrtinaea* and the 'eucalyptoid' material, the peak probability was approx. 1·5 times the age of the fossil, allowing the possibility that the node is substantially older than the fossil constraint. A narrower prior probability distribution was used for *Myrtacedeites*, given that age estimates for the Myrtales crown node are generally younger than 121 Ma, i.e. the upper root constraint (e.g. Magallón and Sanderson, 2001; Sytsma *et al.*, 2004; Davies *et al.*, 2004). Therefore, the upper 95 % CI of the prior probability distribution corresponds to an age of approx. 100 Ma (Table 1). Using the stem node to calibrate molecular rates provides an objective criterion for fossil assignment where there is uncertainty in the correct nodal placement (Renner,

TABLE 1. *Calibrations used for the molecular dating analyses of Myrtaceae*

	Calibration	Prior distribution	Prior (mean [95 % CI])	Joint prior (mean [95 % CI])	Posterior (mean [95 % HPD])
1. Myrtaceae stem	***Myrtacedietes* 86 Ma**	**Log-normal**	**92 (86–100)**	**93 (86–101)**	**94 (87–102)**
Myrtaceae				87 (75–100)	86 (74–96)
2. Eucalypteae stem	**Eucalyptus 48 Ma**	**Log-normal**	**65 (52–86)**	**58 (45–73)**	**60 (53–68)**
Eucalypteae				36 (15–57)	40 (28–50)
3. Myrteae stem (BKMMST clade)	***Paleomyrtineae* 56 Ma**	**Log-normal**	**67 (55–89)**	**69 (55–84)**	**59 (53–67)**
Myrteae				50 (30–68)	34 (25–43)
4. Metrosidereae	***Metrosideros* 20 Ma**	**Normal**	**20 (10–31)**	**20 (11–33)**	**20 (13–28)**
5. Kanieae	***Tristaniandra* 45 Ma**	**Normal**	**45 (30–52)**	**34 (21–48)**	**39 (28–50)**

For each fossil, the calibration node is highlighted in bold, and alternative, reasonable fossil placements are indicated. The prior probability distribution for the constrained node, and the joint prior and posterior probability distributions of the constrained node and alternative fossil placements are indicated (millions of years). Numbering corresponds to node numbers in Fig. 3.

2005; for discussion of Myrtaceae fossils, see Rutschmann *et al.*, 2007).

For two fossils (*Tristaniandra* and *Metrosideros*), the associated lineages (Kanieae and Metrosidereae, respectively) are resolved within a well-supported polytomy that includes Myrteae (Fig. 3). The *Paleomyrtinaea* fossils provide the oldest known minimum age for that clade and the *Tristaniandra* and *Metrosideros* fossils were therefore used to constrain the crown group age of their associated lineage (Kanieae and Metrosidereae, respectively) using a normal prior probability distribution with the peak probability equivalent to the fossil age, and a broad CI with 'soft' lower and upper bounds allowing the possibility that the calibration node is older, or younger, than the fossil age (Table 1 and Fig. 3).

A specific concern with Bayesian statistical approaches is the influence of the priors on the posterior probabilities (e.g. Welch *et al.*, 2005) and it is good practice to consider the distribution of the joint prior on posterior density estimates (Drummond *et al.*, 2006). Here, it has been argued that a stem node placement is the most objective criterion for fossil nodal placement. Analyses were run (with calibrations and model settings as outlined above), sampling entirely from the prior, to assess the influence of the priors on the posterior estimate for alternative (more nested) fossil nodal placements and, also, to test whether the data are sufficiently informative to update the priors (Table 1).

Diversification rates of Myrtaceae

Based upon the phylogenetic data, species richness was estimated for clades of interest from the World Checklist of Myrtaceae (Govaerts *et al.*, 2008). For taxa not included in the present analysis, the scheme of Wilson *et al.* (2005) was used to estimate the tribal affinities. *Cloezia* was not placed by Wilson *et al.* (2005), but in the present study it is resolved in a clade including Tristanieae (see Fig. 1).

For selected clades, clade-specific diversification rates (i.e. the rate of lineage accumulation/unit time) were derived using the crown node method-of-moments estimators described by Magallón and Sanderson (2001) assuming a relative extinction rate of 0·9. For a given diversification rate, and relative extinction rate, Magallón and Sanderson (2001) describe a method by which it is possible to estimate a CI on the expected number of species included within a hypothetical crown group for each interval of time from its origin onwards. Following Magallón and Sanderson (2001), a 95 % CI (upper and lower boundary value within which 95 % of the results of the replicates of the stochastic process will fall) was calculated for intervals of 2 million years from time = 0 to time = 70 Ma, assuming the estimated diversification rate for subfamily Myrtoideae (*sensu* Wilson *et al.*, 2005) and a relative extinction fraction of 0 and 0·9. Standing diversity for the tribes of Myrtoideae was then compared with these sets of critical values. The null hypothesis is that all lineages have diversified at a rate consistent with the overall Myrtoideae radiation. Standing diversities that exceed the upper or lower critical values can be considered unexpectedly species-rich or -poor, respectively, in the context of the Myrtoideae radiation. All calculations were performed using the R package GEIGER (Harmon *et al.*, 2008).

Shifts in diversification rate within Myrtaceae were explored using the LASER package (Rabosky, 2006) for the R programming language, which implements the methods described by Sanderson and Wojciechowski (1996). Briefly, this approach uses phylogenetic (topology and branch length) and taxonomic (species richness) data first to test the null hypothesis that all lineages have diversified under a homogeneous rate and secondly, if a homogeneous rate is rejected, to identify the most likely node at which a diversification rate shift has occurred. Given an ultrametric topology (i.e. the BRC topologies; see Fig. 2) with species richness estimates for the terminals, LASER contrasts the likelihood of the data under a model that assumes that all lineages have diversified at a constant rate (one-rate model) with the likelihood of a model in which an ancestral diversification rate shifts at some point to a new diversification rate (flexible-rate model). The flexible-rate model estimates branch-specific diversification rates and the maximum likelihood (ML) shift point is the node with the highest combined likelihood determined by sequentially splitting the tree at each node and optimizing the diversification rate onto the two resulting subtrees (Rabosky *et al.*, 2007).

Tests for diversification rate shifts were conducted at the tribal level derived by pruning all but two taxa per tribe from ultrametric (BRC) topologies, and assigning half the estimated species richness per tribe to each terminal. To avoid conditioning results on a particular topology and branch lengths, trees were sampled from the 95 % HPD of the BRC analyses in proportion to the auto-correlation time (determined using Tracer v. 1·4), i.e. the number of steps (generations) between independent draws from the posterior probability distribution. Because taxon sampling density can influence divergence time estimates (Cook and Crisp, 2005; Linder *et al.*, 2005), the effect of taxon pruning on branch lengths was assessed by summarizing divergence time estimates from the pooled sample of tribal level topologies for comparison with the estimates derived from the complete taxon sample.

Character evolution

Character states for 'fruit-type' (dry or fleshy pericarp) were scored from the literature for the complete taxon sample and a Bayesian approach was used to infer the ancestral states for fruit-type. BayesTraits V1·0 (Pagel and Meade, 2006) simultaneously accounts for phylogenetic uncertainty and uncertainty associated with the estimation of rate parameters upon alternative trees (Pagel and Lutzoni, 2002; Pagel *et al.*, 2004).

Input trees were derived from the Bayesian 'non-clock' analyses of the combined concatenated Myrtaceae data, following 'thinning' to remove autocorrelated samples, as previously described (263 effectively independent topologies were retained). Prior to analyses, the 'ratedev' parameter, which controls the rate at which new states are accepted, was manually set so that the acceptance rate ranged between 20 and 50 % following the authors' recommendations. Priors of the rate parameters were estimated using a hyperprior approach (Pagel *et al.*, 2004) with an exponential distribution, its mean seeded from a uniform distribution on the interval of 0–10·0. A reversible-jump MCMC method was used, in which the Markov chain searches the posterior distribution

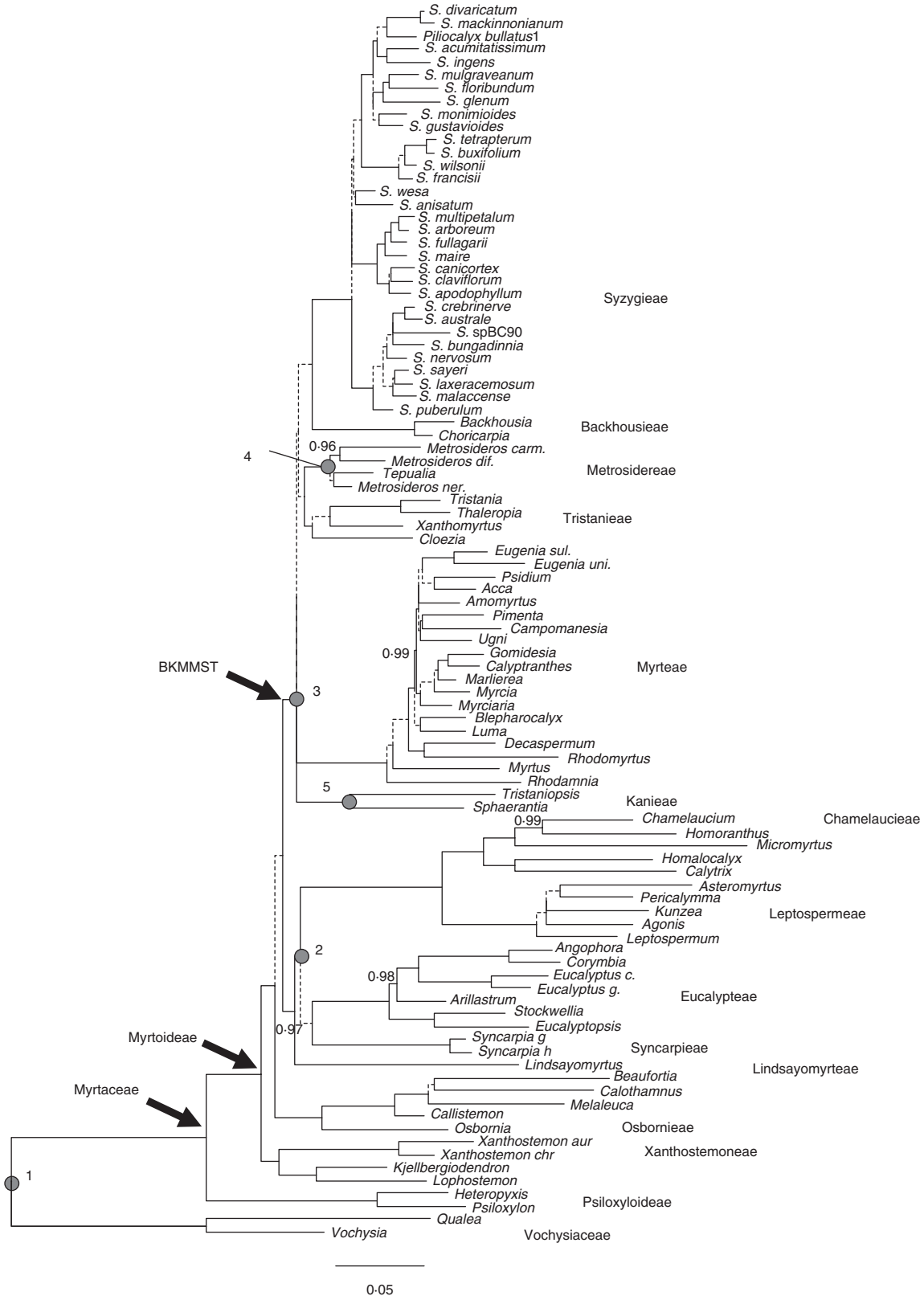

FIG. 1. Relationships of Myrtaceae inferred from the Bayesian analysis of the concatenated ITS and plastid sequence data. Majority rule consensus topology, branch lengths proportional to the inferred number of changes along that branch. Dashed branches have a PP $\leq$ 0·95, PP values between 0·8 and 0·95 are indicated adjacent to the branch. Otherwise the PP = 1·0. Subfamilies and tribal groups follow Wilson *et al.* (2005), and the family Myrtaceae, subfamily Myrtoideae and BKMMST clade (this study) are indicated. Numbered nodes refer to fossil calibrations used for the molecular dating analyses: 1, Myrtaceae stem; 2, Eucalypteae stem; 3, Myrteae stem (BKMMST clade); 4, Metrosidereae; 5, Kanieae (refer to Table 1).

of different models of evolution and the posterior distributions of the parameters of these models (Pagel and Meade, 2006). Because not all of the trees necessarily contain the internal nodes of interest, reconstructions were performed using a 'most recent common ancestor' (MRCA) approach that identifies, for each tree, the MRCA to a group of species and reconstructs the state at the node, then combines this information across trees (Pagel *et al.*, 2004). Three separate analyses were run over 10^7 generations. The 'fossil' command was used to contrast the level of support for each character state at a given node using Bayes factor comparisons (for an interpretation of Bayes factors, see Kass and Rafferty, 1995).

RESULTS

Phylogenetic relationships in Myrtaceae

The analyses of ITS (Fig. S1 in Supplementary data, available online) and the concatenated plastid data (Fig. S2 in Supplementary data) produced broadly consistent topologies, at least to the extent that well-supported nodes did not conflict among data sets, and consequently the data sets were analysed simultaneously. The 50 % majority-rule consensus topology inferred from the MrBayes analyses of the concatenated ITS and plastid data is shown in Fig. 1. The relationships inferred using BEAST, under a BRC and partitioned $4 \times \mathrm{GTR} + \mathrm{I} + \Gamma$ substitution model, show little variation from the MrBayes consensus topology, with only minor differences in PP values among weakly supported nodes (Fig. 2).

Although the monophyly of Myrtaceae *s.l.* was not specifically assessed, the two subfamilies proposed by Wilson *et al.* (2005) (Psiloxyloideae and an expanded subfamily Myrtoideae) are resolved as monophyletic, as are their proposed tribal groupings within Myrtoideae (Wilson *et al.*, 2005). The inferred relationships among the tribes are largely consistent with those reported by Sytsma *et al.* (2004) and Wilson *et al.* (2005), although relative to these, there is a higher level of confidence in some of the inter-tribal groupings. Examples include the grouping of Chamelaucieae, Eucalypteae, Leptospermeae and Syncarpieae (PP = 0·97) and a clade including Backhousieae, Kanieae, Metrosidereae, Myrteae, Syzygieae and Tristanieae (PP = 1·0) (BKMMST clade, Figs 1 and 2). Inter-tribal relationships within the BKMMST clade are generally poorly resolved, although a novel resolution is the inclusion of the New Caledonian-centred *Cloezia* within the BKMMST clade, and a strong association of *Cloezia* with Tristanieae (Figs 1 and 2).

Molecular dating

Figure 2 shows the maximum credibility topology derived from the three independent MCMC runs in BEAST, with median node heights and the 95 % HPD of divergence times illustrated. Analyses were performed without the sequence data (i.e. sampling from the prior) in order to examine the influence of the priors on the posterior probability of divergence time estimates. Table 1 compares the 95 % CI of prior probability distributions and 95 % HPD of posterior probability densities of the Myrtaceae calibrations, and where stem group nodes were used, the prior and posterior densities of the crown group age associated with each of the fossil calibrations. Note that in each instance, the prior distribution for the crown node includes the associated fossil age for that lineage, i.e. a crown node placement is not ruled out *a priori*. Comparison of the 95 % CI of the prior and 95 % HPD estimates suggests that the data are sufficiently informative to update the priors, and, for example, the prior mean for the Myrteae crown node is some 20 Ma older than the median value estimated from the posterior (Table 1).

Diversification rates and diversification rate shifts

The hypothesis that the extant diversities of the tribes of Myrtaceae are not unexpected was tested under the assumption that the entire Myrtoideae radiation has diversified at a constant rate [0·084 net species/million years, assuming 5656 species, an age of 75 million years for the Myrtoideae crown (Fig. 2), and a relative extinction rate of 0·9]. Of the tribal lineages included in the comparisons (Fig. 3), only Syzygieae (1189 species) and Myrteae (2379 species) have standing diversities significantly exceeding the upper 95 % CI of the expected number of species given the assumptions used, regardless of the relative extinction fraction ($e = 0$ and 0·9) and for all estimates included within the 95 % HPD of divergence time estimates for that clade ($P < 0{\cdot}00015$ and $P < 0{\cdot}0006$, respectively, at $e = 0{\cdot}9$, using the upper age estimate for the crown group included within the 95 % HPD of divergence times). In support of these findings, the analyses using LASER (repeated over 300 sampled tribal-level topologies; Fig. 4) strongly reject a homogeneous diversification rate for Myrtaceae in favour of a flexible-rate model ($\Delta\mathrm{AIC} > 30{\cdot}7$; $\Delta\mathrm{LH} < 2{\cdot}91 \times 10^{-8}$).

There is some ambiguity in the location of the reconstructed ML shift point under the flexible-rate model, although a few generalizations can be made (Table 2). First, the ML shift point is associated with, or nested within, the BKMMST clade across all sampled topologies, and secondly, the clade associated with the shift always includes the tribes Syzygieae and Myrteae, or only Syzygieae or Myrteae. Generally, this ambiguity is a reflection of the poor resolution of relationships among the BKMMST tribes (Figs 1 and 2).

In Table 2, the ML shift point is represented as the proportion of the 300 sampled topologies associated with that clade. Perhaps a more meaningful measure is a 'corrected' clade-specific ML shift-point proportion, derived by dividing the proportion of sampled topologies by the posterior probability of that clade, i.e. the proportion of topologies that contain that clade and also include the ML shift point at that node. For this value, only the topologies that include a monophyletic Syzygieae + Myrteae contain the ML shift point in 100 % of the sampled trees (Table 2). Figure 5 shows the differences in AIC (ΔAIC) values obtained by subtracting the AIC score for the reconstructed ML shift point on each of the included topologies with the best AIC score for a rate shift estimated from the overall sample. The best AIC (576·6) was associated with the MRCA of Syzygieae + Myrteae, and in Fig. 5, the ΔAIC scores for topologies with this resolution are highlighted for comparison with all other reconstructed ML shift points. In general, the lowest ΔAIC

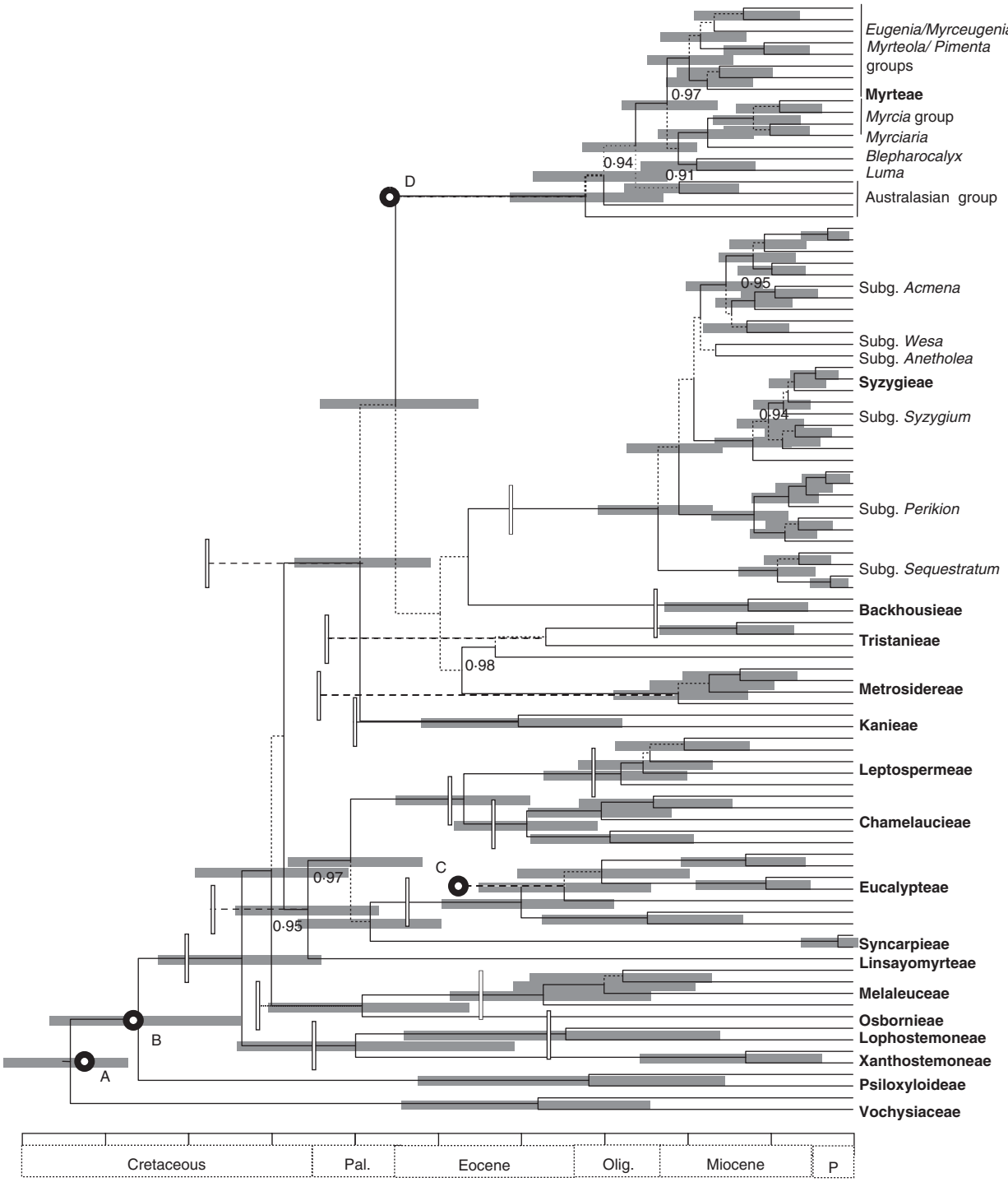

FIG. 2. Maximum credibility chronogram inferred using BRC methods. The posterior probability of the branches is as in Fig. 1. Horizontal bars represent the 95 % HPD of divergence times for nodes receiving a PP $\geq$ 0·5. Vertical bars indicate the estimated divergence time for the equivalent node from Sytsma *et al.* (2004). Fossil calibrations from Sytsma *et al.* are also indicated (open circles: A, PHMV clade, 93 Ma; B, *Myrtacedeites*, 86 Ma; C, 'eucalypt' fruit, 48 Ma; D, *Paleomyrtineae*, 56 Ma). Groupings within Syzygieae and Myrteae are according to Craven and Biffin (2010) and Lucas *et al.* (2007), respectively. Each division in the scale bar is equal to 10 million years.

values are associated with the former and, for instance, the mean ($\pm$ s.d.) AIC score for shifts on Syzygieae + Myrteae was 589·1 (6·2) versus a mean of 610·2 (10·7) for the AIC score derived from all alternative ML shift points.

Character evolution

From our Bayesian reconstructions of ancestral fruit types, the probability of a single origin for the fleshy pericarp (i.e. the MRCA of Myrteae, Syzygieae and Tristanieae had fleshy fruit)

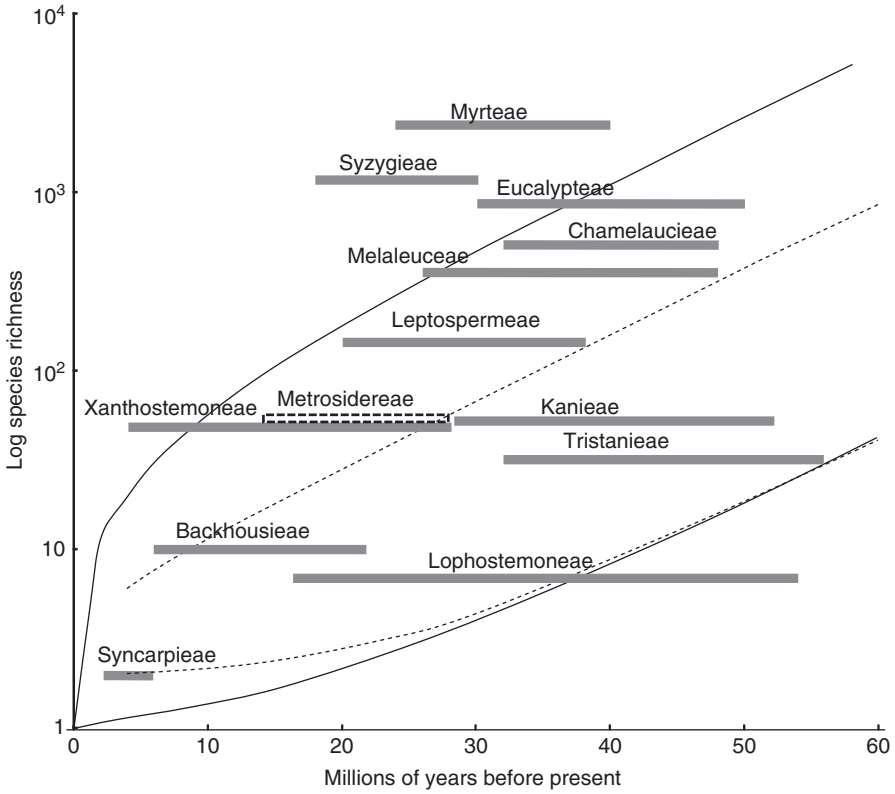

FIG. 3. Confidence intervals of expected diversity (log scale) according to age of crown group, with the sets of lines representing the upper and lower limits of the 95 % CI of expected species numbers assuming a diversification rate of 0·084 (Myrtoideae median) and a relative extinction rate of 0 (broken lines) and 0·9 (continuous lines). Tribes of Myrtaceae are mapped according to estimated standing diversity and the age of the crown group (95 % HPD of divergence time estimates shown as horizontal bars).

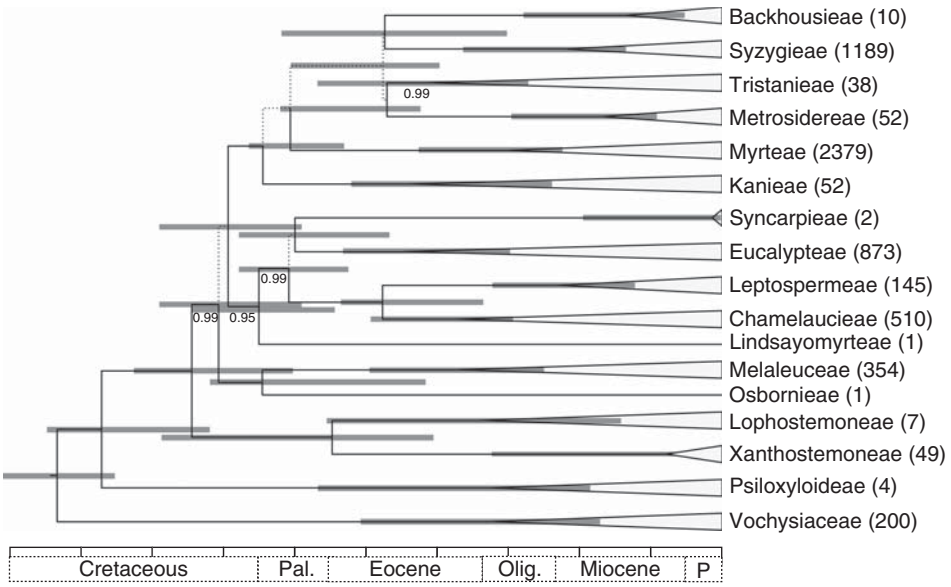

FIG. 4. Consensus topology of 300 trees obtained from the BRC analyses (see Fig. 2) and pruned to represent tribal diversity in Myrtaceae. Diversity per tribe according to Govaerts *et al.* (2008) is indicated adjacent to the terminal. Clade support is as in Fig. 1. Vertical bars represent the range of divergence times obtained from the 300 sampled topologies for all nodes receiving a PP $\geq$ 0·5. Each division in the scale bar is equal to 10 million years.

is $<$0·19, and the probability that a fleshy pericarp has arisen twice within the BKMMST clade (i.e. once within *Xanthomyrtus* and once for the MRCA of Syzygieae and Myrteae) has a probability of $<$0·21. Bayes factor comparisons was used to test the relative support for one state over the other for each of these groupings. For the MRCA of Myrteae,

TABLE 2. *The distribution of reconstructed ML shift point under the flexible-rate model amongst nodes from 300 sampled tribal level topologies, the posterior probability of each node, and the proportion of topologies containing the ML shift point on that node (used to derive a corrected ML shift statistic by dividing the two values)*

	Node*							
	BKMeMST	BMeMST	MeMST	MeMS	SMT	SM	M	S
Posterior probability	1·0	0·61	0·02	0·02	0·03	0·18	1·0	1·0
Proportion of topologies containing ML shift	0·06	0·43	0·13	0·13	0·27	0·18	0·17	0·1
Corrected ML shift	0·06	0·71	0·66	0·66	0·89	1·0	0·17	0·1

* B, Backhousieae; K, Kanieae; Me, Metrosidereae; M, Myrteae; S, Syzygieae; T, Tristanieae.

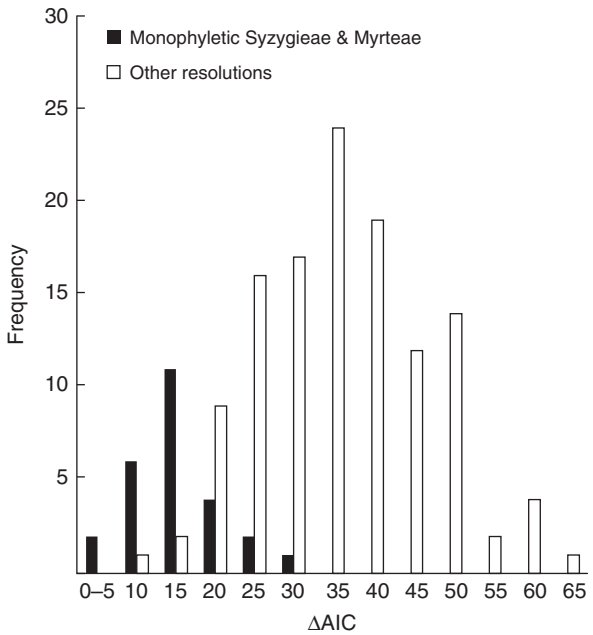

FIG. 5. Frequency distribution of AIC differences obtained by subtracting the AIC score for the ML shift point estimated under a flexible-rate diversification model on each of 300 sampled topologies (see Fig. 4) with the best AIC score from the overall sample. The black columns represent the ΔAIC for sampled topologies that resolve monophyletic Syzygieae and Myrteae while the white columns represent the ΔAIC for all other resolutions (see Table 2).

Syzygieae and *Xanthomyrtus*, there is strong support for the dry fruit state [$2\log_e(B^0) = 8{\cdot}8$] whereas for the MRCA Syzygieae + Myrteae, the Bayes factor comparison has a $2\log_e(B^0)$ of 7·3, again favouring the dry-fruited state at this node.

DISCUSSION

Phylogenetic relationships

Our analyses of the concatenated data (Figs 1 and 2) produced a well-supported hypothesis of relationships in Myrtaceae and, in several instances, a high level of confidence for groupings that were not strongly supported in previous molecular studies (Sytsma *et al.*, 2004; Wilson *et al.*, 2001, 2005). This may be, in part, a consequence of different analytical approaches and, in particular, several studies have found that the Bayesian posterior probabilities of clades tend to be higher than support from non-parametric bootstrapping (BS) for the same set of data (e.g. Erixon *et al.*, 2003; Simmons *et al.*, 2004). The studies of Sytsma *et al.* and Wilson *et al.* used the latter approach to assess statistical support for clades. However, considering the plastid-only Bayesian analysis (Fig. S2 in Supplementary data, available online), which is most comparable to the study of Sytsma *et al.*, there are several nodes receiving relatively weak support (PP $< 0{\cdot}95$) that are robustly supported in the analysis of the concatenated data. For instance, the grouping of Chamelaucieae, Eucalypteae, Leptospermeae, Lindsayomyrteae and Syncarpieae has a PP $= 0{\cdot}83$ in the analysis of the plastid data, and for the ML estimate of Sytsma *et al.* receives a BS of $<70\,\%$. In the Bayesian analyses of the concatenated dataset, this clade is statistically well supported (Fig. 1). Similarly, Sytsma *et al.* (2004) identified a clade including Backhousieae, Kanieae, Metrosidereae, Myrteae, Syzygieae and Tristanieae, but with low statistical support. An equivalent grouping (Fig. S2 in Supplementary data) is weakly supported by the Bayesian analysis of the plastid data (PP $= 0{\cdot}89$), but is strongly supported in the concatenated data analyses (BKMMST clade; Fig. 1). These findings suggest a direct positive effect from the addition of the ITS data rather than, or in addition to, the contrasting measures of statistical support employed in this versus previous molecular studies of Myrtaceae.

Molecular dating

In their comparable study, Sytsma *et al.* (2004) used rate-variable molecular dating analyses to estimate divergence times among Myrtaceae, and, in addition to fixing the age of the root using a 'derived' date (93 Ma), the 'eucalypt' crown group (including *Eucalyptus*, *Angophora* and *Arillastrum*) was fixed at 48 Ma [based upon the older of two possible ages that have been suggested for the Nelly Creek Formation fossils from central Australia described in Lange (1978) and Ambrose *et al.* (1979); see Rozenfelds (1996)]; the Myrteae crown node was fixed at 56 Ma (based on the age of the *Paleomyrtinaea* fossil fruit); and the *Myrtaceidites* pollen taxon was used to provide a maximum age of 86 Ma for the Myrtaceae crown node.

The calibration points used by Sytsma *et al.* (2004) are compared with the divergence time estimates from the BEAST analyses, for the equivalent node, in Fig. 2. Of these, the age of the root and the Myrtaceae crown node are highly consistent with the fossil constraints of Sytsma *et al.*, whereas the estimated 'eucalypt' crown group age is at least comparable with their fossil placement (95 % HPD 35–45 Ma). However, there is

considerable discrepancy with respect to the age of the Myrteae crown node, which in the present study is approx. 10–30 Ma younger (95 % HPD) than the age implied by the placement of the *Paleomyrtinaea* fossil fruit by Sytsma *et al.* More generally, the age estimates from the two studies [compare Fig. 5 (S93), Sytsma *et al.* (2004) and Fig. 2] are reasonably consistent across much of the Myrtaceae phylogeny, although there are large discrepancies with respect to the BKMMST clade with Sytsma *et al.* reporting divergence time estimates for the relevant taxa that are generally older than those estimated here. We hypothesize that these differences are driven primarily by the contrasting treatment of the *Paleomyrtinaea* fossil constraint among studies. On the one hand, constraining the stem group age with the fossil constraint could force a younger age on more nested nodes or, alternatively, using a fixed age for the crown node rules out the possibility that the associated fossil lineage may in fact be older than the extant crown radiation (e.g. an extent stem lineage).

To explore this hypothesis, BRC analyses were performed with settings, as described above, and the following age constraints: using uniform priors, the age of the root was fixed at 92–94 Ma, the Myrtaceae crown node at 87–85 Ma, and the 'eucalypt' crown at 49–47 Ma. All values within these bounds are equally probable, whereas there is zero probability associated with values outside of the bounds, i.e. approximating a 'fixed' node age, as used by Sytsma *et al.* (2004). From this analysis (full results not shown), the age of the Myrteae crown group was estimated at 32 (95 % HPD 23–39) Ma, and the age of the BKMMST clade was 55 (95 % HPD 44–66) Ma, which are highly consistent with the divergence time estimates obtained for these nodes using a log-normal prior to constrain the stem group age (Table 1). This suggests that an early stem group lineage is the most appropriate placement for *Paleomyrtinaea*, and that Sytsma *et al.* may have substantially overestimated the age of the Myrteae and lineages within the BKMMST clade by constraining the crown node age.

The 'likely vicariance' hypothesis of Sytsma *et al.* (2004) to explain intercontinental disjunctions in Myrteae needs reassessment in light of the estimated Oligocene–Miocene (95 % HPD 34–22 Ma) radiation of the American Myrteae (Table 1 and Fig. 2), which cannot rule out an early widespread South American distribution and subsequent extinction of (an) ancestor(s) of modern Myrteae (represented by *Paleomyrtinaea*). Modern Myrteae may then have recolonized South America from Australasia, possibly post-dating the opening of the Drake Passage (approx. 28 Ma; McLoughlin, 2001).

Diversification rates

Strong evidence was found for a positive diversification rate shift within Myrtaceae that was consistently associated with the BKMMST clade (Table 2 and Fig. 4), and in particular with Syzygieae and Myrteae (Table 2 and Figs 3 and 5). The vast majority of lineages within the BKMMST clade are woody rainforest trees whereas all of Backhousieae, Kanieae, Metrosidereae and Tristanieae (excluding *Xanthomyrtus*) have dry capsular fruits indicative of abiotic dispersal. All of Myrteae, Syzygieae (excluding the monotypic subgenus *Anetholea* of *Syzygium*) and *Xanthomyrtus* develop a fleshy pericarp, which is here considered indicative of biotic dispersal. Biotic dispersal has been variously proposed as a mechanism promoting elevated rates of cladogenesis among angiosperms, through adaptive divergence in response to different dispersal vectors and/or by promoting allopatry among plant populations due to the movement behaviour of biotic dispersers (e.g. Tiffney and Mazer, 1995; Smith, 2001). Several studies have failed to find a general effect of biotic dispersal on extant species numbers within angiosperms (Herrera, 1989; Midgley and Bond, 1991; Eriksson and Bremer, 1992; Davies *et al.*, 2004), but there does appear to be significant interaction between diversification rates, dispersal syndromes and the specific ecological context (Tiffney and Mazer, 1995; Smith, 2001; de Quieroz, 2002). Tiffney and Mazer (1995), for example, argue that among angiosperms, an arborescent habit favours large seed size and biotic dispersal. In spatially unpredictable closed forest communities, lineages with these characteristics may experience higher recruitment success and lower extinction rates, relative to woody arborescent lineages with unassisted dispersal.

In light of the present findings (Table 2 and Figs 3 and 5), it is tempting to suggest that the possession of fleshy fruits *per se* may be related to elevated diversification rates within Syzygieae and Myrteae relative to the other lineages of Myrtoideae. This hypothesis would gain support if there were multiple shifts from dry to fleshy fruits associated with significant positive diversification shifts. Although the relationships among Syzygieae and Myrteae are not well resolved, the separation of *Xanthomyrtus* (Tristanieae) from traditional Myrtoideae is strongly supported (Wilson *et al.*, 2005; Figs 1 and 2), suggesting at least paraphyly of the fleshy fruited lineages. The condition for paraphyly of Myrtoideae *s.s.* would require that that Tristanieae, Syzygieae and Myrteae form a clade (PP = 0·03, Table 2) and that *Xanthomyrtus* is sister to the capsular-fruited Tristanieae, whereas alternatively there could be two or three separate origins of fleshy fruits if Syzygieae and Myrteae are not resolved as sister lineages (PP = 0·18 for this monophyly; Table 2). The evolution of fruit type in Myrtaceae was estimated using a method that simultaneously accounts for phylogenetic and branch-length uncertainty (Pagel *et al.*, 2004). The ancestral state reconstructions of fruit morphology strongly support at least two, and probably three, separate origins of fleshy fruits within the BKMMST clade suggesting that Syzygieae and Myrteae have undergone independent shifts from dry to fleshy-fruited states. Furthermore, it was found that the highest AIC shift scores were consistently associated with a monophyletic Syzygieae + Myrteae (Table 2 and Fig. 5), suggesting that both of these lineages have experienced higher diversification rates than Myrtaceae in general compared with a less parsimonious hypothesis that a rate shift has occurred at a deeper node and Syzygieae and Myrteae have merely retained a high ancestral rate (see Rabosky *et al.*, 2007). While these findings imply causality, further sampling of *Xanthomyrtus* (here, represented by a single terminal but including 23 species; Govaerts *et al.*, 2008) would help to clarify the association between fleshy fruits and diversification rate shifts in the BKMMST clade and Myrtaceae.

A further consideration is the diversity within both Syzygieae and Myrteae, as both lineages include species-rich groups. In Myrteae, *Eugenia* has an estimated 1050+ species, and *Myrcia s.l.* (Lucas *et al.*, 2007) includes approx. 750 species (Govaerts *et al.*, 2008). For Syzygieae, comprising the single genus *Syzygium* (Craven *et al.*, 2006), the six subgenera proposed by Craven and Biffin (2010) include two monotypic lineages, and it has been suggested that subgenus *Syzygium* includes approx. 90–95 % (or approx. 1000 species) of the total species richness of Syzygieae (Parnell *et al.*, 2006). Given these estimates, and in light of the timing of radiation of the corresponding crown groups (95 % HPD; Fig. 2), the estimated diversification rates are 0·29–0·93, 0·25–0·61 and 0·27–0·58 net speciation events per million years (assuming $e = 0{\cdot}9$) for *Eugenia*, *Myrcia s.l.* and subgenus *Syzygium*, respectively. These values are high in the context of angiosperms in general (Magallón and Sanderson, 2001) and rival the values inferred for island plant radiations (e.g. Baldwin and Sanderson, 1998). They are also significant in light of predictions that woody arborescent angiosperm lineages in general should have low rates of diversification, for example, relative to herbaceous lineages (reviewed by Petit and Hampe, 2006). In terms of the present study, it is plausible that the high diversification rates reported for the Syzygieae and Myrteae crown groups are a consequence of 'trickle down' effects (Moore *et al.*, 2004) driven by these species-rich, more deeply nested lineages. Therefore, a simple correlation between high species richness and the evolution of fleshy fruit is contingent on more detailed studies of the evolutionary relationships and timing of lineage diversification events within Syzygieae and Myrteae.

Additional factors for consideration (alone or in conjunction) as potential drivers of rapid speciation in large genera of Syzygieae and Myrteae are pollination strategy and embryo specialization. *Syzygium* and most genera of Myrteae display relative homogeneity of primarily bee-pollinated flower types with flexibility in flowering strategy. Flowering, particularly in the three largest genera, is showy but timing varies from mass-flowering in a few days, to pulsed or steady flowering lasting up to 3 months (Proença and Gibbs, 1994). This faithful but flexible bee pollination may allow species to exploit a wide variety of bee species and behaviour (e.g. trap-lining and buzz pollination) and may be a shared source of success with large genera in other families (e.g. Melastomataceae and Solanaceae). Morphological divergence in seeds types from small, wind-dispersed or hard, C-shaped seeds embedded in fleshy pulp to larger, more complex architectures may also convey evolutionary benefit to the genera in question. The embryonic cotyledons of *Myrcia s.l.* are folded, green and ready to photosynthesize, the embryos of *Eugenia* and *Syzygium s.l.* are energy-rich homogeneous structures derived from swollen and fused cotyledons. Presence of the putative evolutionary drivers described above, including those linked to fleshy fruits such as endozoochory, are strongly correlated with large genera of Myrtaceae established in the moist lowland tropics. Fruit dispersal by birds, bats or larger marsupials is reported in *Syzygium* (Nic Lughadha and Proença, 1996), whereas *Eugenia* fruits are mainly dispersed by birds (Snow, 1981). The implication then is that independent ancestral lineages of Myrtaceae encountered similar niches available in separately developing tropical forest and where once established, and seemingly in parallel, their shared potential for speciation on a remarkable scale was exploited.

Conclusions

Traditionally, the fleshy-fruited Myrtaceae have been treated as a monophyletic group, although phylogenetic studies suggest that para- or polyphyly is likely, with *Xanthomyrtus*, the predominantly American Myrteae and the predominantly Australasian Syzygieae forming distinct, well-supported lineages. The results of this study suggest a relatively recent (Oligocene–Miocene) radiation of these tribes and multiple origins of fleshy fruits within the more inclusive BKMMST clade. There is strong support for exceptionally high diversification rates for both Syzygieae and Myrteae, and a highly significant positive shift in diversification rates associated with both of these lineages relative to the overall radiation of Myrtaceae. Taken together, these factors suggest a link between the evolution of fleshy fruits and elevated rates of lineage accumulation within the BKMMST clade. An alternative hypothesis is that the high species richness within Syzygieae and Myrteae is driving the elevated speciation rates, i.e. comparisons at the tribal level are insensitive to *bona fide* shifts at more nested nodes and, in terms of formulating causal hypotheses, are potentially misleading (Moore *et al.*, 2004). Future studies are required, focusing specifically on the evolutionary relationships and the timings of diversification in Syzygieae and Myrteae. For instance, significant shifts in diversification rate within these groups would suggest that, at a minimum, more complex hypotheses than those suggested above are required to account for the disparate lineage diversities among Myrtaceae, although these elevated diversification rates may be contingent on the evolution of fleshy fruits in rainforest tree lineages.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following figures. Figure S1: Relationships of Myrtaceae inferred from the Bayesian analysis of the ITS data. Figure S2: Relationships of Myrtaceae inferred from the Bayesian analysis of the combined *matK* and *ndhF* data.

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APPENDIX

Taxa studied, GenBank accessions and voucher information

Taxon		*matK*	*ndhF*	ITS	Voucher
Acca sellowiana (O.Berg) Burret	Myrteae	AY525128	AY498783	AM234067	
Agonis flexuosa (Muhl. ex Willd.) Sweet	Leptospermeae	AF184711	AY498762	DQ499115	
Amomyrtus meli (Phil.) D.Legrand & Kausel	Myrteae	AM489976		AM234069	
Angophora hispida (Sm.) Blaxell	Eucalypteae	AF368196	AY498763	AF190357	
Arillastrum gummiferum (Brong. & Gris) Panch. ex Baill.	Eucalypteae	AF368198	AY498765	AF058454	
Asteromyrtus arnhemica (Byrnes) Craven	Chamelaucieae	EF026603			
Asteromyrtus lysicephala (F.Muell. & F.M.Bailey) Craven	Chamelaucieae	AF184718	AY498766		
Backhousia myrtifolia Hook. & Harv.	Backhousieae	AF368200	DQ088472	DQ088408	
Beaufortia orbifolia F.Muell.	Melaleuceae	AY521530	AY498771	AF048888	
Blepharocalyx tweediei (Hook. & Arn.) O.Berg	Myrteae	AY521531	AY498772	AM234084	
Callistemon polandii F.M.Bailey	Melaleuceae	AF184705	AY498773		
Callistemon viminalis (Sol. ex Gaertn.) G.Don ex Loudon.	Melaleuceae			EF041510	
Calothamnus quadrifidus R.Br. ex W.T.Aiton	Melaleuceae			EF041511	
Calothamnus validus S.Moore	Melaleuceae	AF184704	AY498774		
Calyptranthes concinna DC.	Myrteae	AF368201	AY498775	AM234103	
Calytrix tetragona Labill.	Chamelaucieae	AF489396	AY498776	HM160102/03	UNSW21772
Campomanesia guazumifolia (Cambess.) O.Berg	Myrteae	AY521532	AY498777	AM234076	
Chamelaucium uncinatum Schauer	Chamelaucieae	AY259816		EF026605	
Choricarpia subargentea (C.T.White) L.A.S.Johnson	Backhousieae	AF368202	DQ088473	DQ088409	
Cloezia floribunda Brongn. & Gris	Unplaced	AY521533		AF172767	
Corymbia variegata (F.Muell.) K.D.Hill & L.A.S.Johnson	Eucalypteae	AF368203		DQ993141	
Decaspermum humile (G.Don) A.J.Scott	Myrteae	AY521534	AY498780	AM234128	
Eucalyptopsis papuana C.T.White	Eucalypteae	AF368205		AF190354	

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APPENDIX *Continued*

Taxon		*matK*	*ndhF*	ITS	Voucher
Eucalyptus curtisii Blakely & C.T.White	Eucalypteae	AF368206	AY498781	AF390525	
Eucalypus globulus Labill.	Eucalypteae	AY521535	AY780259	AF058467	
Eugenia sulcata Spring ex Mart.	Myrteae	AM489987	HM160097	AM234089	Lucas 68
Eugenia uniflora L.	Myrteae	AF368207	DQ088457	AY487284	
Gomidesia flagellaris D.Legrand	Myrteae	AM489989	HM16009	AM234113	
Heteropyxis natalensis Harv.	Heteropyxideae	AF368208	AY498824	HM160104/05	PGW 1475- NSW
Homalocalyx aureus (C.A.Gardner) Craven	Chamelaucieae	AF489398	AY498785	HM160106/07	UNSW22947
Homoranthus darwinioides Cheel	Chamelaucieae	AF489399	AY498786	HM160108	UNSW23267
Kjellbergiodendron celebicum (Koord.) Merr.	Lophostemoneae	AF368209	AY498788	HM160109/10	Zich s.n.
Kunzea capitata (Sm.) Heynh.	Leptospermeae	AF184723	AY498790		
Kunzea sinclairii (Kirk) W.Harris	Leptospermeae			AY772399	
Leptospermum scoparium J.R.Forst & G.Forst	Leptospermeae	AM489991	AM235423	AY772398	
Lindsayomyrtus racemoides (Greves) Craven	Lindsayomyrteae	AF184706	AY498793	HM160111/12	
Lophostemon confertus (R.Br.) P.G.Wilson & J.T.Waterh.	Lophostemoneae	AF184707	AY498794	AF390444	
Luma apiculata (DC.) Burret	Myrteae	AY521540	AY498795	AY463105	
Marlierea eugeniopsoides (D.Legrand & Kausel) D.Legrand	Myrteae	AM489996	HM160099	AM234107	Lucas 61
Melaleuca viridiflora Sol. ex Gaertn.	Melaleuceae	AY498798	AF184708	AF294611	
Metrosideros carminea W.R.B.Oliv.	Metrosidereae	AY521541	AY498799	AF211498	
Metrosideros macropus Hook. & Arn.	Metrosidereae	AF368212	AY498801	AF172745	
Metrosideros nervulosa C.Moore & F.Muell.	Metrosidereae	Q088535	DQ088458	DQ088395	
Micromyrtus ciliata (Sm.) Druce	Chamelaucieae	AF489400		HM160113/14	UNSW23860
Myrcia saxatilis (Amshoff) McVaugh	Myrteae	AM490004	HM160100	AM234119	Lucas 98
Myrciaria cauliflora (Mart.) O.Berg	Myrteae			AM234093	
Myrciaria vexator McVaugh	Myrteae	AY521544	AY498804		
Myrtus communis L.	Myrteae	AY525136	AF215593	AF215628	
Osbornia octodonta F.Muell.	Osbornieae	AF368213	AY498805	EF041844	
Pericalymma ellipticum (Endl.) Schauer	Melaleuceae	AF184740	AY498806	EF026604	
Piliocalyx bullatus Brong. & Gris	Syzygieae	DQ088552	DQ088478	DQ088413	
Pimenta racemosa (Mill.) J.W.Moore	Myrteae	DQ088554	AY498808	EF026631	
Psidium cattleianum Afzel. ex Sabine	Myrteae	AM490014	HM160101	AM234080	Lucas 213
Psiloxylon mauritianum (Bouton ex Hook.f.) Baill.	Psiloxyloideae	AF368215	AY498825	EF026606	
Qualea grandiflora Mart.	Vochysiaceae (outgroup)	AF368216			
Qualea sp.	Vochysiaceae (outgroup)		AY498829		
Rhodamnia argentea Benth.	Myrteae	AF368217	AY498810	AY487302	
Rhodomyrtus macrocarpa Benth.	Myrteae	AY498811	AY525137		
Rhodomyrtus psidioides (G.Don) Benth.	Myrteae			AM234134	
Sphaerantia chartacea P.G.Wilson & B.Hyland	Kanieae	AY521547		HM160115/16	PGW 1348
Stockwellia quadrifida D.J.Carr, S.G.M.Carr & B.Hyland	Eucalypteae	AY498812	AY525138	AF390445	
Syncarpia glomulifera (Sm.) Nied.	Syncarpieae	AY498813	AF368220	HM160117/18	UNSW23246
Syncarpia hillii F.M.Bailey	Syncarpieae	AY525139			
Syzygium acuminatissimum DC	Syzygieae	DQ088537	DQ088462	EF026611	
Syzygium anisatum (Vickery) Craven & Biffin	Syzygieae	AF368195	DQ088471	DQ088407	
Syzygium apodophyllum (F.Muell.) B.Hyland	Syzygieae	DQ088558	DQ088482	DQ088417	
Syzygium arboreum (Baker f.) J.W.Dawson	Syzygieae	DQ088560	DQ088484	DQ088418	
Syzygium bungadinnia (F.M.Bail.) B.Hyland	Syzygieae	DQ088568	DQ088490	DQ088423	
Syzygium buxifolium Hook. & Arn.	Syzygieae	DQ088569	DQ088491	DQ088424	
Syzygium canicortex B.Hyland	Syzygieae	DQ088570	DQ088492	DQ088425	
Syzygium claviflorum (Roxb.) Wall. ex Stued.	Syzygieae	DQ088546	DQ088470	DQ088406	
Syzygium crebrinerve (C.T.White) L.Johnson	Syzygieae	DQ088574	DQ088495	DQ088428	
Syzygium divaricatum (Merr. & L.M.Perry) Craven & Biffin	Syzygieae	DQ088538	DQ088463		
Syzygium floribundum F.Muell.	Syzygieae	DQ088620	DQ088531	DQ088453	
Syzygium francisii (F.M.Bail.) L.Johnson	Syzygieae	DQ088578	DQ088498	DQ088430	
Syzygium fullagarii (F.Muell.) Craven	Syzygieae	DQ088579	DQ088499	DQ088431	
Syzygium glenum Craven	Syzygieae	DQ088539	DQ088464	AY187162	
Syzygium gustavioides (F.M.Bail.) B.Hyland	Syzygieae	DQ088582	DQ088501	DQ088433	
Syzygium ingens (F.Muell. ex C.Moore) Craven & Biffin	Syzygieae	DQ088542	DQ088466	DQ088402	
Syzygium laxeracemosum (Guillaumin) J.W.Dawson	Syzygieae	DQ088586	DQ088505	DQ088436	
Syzygium mackinnonianum (B. Hyland) Craven & Biffin	Syzygieae	DQ088543	DQ088467	DQ088403	
Syzygium maire (A.Cunn.) Sykes & P.J.Garnock-Jones	Syzygieae	DQ088589	DQ088508	DQ088438	
Syzygium malacense (L.) Merr. & Perry	Syzygieae	DQ088590	DQ088509	AY187199	
Syzygium monimioides Craven	Syzygieae	DQ088544	DQ088468	DQ088404	
Syzygium mulgraveanum (B.Hyland) Craven & Biffin	Syzygieae	DQ088622	DQ088533	DQ088455	
Syzygium multipetalum Pancher ex Brongn. & Gris	Syzygieae	DQ088594	DQ088512	DQ088440	
Syzygium nervosum D.C.	Syzygieae	DQ088595	DQ088513	EF026636	
Syzygium paniculatum Gaertner	Syzygieae	DQ088598	DQ088515	AY187204	
Syzygium puberulum Hartley & Perry	Syzygieae	DQ088601	DQ088517	AY187207	

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APPENDIX *Continued*

Taxon		*matK*	*ndhF*	ITS	Voucher
Syzygium sp. 'Sulawesi 2'	Syzygieae	DQ088611	DQ088524	EF026649	
Syzygium sayeri (F.Muell.) B.Hyland	Syzygieae	DQ088607	AY187209		
Syzygium tetrapterum (Miq.) Chantaranothai & J.Parn.	Syzygieae	DQ088615	DQ088527	DQ088448	
Syzygium wesa B.Hyland	Syzygieae	DQ088617	DQ088529	DQ088450	
Syzygium wilsonii (F.Muell.) B.Hyland subsp. *wilsonii*	Syzygieae	DQ088618	DQ088530	DQ088451	
Tepualia stipularis Griseb.	Metrosidereae	AF368222		AM234071	
Thaleropia queenslandica (L.S.Sm.) Peter G.Wilson	Tristanieae	AF368223	DQ088460	DQ088397	
Tristania neriifolia (Sims) R.Br.	Tristanieae	AF368224	DQ088461	EF026608	
Tristaniopsis laurina (Sm.) Peter G.Wilson & J.T.Waterh.	Kanieae	AF184710	AY498818	EF041514	
Ugni molinae Turcz.	Myrteae	AM490018	AY498819	AM234143	
Vochysia hondurensis Sprague	Vochysiaceae (outgroup)	AY572446	AY498832		
Xanthomyrtus montivaga A.J.Scott	Tristanieae		AM234147		
Xanthomyrtus papuana Merr. & L.M.Perry	Tristanieae	AF368226	AY498822		
Xanthostemon aurantiacus (Brongn. & Gris) Schltr.	Xanthostemoneae	AY525144			
Xanthostemon chrysanthus (F.Muell.) Benth.	Xanthostemoneae	AF368227	AY498823	EF041515	