

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 timecalibrated 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

© The Author 2010. Published by Oxford University Press on behalf of the Annals of Botany Company. All rights reserved. For Permissions, please email: journals.permissions@oxfordjournals.org 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 $(GTR) + I + \Gamma$ 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 | - | 0 | | 87 (75-100) | 86 (74-96) |
| 2. Eucalypteae stem | Eucalyptus 48 Ma | Log-normal | 65 (52-86) | 58 (45-73) | 60 (53-68) |
| Eucalypteae | • | 0 | | 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 | J. | 8 | · / | 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 flexiblerate 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 $0-10\cdot0$. A reversible-jump MCMC method was used, in which the Markov chain searches the posterior distribution Downloaded from https://academic.oup.com/aob/article/106/1/79/95434 by guest on 18 April 2024

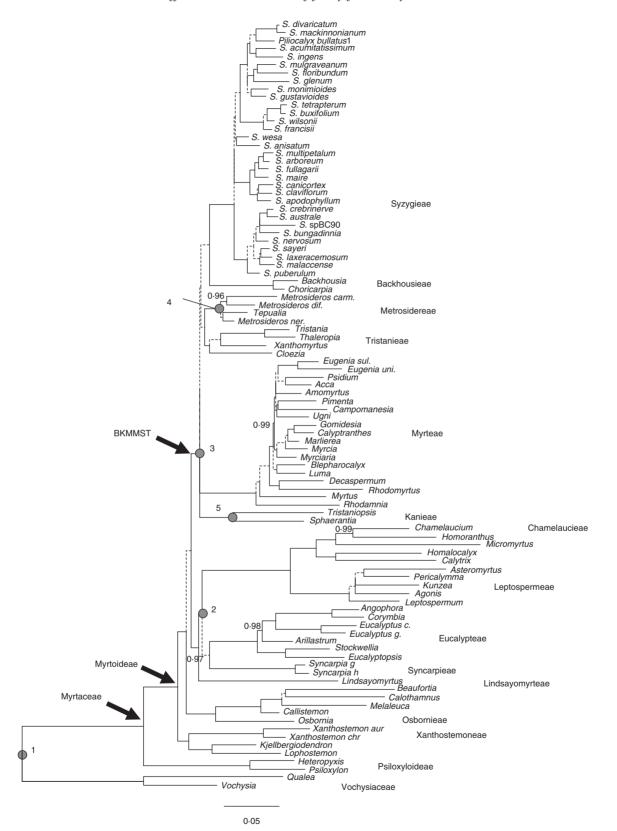


FIG. 1. Relationships of Myrtaceae inferred from the Bayesian analysis of the concatenated ITS and plastid sequence data. Majority rule consensus topology, branch lengths proportional to the inferred number of changes along that branch. Dashed branches have a $PP \le 0.95$, PP values between 0.8 and 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 $4 \times \text{GTR} + \text{I} + \Gamma$ 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. (Psiloxyloideae and an expanded subfamily (2005)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 Caledoniancentred 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 and0.9) and for all estimates included within the 95 % HPD of divergence time estimates for that clade (P < 0.00015 and P < 0.0006, respectively, at e = 0.9, 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 ($\Delta AIC >$ 30.7: $\Delta LH < 2.91 \times 10^{-8}$).

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 (Δ AIC) 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 Δ AIC scores for topologies with this resolution are highlighted for comparison with all other reconstructed ML shift points. In general, the lowest ΔAIC

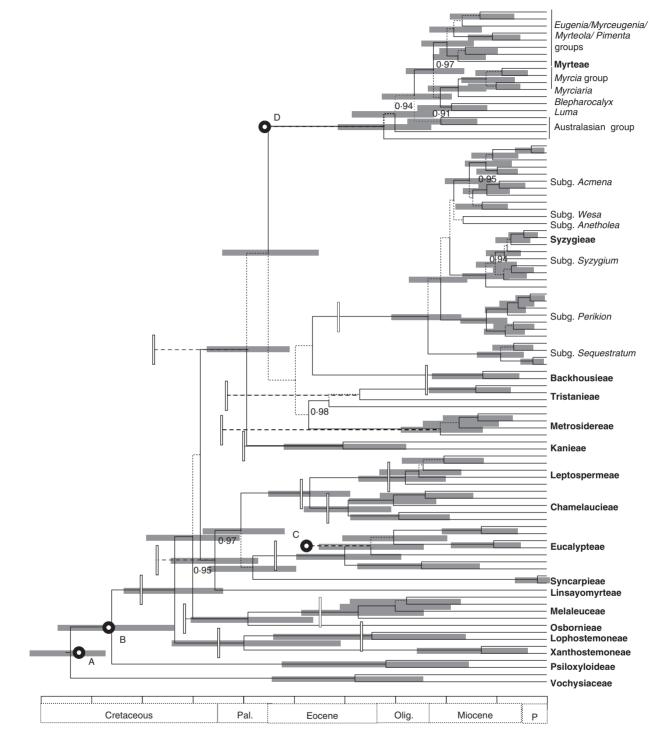


FIG. 2. Maximum credibility chronogram inferred using BRC methods. The posterior probability of the branches is as in Fig. 1. Horizontal bars represent the 95 % HPD of divergence times for nodes receiving a PP ≥ 0.5. Vertical bars indicate the estimated divergence time for the equivalent node from Sytsma *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)

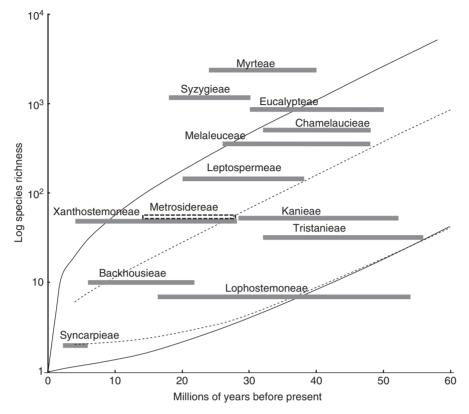


FIG. 3. Confidence intervals of expected diversity (log scale) according to age of crown group, with the sets of lines representing the upper and lower limits of the 95 % CI of expected species numbers assuming a diversification rate of 0.084 (Myrtoideae median) and a relative extinction rate of 0 (broken 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).

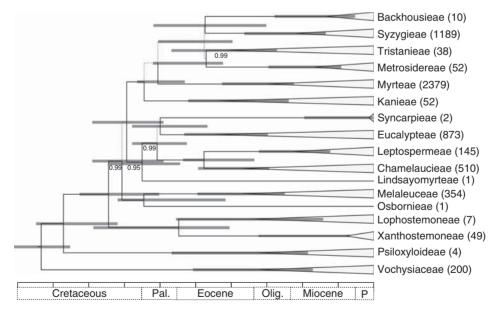


FIG. 4. Consensus topology of 300 trees obtained from the BRC analyses (see Fig. 2) and pruned to represent tribal diversity in Myrtaceae. Diversity per tribe according to Govaerts *et al.* (2008) is indicated adjacent to the terminal. Clade support is as in Fig. 1. Vertical bars represent the range of divergence times obtained from the 300 sampled topologies for all nodes receiving a PP ≥ 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 | М | 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.

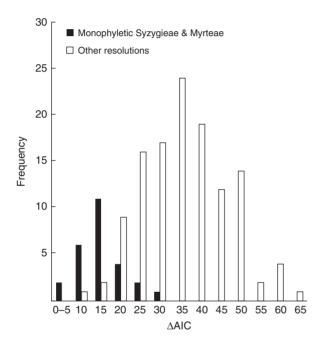


FIG. 5. Frequency distribution of AIC differences obtained by subtracting the AIC score for the ML shift point estimated under a flexible-rate diversification model on each of 300 sampled topologies (see Fig. 4) with the best AIC score from the overall sample. The black columns represent the Δ AIC for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

Syzygieae and *Xanthomyrtus*, there is strong support for the dry fruit state $[2log_e(B^0) = 8.8]$ whereas for the MRCA Syzygieae + Myrteae, the Bayes factor comparison has a $2log_e(B^0)$ 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 < 0.95) 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 = 0.83 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 = 0.89), 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 ratevariable 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; Midglev 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 = 0.9) 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

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| Metrosideros carminea W.R.B.Oliv. Metrosideresa AY521541 AY498790 AF211498 Metrosideros nervalosa C'Moore & F.Muell. Metrosideresa Q088355 DQ088455 DQ088455 Metrosideros nervalosa C'Moore & F.Muell. Metrosideresa AH494000 HM1601131/1 UNSV23860 Myrciaria catañis (Amshoff) McVaugh Myreae AM234003 AM234003 AM234003 Myrciaria vexator McVaugh Myreae AY25154 AY21559 AF21553 AF21553 AF21550 AF215628 Cibornia cridonta F.Muell. Osborniae AF368213 AY498805 EF024604 EF024614 EF024614 EF024614 EF024614 EF0248704 EF024870 EF0248704 | | | | | | Lucas 61 |
| Metrosiders macropus Hook, & Am, Metrosiders A PA36212AF36212AF36213AF36213Metrosiders convulsos C.Move & F.Muell.ChamelauciaeQU88355DQ08435UNS23860Myrcia scattift (Amshoff) McVanghMyreaeAM234119Lucas 98Myrciaria caulifont (Mart.) O.BergMyreaeAV235146AV249804AV2491804Myrciaria caulifont MeVanghMyreaeAY25154AV249805EP041814Myricaria vaculifont MeVanghMyreaeAY25154AV498806EP041814Cohornia cordonate I.Muell.Osbornia cordonate I.Muell.Osbornia cordonate I.Muell.AV498806EP0426611Princaly multimus Brong, & GrisSyrgigicaeQU88552DQ088451AV498806EP026661Pilocaly multimus Brong, & GrisSyrgigicaeMyreaeAF368215AV498806EF026616Pilocaly multimus Mozie.SabineMyreaeMyreaeAF368216AV498820EF026616Pullar cardington Mart.Vodhysiaccar (outgroup)AF368217AV48820AV487302Lucas 213Pilocaly multimus macrocarp Benth.MyreaeAY498811AY362137AY487302Lucas 214Rhodomyrus pidiodar (I.Donn Benth.MyreaeAY498812AY25137AF36820HM160115716PGW 1348Sockwellin quadrified D.J.Carr, S.G.M.Carr, & BrlylandEucalyptaeAY498813AF36820HM160115716PGW 1348Sockwellin quadrified D.J.Carr, S.G.M.Carr, & BrlylandSyrgigicaQU88557DQ088462EF026611Syrgigina michandifor (Min, Nied,Syrgigi | | | | | | |
| Metrosideros nervalios C.Moore & F.Muell. Metrosideras Q088353 DQ088455 QU88305 Micramyrus citiaa (Sm.) Dunce AM490004 HM16011104 AU324003 AU324003 Myricaira caudifion (Mart.) O.Berg Myreae AV521544 AV848004 AU324003 Myricaira vector McVaugh Myreae AV52156 AF215593 AF21550 AF | | | | | | |
| Micronyrus ciliau (Sm.) DruceChandbauciae \bar{A} 4494000HM 160113/14UNSW23860Myrcia xaulit (Anshoff) McNaphMyrteaAM234093AM234093Myrciari aculifloru (Mart) O.BergMyrteaAY521544AY498804Myrciari aculifloru (Mart) O.BergMyrteaAY52153AF215533AF21503AF21503AF21503AF21503Abornia actoromics L.OsborniaeAF368213AY498806Pricacly Multura Brong, & GrisSyrygieaeDQ88552DQ088552DQ088574Policacly Multura Brong, & GrisMyrteaeAM490014HM160101AM234090Lucas 213Pilicacly Multura Brong, & SabineMyrteaeAP368216AY498808EF026601Pultura accentors (MII) J.W.MooreMyrteaeAF368216EF026606EF026606Pultura accentors (Marting BrankMyrteaeAF368216MyrteasAY498809Pultura accentor Benth.MyrteaeAY498810AY497802EF026606Pultura accentor Benth.MyrteaeAY498811AY49820AY497302Phodamira accentor Bolth.MyrteaeAY498813AF368216MH160115/16PGW 1348Fa68207HM160115/16PGW 1348Phodamyrta paindards (Don Benth.MyrteaeAY498813AF36820HM160117/18NaceaeAY498813AF368207DQ088471DQ088471Syrgytiam achandur (Vickery) Craven & BriftinSyrgyteaeDQ088575DQ088471Syrgytiam achandur (Vickery) Craven & BriftinSyrgyteaeDQ088570DQ088470 </td <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> | | | | | | |
| Myrcia caxalitis (Amisoff) McVaughMyreaeAM49000HM16010AM23409Lacas 98Myrciaria vacutor McVaughMyrteaeAY52154AV23803HMyrtea or X52156AF215503AF215503AF215503AF215503Osbornia catodonta F Muell.OsborniaceAF368213AY498805EF026604Princalymme ellipticum (Endl) SchuzerMyrteaeAV49800EF026604LPlincculy Inducts Brong, & GrisSyzygicaeD0088552AV498808EF026601Plincculy Inducts Brong, & SabineMyrteaeAV490014HM160101AK23400Lucas 213Plincculy Inductor School or Scho | | | | DQ088458 | | LINGWARD |
| Myrciaria cauliflora (Mart) O.BergMyrcaeMyrcaeMyrca< | | | | ID (1 (0100 | | |
| MyrciaeAYS2136AY2152593AY215628Osbornia octodonta F.Muell.OsborniaeAF368213AY498805EF041844Pericalymma ellipticum (Endl.) SchauerMelaleuccaeAF184710AY498805EF026604Plincadys bullatus Brong, & GrisSyzygicaeDQ088552DQ088473DQ088413Pinnetta racemosa (Mill.) J.W.MooreMyrteaeAV498004EH01010AH234080Lacas 213Psilturo calt featureColson ex Book, J. Baill.PsiloxyloideaeAF368216AY498829EF026601Psilturo calt featureVochysiaceae (outgroup)AY498810AY487302AY49810AY487302Phodamyrits macrocarpa Benth.MyrteaeAY39811AY497302AY497302Phodamyrits macrocarpa Benth.MyrteaeAY39811AY487302AY497302Phodamyrits macrocarpa Benth.MyrteaeAY39811AY487302AY487302Stockwellia quadrifida D.J.Carr, S.G.M.Carr & B.HylandSucarpitaeAY49813AF368210HM160115/16PGW 1348Stockwellia quadrifida D.J.Carr, S.G.M.Carr & B.HylandSyncarpitaeAY25137TUNSW22246Syncarpia folmulifera (Sm.) Nicd.SyncarpitaeAY39812AY39812AY487302Syncarpia folmulitif. F.M.BaileySyncarpitaeAY355137DQ088471DQ088407Syngium antoinatistististum DCSyngigeaDQ088570DQ088472DQ088417Syngium antoinatistististum DCSyngigeaDQ088570DQ088482DQ088413Syngium antoinatististum DCSyngigeaDQ088470 </td <td></td> <td></td> <td>AM490004</td> <td>HM160100</td> <td></td> <td>Lucas 98</td> | | | AM490004 | HM160100 | | Lucas 98 |
| MyrtaeAY25213AY215293AF215282Oksornia octodnut F.Muell.Osbornia octodnut F.Muell.Osbornia octodnut F.Muell.Pricalysma ellipticum (Endl.) SchauerMelaeuceaeAF18470Prilicolys bullatus Brong, & GrisSyrgigaeDQ088552DQ088478DQ088413Pimenia racemosa (Mill.) J.W.MooreMyrteaeDQ088554AY498806EF026601Psilox of marinianus (Bouton ex Hook,f.) Baill.MyrteaeAM490011AM234080Lucas 213Palaxyon marinianus (Bouton ex Hook,f.) Baill.Vochysiaceae (outgroup)AF368215AY498825EF026606Qualea grandiflora Mart.Vochysiaceae (outgroup)AF368217AY498810AY2487302Rhodamyrita psiloidise (G.Don) Benth.MyrteaeAF368217AY498811AY25137Rhodamyrita psiloidise (G.Don) Benth.MyrteaeAY498812AY521547HM160115/16PGW 1348Spncarpia chartece OR, GWilson & B.HylandKanicaeAY498812AY521547HM160117/18UNSW23246Syncarpia poundifera (Sm.) Nied.SyrgigaeDQ088575DQ088472DQ088471DQ088471Syrgigina anisatismi mub CSyrgigaeSyrgigaeAF36820HM11011718UNSW23246Syrgigina anisatism (Vickery) Craven & BiffinSyrgigaeDQ088546DQ088470DQ08842Syrgigina charlen (Baler 1, J.W.DawsonSyrgigaeDQ088540DQ088470DQ08842Syrgigin angolophyllum (F.Muell, B.HylandSyrgigaeDQ088540DQ088470DQ08842Syrgigin angolophyllum (F.Muell, D.HylandSyrgigae <td></td> <td></td> <td></td> <td></td> <td>AM234093</td> <td></td> | | | | | AM234093 | |
| Oxbornia octodonta F.Muell.OxborniaeAT368210AT498806EF041844Pericaclymar outini accentosa (Mill) SthaterMelaleucaceAT184740AT498806EF026604Plineadyx bullatus Brong, & GrisSyzygieaeDQ088552DQ088478DQ088413Pinentia racentosa (Mill) J.W.MooreMyrteaeAV49800HM16101AM234080Lucas 213Psilour catilediman Atzel, ex SabineMyrteaeAT368216AT498825EF026604Qualea grandflora Mart.Vochysiacea (outgroup)AT498810AY487302AT498810Paleoxytion mauritiaum ageneta Benth.MyrteaeAT498811AY487302Rhodomyrits macrocarpa Benth.MyrteaeAT498811AY525137Rhodomyrits spiciolaes (C)on Benth.MyrteaeAY49813AF368217AT498810AY487302Spockwellia quadrifida DJ.Carr, S.G.M.Carr & B.HylandEncalypteaeAY49813AF368217HM160115/16PGW 1348Spockwellia quadrifida DJ.Carr, S.G.M.Carr & B.HylandSyncarpicaeAY498813AF36820HM160117/18UNSW23246Syzygtian anisatiam Wickery) Craven & BiffinSyzygieaeDQ088570DQ088471DQ088407Syzygian arboream (Baker f, J.W.DawsonSyzygieaeDQ088570DQ088482DQ088413Syzygtiam arboream (Boxh) Wall, ex Stued,SyzygieaeDQ088570DQ088470DQ088423Syzygiam arboream (Baker f, J.W.DawsonSyzygieaeDQ088570DQ088470DQ088413Syzygtiam arboream (Boxh) Wall, ex Stued,SyzygieaeDQ088570DQ088470DQ088413 <td></td> <td><i>.</i></td> <td></td> <td></td> <td>1 221 2 (20)</td> <td></td> | | <i>.</i> | | | 1 221 2 (20) | |
| Perically bullatus Brong, & GrisMelaleuceaeAF1400AY498806EF026604Plinocalyb bullatus Brong, & GrisSyzygieaeDQ088552DQ088173DQ088174Plinocalyb bullatus Brong, & GrisMyrteaeDQ088554AY49800EF026601Psilovlon mauritianum (Bouton ex Hock.f.) Baill.PrilovyloideaeAF368215AY498825EV026606Qualea grandiflora Mart.Vochysiacea (outgroup)AY49825X4749825X4749825Rhodomyritus macroccarpa Benth.MyrteaeAF368217AY498810AY487302Rhodomyritus psidioides (G.Don) Benth.MyrteaeAY498811AY487302Sphaernatic chartacea PG.Wilson & B.HylandEucalypteaeAY498813AF368240Syncarpia glonulifera (Sm.) Nied.SyncarpiaeaAY39837DQ088471DQ088471Syrgyium actimitii FM.BaileySyncarpiaeaAY498813AF368240HM160117118UNSW23246Syrgyium actimitii FM.BaileySyrgyieaeDQ088576DQ088471DQ088471DQ088471Syrgyium actimitii FM.BaileySyrgyieaeDQ088568DQ088471DQ088471DQ088402Syrgyium actimitii FM.BaileySyrgyieaeDQ088568DQ088470DQ088424Syrgyium activatur (Yickery) Craven & BiffinSyrgyieaeDQ088568DQ088470DQ088424Syrgyium activatur (Kok.h) Wall. e. Stued.SyrgyieaeDQ088568DQ088463DQ088424Syrgyium activatur (Merk. & Arm.SyrgyieaeDQ088568DQ088464DQ088464Syrgyium fulcatior (M.Meell, B.HylandSyrgyieae <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> | | | | | | |
| Pillocalyx bullarus Brong, & GrisSyzygicaeDQ08852DQ088478DQ088413Pinenta raccenosa (Mil.) J.W.MooreMyrteaeAM49808Evo26631Psidiany canticianum Afzel, ex SabineMyrteaeAF368215AY49808Evo26630Psidoxylon mauritianum (Bouton ex Hook,f.) Baill,PsiloxyloideaeAF368215AY49829EVo26606Qualea grandfloru Mar.Vochysiacea (outgroup)AF368217AY49820AY487302Rhodomyrita argentea Benth,MyrteaeAF368217AY49810AY487302Rhodomyrita succrocarpa Benth,MyrteaeAY49811AY252138AY247302Spockwellia quadrifida DJ.Car, S.G.M.Carr & B.HylandKneineaeAY29812AY252138AF36820Spockwellia quadrifida DJ.Carr, S.G.M.Carr & B.HylandEucalypteaeAY49813AF36820HM16011718UNSW23246Syncarpia killii F.M.BaileySyncarpieaeAY39813AF36820HM16011718UNSW23246Syzygium anisatium (Vickery) Craven & BiffinSyzygicaeDQ08853DQ088471DQ088471Syzygium anogatimia (F.M.Bail, B.HylandSyzygicaeDQ088560DQ088484DQ088418Syzygium anguimia (F.M.Bail, B.HylandSyzygicaeDQ088560DQ088470DQ088425Syzygium andioniur (Mach, B.LylandSyzygicaeDQ088560DQ088470DQ088425Syzygium forbindum FMuell, S. SyzgiamSyzygiam GN088570DQ088462DQ088425Syzygium forbindum FMaellSyzygiam forbindum FMaellSyzygiam SyzygiaeDQ088570DQ088443Syzygium anogatimia | | | | | | |
| Pinemia racemosa (Mill.) J.W.MooreMyricaeDQ88554AY49808EF026631Psidum catticianum AZat. ex SabineMyricaeAM49001AM23400Lucas 213Psiloxylon mauritianum (Bouton ex Hook.f.) Baill.PsiloxyloideaeAF368215AY498825EF026606Qualea grandiflora Mart.Vochysiaceae (outgroup)AY498829AY498829Rhodammia argentea Benth.MyrteaeAY498810AY498810Rhodamyrtus psidioides (G.Don) Benth.MyrteaeAY498812AY252137Rhodamyrtus psidioides (G.Don) Benth.MyrteaeAY498812AY252138Sphaerantia chartacea P.G.Wilson & B.HylandEucalypteaeAY498813AF368220Syncarpia glomulifera (Sm.) Nied.SyncarpiaeaAY498813AF368220Syncarpia glomulifera (Sm.) Nied.SyncarpiaeaDQ088437DQ088407Syrgium anisatum (Vickery) Craven & BiffinSyzygiaeaDQ088570DQ088417Syrgium anisatum (Vickery) Craven & BiffinSyzygiaeaDQ088570DQ088418Syrgium angdiming (F.M.Bail) B.HylandSyzygiaeaDQ088570DQ088423Syrgium canciner B.HylandSyzygiaeaDQ088570DQ088424Syzgium canciner B.HylandSyzygiaeaDQ088570DQ088426Syzgium canciner B.HylandSyzygiaeaDQ088570DQ088426Syzgium canciner B.HylandSyzygiaeaDQ088570DQ088428Syzgium functifur M.Roch.) Wall. e. Stued.SyzygiaeaDQ088570DQ088428Syzgium functifur M.Roch.) Wall. e. Stued.SyzygiaeaDQ088570DQ088430< | | | | | | |
| Psidium cartleianum Afzel. ex SabineMyrteaeAM49014HM160101AM234080Lucas 213PsiloxyloideaePsiloxyloideaeAF368215AY498825EF026606Qualea grandifora Mart.Vochysiaceae (outgroup)AF368216AY498829Rhodamnia argentea Benth.MyrteaeAF368217AY498810Rhodamyrtus macrocarpa Benth.MyrteaeAY498811AY525137Rhodamyrtus macrocarpa Benth.MyrteaeAY498811AY525138Sphaerantia chartacea P.G.Wilson & B.HylandEucalypteaeAY49812AY525138Syncarpia glomulifera (Sm.) Nied.SyncarpiaeaAY3252138AF368210Syncarpia glomulifera (Sm.) Nied.SyncarpiaeaAY3252138AF368220Syrogtian acuminatissimum DCSyzygiaeDQ088471DQ088407Syzygium anisatum (Vickery) Craven & BiffinSyzygiaeaDQ088560DQ088471DQ088407Syzygium achorphyllum (FM-Bail) B.HylandSyzygiaeDQ088560DQ088424DQ088418Syzygium achorum (Baker f.) J.W.DawsonSyzygiaeDQ088570DQ088425DQ088425Syzygium divaricatum (Merr. & LM-Perry) Craven & BiffinSyzygiaeDQ088578DQ088426DQ088426Syzygium divaricatum (Merr. & LM-Perry) Craven & BiffinSyzygiaeDQ088578DQ088426DQ088430Syzygium divaricatum (Merr. & LM-Perry) Craven & BiffinSyzygiaeDQ088578DQ088426DQ088431Syzygium divaricatum (Merr. & LM-Perry) Craven & BiffinSyzygiaeDQ088578DQ088436SyzygiaeSyzygiam forbindum F.Muel | | | | ~ | | |
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| Qualea grandiffora Mart.Vochysiaceae (outgroup)AF368216Qualea sp.Vochysiaceae (outgroup)AY49829Rhodomnia argentea Benth.MytteaeAF368217AY498810Rhodomyrtus macrocarpa Benth.MytteaeAY498811AY525137Rhodomyrtus macrocarpa Benth.MytteaeAY498810AY487302Sphaerantia chartacea P.G.Wilson & B.HylandKanicaeAY498813AY525137Spockovelia quadrifida D.L Carr, S.G.M.Carr & B.HylandEucalyptaeAY498813AF368220Syncarpia fullii F.M.BaileySyncarpieaeAY298831AF368220HM160117/18UNSW23246Syncarpia nuinitatissimum DCSyzygitan eunimatissimum DCSyzygitaeDQ088575DQ088442DQ088407Syzygium anosatum (Vickery) Craven & BiffinSyzygicaeDQ088560DQ088442DQ088407Syzygium anoreum (Baker f.) J.W.DawsonSyzygicaeDQ088569DQ088442DQ088417Syzygium anoreum (Baker f.) J.W.DawsonSyzygicaeDQ088569DQ088440DQ088423Syzygium chariforum (Roxh) Walt & Stued.SyzygicaeDQ088579DQ088420DQ088426Syzygium chariforum (Roxh) Walt & Stued.SyzygicaeDQ088579DQ088430DQ088430Syzygium floribundum F.Muell.SyzygicaeDQ088579DQ088431DQ088431Syzygium floribundum F.Muell.SyzygicaeDQ088579DQ088430Syzygium floribundum F.Muell.Syzygium and characeux (F.M.Bail.) L.JohnsonSyzygicaeDQ088579DQ088431DQ088431Syzygium floribundum F.Muell. | | | | | | Lucas 213 |
| Qualea sp.Vochysiaceae (outgroup)AY498829Rhodamnia argentea Benth.MyrteaeAY49811AY487302Rhodomyrus macrocarpa Benth.MyrteaeAY498811AY525137Rhodomyrus psidioides (G.Don) Benth.MyrteaeAM234134Sphaernita chartacea P.G.Wilson & B.HylandKanieaeAY521547HM160115/16Stockwellia quadrifida D.J.Carr, S.G.M.Carr & B.HylandEucalypteaeAY498812AY525138Syncarpia glomulifera (Sm.) Nied.SyncarpieaeAY255139HM160117/18UNSW23246Syncarpia inlili F.M.BaileySyncarpieaeAF368125DQ088462EF02611Syzygium actinatum (Vickery) Craven & BiffinSyzygieaeDQ088508DQ088471DQ088407Syzygium arboreum (Baker f.) J.W.DawsonSyzygieaeDQ088560DQ088482DQ088418Syzygium chariter H.YlandSyzygieaeDQ088570DQ088420DQ088423Syzygium chariter K.H.YlandSyzygieaeDQ088570DQ088420DQ088423Syzygium chariter K.H.YlandSyzygieaeDQ088570DQ088420DQ088423Syzygium chariter K.T.M.Herry Craven & BiffinSyzygieaeDQ088570DQ088420DQ088428Syzygium chariter K.L.M.Perry Craven & BiffinSyzygieaeDQ088578DQ088470DQ088428Syzygium chariter W.C.T.White) L.JohnsonSyzygieaeDQ088578DQ088408DQ088428Syzygium failagerii (F.Muell.) CravenSyzygieaeDQ088578DQ088498DQ088433Syzygium failarear (H.Muell.)SyzygieaeDQ088578DQ088498 | | | | AY498825 | EF026606 | |
| Rhodamita argentea Benh.MyrteaeAF368217AY49810AY487302Rhodomyrtus macrocarpa Benh.MyrteaeAY498811AY255137AM234134Sphaerantia chartacea P.G.Wilson & B.HylandKanieaeAY521547HM16011516PGW 1348Spocarpia glonulifera (Sm.) Nied.SyncarpiaeaAY498812AY525138AF390445Syncarpia fillii F.M.BaileySyncarpiaeaAY498813AF368220HM160117/18UNSW23246Syrogtim anisatum (Vickery) Craven & BiffinSyrzygiaeaDQ088575DQ088462EF026611Syrzygiun anisatum (Vickery) Craven & BiffinSyrzygiaeaDQ088568DQ088412DQ088417Syrzygiun arboreum (Baker f.) J.W.DawsonSyrzygiaeaDQ088569DQ088440DQ088418Syrzygiun arboreum (Baker f.) J.W.DawsonSyrzygiaeaDQ088569DQ088440DQ088414Syrzygiun arboreum (Baker f.) LW.DawsonSyrzygiaeaDQ088570DQ088420DQ088421Syrzygiun arboreum (Baker f.) LW.DawsonSyrzygiaeaDQ088570DQ088420DQ088421Syrzygiun arboreum (Roxb.) Wall ex Stued.SyrzygiaeaDQ088570DQ088420DQ088423Syrzygium foribundum (Roxb.) Wall ex Stued.SyrzygiaeaDQ088574DQ088470DQ088426Syrzygium furibundum F.Muell.SyrzygiaeaDQ088578DQ088466Syrzygium furibundum F.Muell.Syrzygium furibundum F.Muell.SyrzygiaeaDQ088578DQ088453DQ088453Syrzygium furibundum F.Muell.SyrzygiaeaDQ088578DQ088453DQ088453Syrzygium furib | | | AF368216 | 137400020 | | |
| Rhodomyrtus macrocarpa Benth.MyrteaAY498811AY525137Rhodomyrtus psidioides (G.Don) Benth.MyrteaAM234134Rhodomyrtus psidioides (G.Don) Benth.MyrteaAM234134Splaerantia chartacea P.G.Wilson & B.HylandEucalypteaeAY521547HM160115/16Stockwellia quadrifyda D.J.Carr, S.G.M.Carr & B.HylandEucalypteaeAY498812AY526138Syncarpia gionulifera (Sm.) Nied.SyncarpiaeAY49813AF306420HM160117/18Syncarpia gionulifera (Strey) Craven & BiffinSyzygieaeA7636155DQ088471DQ088407Syzygium acuinitatissimum DCSyzygieaeDQ088560DQ088482DQ088418Syzygium aborberum (Baker f, J.W.DawsonSyzygieaeDQ088560DQ088441DQ088442Syzygium chronicortex B.HylandSyzygieaeDQ088570DQ088490DQ088424Syzygium chronicortex B.HylandSyzygieaeDQ088570DQ088491DQ088424Syzygium chronicortex B.HylandSyzygieaeDQ088570DQ088492DQ088425Syzygium chronicortex B.HylandSyzygieaeDQ088574DQ088405DQ088405Syzygium chronicortex C.HylandSyzygieaeDQ088574DQ088405DQ088405Syzygium floribundum F.Muell.SyzygieaeDQ088578DQ088463Syzygium glorini (f.Muell, CravenSyzygieaeDQ088578DQ088404Syzygium glenum CravenSyzygieaeDQ088582DQ088405Syzygium glenum CravenSyzygieaeDQ088586DQ088406Syzygium glenum CravenSyzygieae | | | 152(0217 | | 13/10/2000 | |
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| Sphaerantia characea P.G. Wilson & B. HylandKanieaeAY321547HM160115/16PGW 1348Stockvellia quadrifida D.J.Carre & B. HylandEucalypteaeAY498812AY325138AF390445Syncarpia glonulifera (Sm.) Nied.SyncarpiaeeAY39813AF368220HM160117/18UNSW23246Syncarpia initiatismum DCSyncarpiaeeAY352139AF368125DQ088407UNSW23246Syzygium anisatum (Vickery) Craven & BiffinSyzygieaeDQ088535DQ088412DQ088407Syzygium arboreum (Baker f.) J.W.DawsonSyzygieaeDQ088560DQ088442DQ088418Syzygium abardunia (F.M.Bail.) B. HylandSyzygieaeDQ088569DQ088420DQ088423Syzygium claviforum (Roxb.) Wall. ex Stued.SyzygieaeDQ088570DQ088470DQ088425Syzygium claviforum (Roxb.) Wall. ex Stued.SyzygieaeDQ088574DQ088470DQ088426Syzygium foribundum F.Muell.J.JohnsonSyzygieaeDQ088574DQ088431Syzygium foribundum F.Muell.SyzygieaeDQ088578DQ088430Syzygium granicaiut (F.M.Bail.) B.HylandSyzygium granicaiut (Hert, & L.M.Perry) Craven & BiffinSyzygieaeDQ088574DQ088426DQ088428Syzygium fancisti (F.M.Bail.) LohnsonSyzygieaeDQ088578DQ088430Syzygium granicaiut (Heul.) CravenSyzygium granicaiut (Heul.) CravenSyzygieaeDQ088579DQ088442Syzygium granicaiut (Heul.) Craven & BiffinSyzygium granicaiterH.Muel.) Craven & BiffinSyzygieaeDQ088579DQ088430Syzygium grani | | | A¥498811 | AY525137 | 434024124 | |
| Stockwellia quadrifida D.J.Carr, S.G.M.Carr & B.HylandEucalypteaeAY498812AY525138AF3690445Syncarpia illii F.M.BaileySyncarpie and Syncarpia illii F.M.BaileySyncarpia illii F.M.BaileyHII 60117/18UNSW23246Syzygium acuminatissimum DCSyzygieaeDQ088537DQ088402EF026611Syzygium anisatum (Vickery) Craven & BiffinSyzygieaeDQ088558DQ088471DQ088407Syzygium arboreum (Baker f.) J.W.DawsonSyzygieaeDQ088560DQ088484DQ088418Syzygium arboreum (Baker f.) J.W.DawsonSyzygieaeDQ088560DQ088420DQ088423Syzygium surfolium Hook & Arn.SyzygieaeDQ088570DQ088420DQ088424Syzygium canicortex B.HylandSyzygieaeDQ088570DQ088402DQ088405Syzygium canicortex B.HylandSyzygieaeDQ088570DQ088402DQ088406Syzygium faraicatum (Merr. & L.M.Perry) Craven & BiffinSyzygieaeDQ088570DQ088403DQ088453Syzygium faraicatur (Merr. & L.M.Perry) Craven & BiffinSyzygieaeDQ088579DQ088453DQ088453Syzygium glenum CravenSyzygieaeDQ088579DQ088431DQ088430Syzygium glenum CravenSyzygieaeDQ088579DQ088464AY187162Syzygium glenum CravenSyzygieaeDQ088545DQ088433Syzygium glenum Craven & BiffinSyzygieaeDQ088540DQ088433Syzygium glenum Craven & BiffinSyzygieaeDQ088540DQ088433DQ088433Syzygium glenum Craven & BiffinSyzygieaeDQ088586DQ0884 | | | A 3/501547 | | | DCW 1240 |
| Syncarpia glomulifera (Sm.) Nied.SyncarpiaeAY49813AF368220HM160117/18UNSW23246Syncarpia hillii F.M.BaileySyncarpiaeAY525139SyzygianEF026611Syzygiun acuminatissimum DCSyzygiaeDQ088577DQ088471DQ088407Syzygiun anisatum (Vickery) Craven & BiffinSyzygiaeDQ088585DQ088482DQ088417Syzygiun andodphyllum (F.Muell.) B.HylandSyzygiaeDQ088568DQ088440DQ088418Syzygium bungadinnia (F.M.Bail.) B.HylandSyzygiaeDQ088569DQ088490DQ088423Syzygium cancortex B.HylandSyzygiaeDQ088569DQ088490DQ088424Syzygium claviforum (Roxb.) Wall. ex Stued.SyzygiaeDQ088570DQ088490DQ088425Syzygium claviforum (Roxb.) Wall. ex Stued.SyzygiaeDQ088574DQ088470DQ088426Syzygium farbindum F.Muell.SyzygiaeDQ088579DQ088463Syzygiam farbindum F.Muell.Syzygium farbindum F.Muell.LJohnsonSyzygiaeDQ088579DQ088463Syzygium farbindum F.Muell.SyzygiaeDQ088579DQ088443Syzygium glenum CravenSyzygiaeDQ088579DQ088440Syzygium glenum CravenSyzygiaeDQ088582DQ088451Syzygium gans (F.Muell.) C.Nore Craven & BiffinSyzygiaeDQ088582DQ088464Syzygium gans (F.Muell.) Craven & BiffinSyzygiaeDQ088582DQ088404Syzygium mare (A.Cunn.) Sykes & P.J.Garnock-JonesSyzygiaeDQ088584DQ088403Syzygium malacenes (L.) Mert. & Perry <td></td> <td></td> <td></td> <td>137505100</td> <td></td> <td>PGW 1348</td> | | | | 137505100 | | PGW 1348 |
| Syncarpia hillii F.M.BaileySyncarpieaeAY525139Syzgium acuminatissimum DCSyzygieaeDQ088537DQ088421EF026611Syzygium anisatum (Vickery) Craven & BiffinSyzygieaeDQ088558DQ088422DQ088417Syzygium apodophyllum (F.Muell.) B.HylandSyzygieaeDQ088560DQ088484DQ088413Syzygium abroreum (Baker f. J.W.DawsonSyzygieaeDQ088566DQ088490DQ088423Syzygium buxifolium Hook. & Arn.SyzygieaeDQ088569DQ088490DQ088424Syzygium calcortex B.HylandSyzygieaeDQ088570DQ088492DQ088425Syzygium calcortex B.HylandSyzygieaeDQ088574DQ088495DQ088406Syzygium crebrinerve (C.T.White) L.JohnsonSyzygieaeDQ088574DQ088453DQ088433Syzygium francistii (F.M.Bail.) L.JohnsonSyzygieaeDQ088578DQ088495DQ088430Syzygium francistii (F.M.Bail.) L.JohnsonSyzygieaeDQ088578DQ088499DQ088430Syzygium francistii (F.M.Bail.) L.JohnsonSyzygieaeDQ088579DQ088499DQ088433Syzygium francistii (F.M.Bail.) B.HylandSyzygieaeDQ088539DQ088451DQ088433Syzygium ingens (F.Muell.) CravenSyzygieaeDQ088542DQ088464AY187162Syzygium ingens (F.Muell. ex C.Moore) Craven & BiffinSyzygieaeDQ088543DQ088467DQ088433Syzygium nackimonianum (B. Hyland)SyzygieaeDQ088589DQ088467DQ088402Syzygium mackimonianum (B. Hyland)SyzygieaeDQ088589DQ0885 | | | | | | LINICIN/2224C |
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| 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 | |

APPENDIX Continued