

## Postprint: Phylogenetic Relationships of Myrtales and Its Close Relatives Based on Chloroplast Genomes

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### Abstract

This study analyzed the phylogenetic relationships of Myrtales (6 families, 44 genera, 97 species) and its related groups (Geraniales, 2 families, 5 genera, 25 species) based on chloroplast genome data. The results showed: (1) The genome size of Myrtales ranged from 15.2~17.1 kb, containing 74~90 protein-coding genes, while that of Geraniales ranged from 11.6~24.2 kb, containing 75~132 protein-coding genes; (2) Comparison of phylogenetic trees constructed from chloroplast genome sequences and protein-coding genes revealed significant differences at the inter-order level and within Geraniales, but were essentially consistent within Myrtales; (3) The phylogenetic tree based on protein-coding genes indicated that both Myrtales and Geraniales were monophyletic and formed sister groups; within Myrtales, two major clades were formed, with Myrtaceae, Vochysiaceae, and Melastomataceae constituting one clade, in which Myrtaceae and Vochysiaceae were closely related sister groups, and Onagraceae, Lythraceae, and Combretaceae constituting another clade, in which Onagraceae and Lythraceae were closely related sister groups; at the family level, Myrtaceae, Vochysiaceae, Melastomataceae, Onagraceae, Lythraceae, Combretaceae, and Geraniaceae were all monophyletic (except for families represented by only a single species); (4) Supporting the placement of the genera *Punica* and *Trapa* within Lythraceae; (5) Analysis of sequence variation in protein-coding genes revealed that the number of shared variable genes among 19 genera of Melastomataceae was 53, with a variation percentage ranging from 5.84%~29.53%, while the number of shared variable genes among 9 genera of Myrtaceae was 57, with a variation percentage ranging from 1.31%~15.78%. The results of this study provide a theoretical basis for further investigation into the phylogeny of Myrtales and related families and genera.

## Full Text

# Phylogeny of Myrtales and Related Groups Based on Chloroplast Genome

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## Abstract

This study analyzed the phylogenetic relationships of Myrtales (97 species representing 44 genera in six families) and related groups (Geraniales, 25 species representing five genera in two families) based on chloroplast genome data. The results showed: (1) Myrtales genome sizes ranged from 15.2 to 17.1 kb, containing 74-90 protein-coding genes, while Geraniales genome sizes ranged from 11.6 to 24.2 kb, containing 75-132 protein-coding genes; (2) Phylogenetic trees constructed from whole chloroplast genome sequences and protein-coding genes showed significant differences at the inter-order level and within Geraniales, but were largely congruent within Myrtales; (3) Phylogenetic trees based on protein-coding genes revealed that both Myrtales and Geraniales are monophyletic and sister groups. Within Myrtales, two major clades were identified: one comprising Myrtaceae, Vochysiaceae, and Melastomataceae (with Myrtaceae and Vochysiaceae as sister groups), and the other comprising Onagraceae, Lythraceae, and Combretaceae (with Onagraceae and Lythraceae as sister groups). At the family level, Myrtaceae, Vochysiaceae, Melastomataceae, Onagraceae, Lythraceae, Combretaceae, and Geraniaceae were all monophyletic (excluding families represented by only one species); (4) The placement of *Punica* and *Trapa* within Lythraceae was supported; (5) Analysis of protein-coding gene sequence variation revealed that Melastomataceae shared 53 variable genes across 19 genera, with variation percentages ranging from 5.84% to 29.53%, while Myrtaceae shared 57 variable genes across nine genera, with variation percentages ranging from 1.31% to 15.78%. These results provide a theoretical framework for further phylogenetic studies of Myrtales and related families.

**Keywords:** Geraniales, Myrtaceae, Melastomataceae, protein-coding genes, phylogeny

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## Introduction

In the early stages of molecular systematics, researchers often relied on single or a few genes to resolve phylogenetic relationships. While this approach yielded

satisfactory results for some groups, it encountered obstacles for others, particularly those with slow evolutionary rates or rapid radiations, due to insufficient informative sites. Increasing gene number and employing combined analyses partially improved phylogenetic resolution and support. The advent of next-generation sequencing technologies and reduced sequencing costs has given rise to phylogenomics. Chloroplast genomes have become widely used in phylogenetic analyses due to their moderate size, ease of sequencing and assembly, and good collinearity across different taxa (Zhang and Li, 2011). As of April 2019, the NCBI database contained over 3,000 chloroplast genome sequences, compared to only 146 in October 2010, representing explosive growth that provides unprecedented opportunities for phylogenetic research. Chloroplast genomes have been successfully applied to resolve phylogenetic relationships across various taxonomic levels in angiosperms, including *Citrus* (Carbonell-Caballero et al., 2015), *Gossypium* (Wu et al., 2018), Poaceae (Pessoa-Filho et al., 2018), Orchidaceae (Dong et al., 2018), Caryophyllales (Liu et al., 2018), Zingiberales (Wu et al., 2018), and the broader angiosperm framework (Bausher et al., 2006).

Myrtales, belonging to the rosids, is a monophyletic group supported by both morphological and molecular evidence, though its precise position within the rosids remains unresolved and continues to attract research attention. Analyses based on *rbcL* sequences indicated an uncertain position for Myrtales within rosids (Hilu et al., 2003). Zhu et al. (2007) used combined analysis of one mitochondrial gene, two chloroplast genes, and one nuclear gene fragment, suggesting a possible close relationship between Myrtales and Geraniales (without support), together forming a basal group within rosids. In contrast, Wang et al. (2009) analyzed 12 genes (10 chloroplast and two nuclear) and found that Myrtales and Geraniales formed a moderately supported clade within malvids (eurosids II), serving as sister to the remaining malvid families.

Myrtales comprises nine families, 380 genera, and approximately 13,000 species (The Angiosperm Phylogeny Group, 2016), representing about 6% of core eudicots. Among the nine families, Crypteroniaceae, Alzateaceae, and Penaeaceae contain few species, with over 99% of species distributed among the remaining six families: Myrtaceae, Melastomataceae, Onagraceae, Lythraceae, Combretaceae, and Vochysiaceae. Previous molecular systematic studies include: Conti et al. (1997) based on *rbcL* sequences suggested Myrtaceae might be closely related to Melastomataceae, with Onagraceae and Lythraceae as sister groups, while Combretaceae's position remained unresolved. Sytsma et al. (2004) expanded sampling using *rbcL* and *ndhF* sequences, finding Combretaceae as a possible basal lineage within Myrtales (with low support), Myrtaceae as sister to Melastomataceae + Memecylaceae, and strong support for the Onagraceae-Lythraceae sister relationship. Soltis et al. (2011) analyzed 17 genes and found moderate support for Myrtales and Geraniales as sister groups.

In summary, the closest relatives of Myrtales remain uncertain, and inter-familial relationships within the order require further investigation. Previous molecular systematic studies indicate that single-gene or few-gene analyses

fail to produce stable phylogenetic trees for this group. This study utilizes publicly available chloroplast genome data from six major families of Myrtales and related groups to reconstruct a highly supported and resolved phylogenetic framework for Myrtales, confirming its sister relationship with Geraniales and further establishing Combretaceae as sister to Onagraceae + Lythraceae. Additionally, we analyzed sequence variation in protein-coding genes of Myrtaceae and Melastomataceae to provide reference data for future phylogenetic studies of these families.

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### 1.1 Data Collection

We downloaded complete chloroplast genome sequences and protein-coding genes for 97 species representing 44 genera in six families of Myrtales and 25 species representing five genera in two families of Geraniales from the GenBank database (Table 1). Outgroup taxa included three species from Malvales, two from Brassicales, one from Huerteales, and five from Sapindales (Table 1). We used Excel to record the size of each chloroplast genome and the number of protein-coding genes.

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### 1.2 Matrix Construction

Whole-genome sequences were aligned using MAFFT v7.394 (Kato & Standley, 2013) via the CIPRES Science Gateway (Miller et al., 2010) with default parameters. Protein-coding genes for each species were sorted alphabetically, concatenated, and aligned using MAFFT v7.394 through CIPRES Science Gateway. Alignments were manually refined in MEGA 7.0 software (Kumar et al., 2016).

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### 1.3 Phylogenetic Analysis

Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian inference (BI) methods. ML analysis employed RAxML ver. 8.2.8 (Stamatakis, 2014) with the GTRGAMMA model and rapid bootstrap analysis with 1,000 replicates (BS). BI analysis was conducted in MrBayes v3.2.5 (Ronquist & Huelsenbeck, 2003) using the GTR+GAMMA model. BI parameters included: MCMC algorithm running for 1,000,000 generations, sampling every 1,000 generations, discarding the first 25% as burn-in, and constructing the majority-rule consensus tree from remaining samples to calculate posterior probabilities (PP).

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## 2.1 Genome Size

Myrtales chloroplast genomes ranged from 152,049 to 171,315 bp (mean = 15.9 kb), with protein-coding gene numbers ranging from 74 to 90 (mean = 85) (Table 2, Figure 1 [Figure 1: see original paper]). Geraniales chloroplast genomes ranged from 116,935 to 242,575 bp (mean = 17.0 kb), with protein-coding gene numbers ranging from 75 to 132 (mean = 97) (Table 2, Figure 1).

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## 2.2 Matrix Analysis

To evaluate the utility of chloroplast genomes for phylogenetic analysis at different taxonomic levels, we constructed two datasets: whole chloroplast genome sequences and protein-coding genes. After alignment and manual refinement, we obtained six matrices: (1) three whole-genome matrices comprising Myrtales + Geraniales + outgroups (139 sequences, Matrix 1), Myrtales only (103 sequences, Matrix 3), and Geraniales only (25 sequences, Matrix 5); (2) three protein-coding gene matrices corresponding to the same taxon sets (Matrices 2, 4, and 6). Matrix details are provided in Table 3. The largest matrix was Matrix 5 (Geraniales whole-genome) at 762,293 bp, with 205,260 variable sites, 93,186 parsimony-informative sites (12.22%), and 77.60% missing data. The smallest was Matrix 4 (Myrtales protein-coding genes only) at 113,097 bp, with 26,162 variable sites, 18,171 parsimony-informative sites (16.07%), and 30.09% missing data (Table 3).

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## 2.3 Phylogenetic Trees from Different Matrices

We compared phylogenetic trees constructed from different datasets. Support values were similar between whole-genome and protein-coding gene trees at the inter-order level and within Myrtales. However, within Geraniales, support decreased markedly in the whole-genome tree, with only 68% of branches receiving 95% bootstrap support compared to 95% in the protein-coding gene tree (Figure 2 [Figure 2: see original paper]).

Topological comparisons revealed that both datasets recovered Myrtales and Geraniales as monophyletic with 100% support, though Malvales did not form a monophyletic group in the whole-genome dataset (Figure 3 [Figure 3: see original paper]). Topologies within Myrtales were largely congruent between datasets, with only minor differences within *Eucalyptus* and *Oenothera*. In contrast, Geraniales showed significant topological differences: the whole-genome dataset failed to recover Geraniaceae, *Erodium*, *Pelargonium*, and *Monsonia* as monophyletic, whereas the protein-coding gene dataset supported monophyly for the family and its constituent genera (Figure 4 [Figure 4: see original paper]).

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## 2.4 Phylogenetic Relationships of Myrtales and Geraniales

Based on these results, we selected the protein-coding gene matrix comprising 139 sequences (136 species including subspecies) from Myrtales, Geraniales, and outgroups (Matrix 2) for ML and BI analyses. This matrix was 186,769 bp long, with 53,589 variable sites, 39,804 parsimony-informative sites (21.31%), and 57.36% missing data. The ML analysis yielded a highly resolved phylogenetic tree with mean bootstrap support of 95% and 87.5% of branches receiving 95% support (Figure 5 [Figure 5: see original paper]).

At the ordinal level, all outgroup orders (Malvales, Brassicales, Huerteales, Sapindales) and ingroup orders (Myrtales, Geraniales) were monophyletic (BS = 100%; PP = 1.0). At the family level, Myrtaceae, Melastomataceae, Onagraceae, Lythraceae, Combretaceae, and Vochysiaceae within Myrtales, and Geraniaceae within Geraniales, were all monophyletic (excluding families represented by single species) (BS = 100%; PP = 1.0). At the generic level, *Eucalyptus*, *Angophora* (Myrtaceae), *Oenothera* (Onagraceae), *Lagerstroemia* (Lythraceae), and *Erodium*, *Pelargonium*, and *Monsonia* (Geraniaceae) were monophyletic (excluding genera represented by single species) (BS = 100%; PP = 1.0). *Corymbia* was not monophyletic.

Myrtales was strongly supported as monophyletic, with resolved inter-familial relationships. Myrtaceae and Vochysiaceae formed a clade that was sister to Melastomataceae. Onagraceae and Lythraceae were sister groups, with Combretaceae sister to this pair. The Lythraceae clade included *Lagerstroemia*, *Punica*, and *Trapa*. *Punica* is placed in Punicaceae in the *Flora of China* but was transferred to Lythraceae; *Trapa* belongs to Trapaceae. The Onagraceae clade included *Oenothera*, *Ludwigia*, and *Epilobium*, with *Ludwigia* as the basal lineage and *Oenothera* + *Epilobium* forming a subclade.

Melastomataceae included 19 genera, representing about 10% of the total genera in the family, with only one species per genus, necessitating expanded sampling for robust phylogenetic inference. Myrtaceae included nine genera: *Eucalyptus*, *Corymbia*, *Angophora*, *Allosyncarpia*, *Stockwellia*, *Syzygium*, *Psidium*, *Acca*, and *Plinia*. Previous *matK* phylogenies divided Myrtaceae into two subfamilies and 17 tribes (Wilson et al., 2005). All our sampled genera belong to subfamily Myrtoideae, distributed across three tribes: Syzygieae (*Syzygium*), Myrteae (*Psidium*, *Acca*, *Plinia*), and Eucalypteae (*Angophora*, *Eucalyptus*, *Allosyncarpia*, *Corymbia*, *Stockwellia*), all monophyletic (BS = 100%; PP = 1.0).

Geraniales was monophyletic, with Vivianiaceae as the basal lineage and Geraniaceae forming a monophyletic group where *Hypseocharis* was sister to the remaining genera, and *Erodium* and *Monsonia* were sister groups.

## 2.5 Sequence Divergence of Protein-Coding Genes

To evaluate the utility of different protein-coding genes for infra-familial phylogenetic analysis, we assessed sequence divergence of genes longer than 200 bp in Melastomataceae and Myrtaceae (other families were excluded due to limited generic sampling). Melastomataceae shared 53 variable genes across 19 genera, with variation percentages ranging from 5.84% to 29.53%. The five most variable genes were *rpl22*, *rps15*, *matK*, *ndhF*, and *rps3*, with 12 genes showing indels (Table 4). Myrtaceae shared 57 variable genes across nine genera, with lower variation percentages ranging from 1.31% to 15.78%. The five most variable genes were *rps12*, *ycf1*, *rpl22*, *rps15*, and *matK*, with 11 genes showing indels (Table 4).

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## 3.1 Conflicts Between Whole-Genome and Protein-Coding Gene Trees

Topological incongruence between whole-genome and protein-coding gene trees at the inter-ordinal level and within Geraniales may arise from two factors. First, gene order conservation decreases with increasing taxonomic scope. Geraniaceae species have experienced extensive plastid gene rearrangements (Blazier et al., 2011), resulting in large interspecific differences in gene order. This causes the same gene to appear in multiple positions during whole-genome alignment. Second, intergenic spacer regions exhibit higher sequence variation than protein-coding genes, and at the ordinal level, excessive variation may cause alignment difficulties. Consequently, previous ordinal-level studies using chloroplast genome data (e.g., Caryophyllales, Liu et al., 2018; Zingiberales, Wu et al., 2018; Saxifragales, Dong et al., 2018) have employed protein-coding genes rather than whole-genome sequences.

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## 3.2 Phylogenetic Relationships of Myrtales and Related Groups

Both Myrtales and Geraniales belong to the rosids, and their systematic positions have long been debated (Wang et al., 2009; Soltis et al., 2011). Our chloroplast genome data robustly support their sister relationship (BS = 100%; PP = 1.0).

Combretaceae's position within Myrtales has been uncertain based on morphological and molecular evidence, though recent studies suggest affinity with Onagraceae + Lythraceae (Soltis et al., 2011). Our analysis of the 139-sequence protein-coding gene matrix supports Combretaceae as sister to Onagraceae + Lythraceae with high support (BS = 93%; PP = 1.00). Analyses of Myrtales-only datasets (103 sequences) from both whole-genome and protein-coding genes also support this relationship (BS = 100%; PP = 1.00).

*Punica* is placed in Punicaceae in the *Flora of China* but was transferred to Lythraceae; our results support *Punica* as sister to remaining Lythraceae genera. *Trapa* belongs to Trapaceae in both the *Flora of China* and other classifications; our results support its placement within Lythraceae.

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### 3.3 Candidate Genes for Phylogenetic Analysis in Melastomataceae and Myrtaceae

According to the English edition of the *Flora of China*, Melastomataceae comprises 156-166 genera and approximately 4,500 species, with 21 genera and 114 species in China. Chloroplast protein-coding genes previously used for Melastomataceae phylogeny include *rbcL*, *ndhF*, and *rpl16* (Clausing & Renner, 2001; Renner, 2004). Myrtaceae contains about 130 genera and 4,500 species, distributed primarily in the Mediterranean, sub-Saharan Africa, Madagascar, tropical and temperate Asia, Australia, Pacific islands, and tropical America, with 10 genera and 121 species in China. Genes previously used for Myrtaceae phylogeny include *rbcL*, *ndhF*, *rpl16*, and *matK* (Sytsma et al., 2004; Wilson et al., 2005; Thornhill et al., 2015; Vasconcelos et al., 2017).

Both families are large and species-rich. Our results identify additional candidate genes for phylogenetic studies. The core DNA barcodes *rbcL* and *matK* show high sequence divergence, with variability percentages of 8.61% and 27.10% in Melastomataceae, and 3.53% and 8.12% in Myrtaceae. The “most promising plastid DNA barcode” *ycf1* (Dong et al., 2015) is missing in 18 Melastomataceae genera but shows 10.45% variability in Myrtaceae. In Melastomataceae, 39 genes exhibited >10% variability and 53 genes showed >5% variability. In Myrtaceae, two genes showed >10% variability and 11 genes showed >5% variability. These genes represent important candidates for resolving infra-familial relationships.

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