

Advanced understanding of phylogenetic relationships, morphological evolution and biogeographic history of the mega-diverse plant genus *Myrcia* and its relatives (Myrtaceae: Myrteae)



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ABSTRACT

Myrcia is the largest exclusively Neotropical genus of the plant family Myrtaceae with c. 770 species. Although several studies have elucidated the relationships within particular sections of the genus, to date no phylogeny has been produced that includes a broad taxonomic and geographic representation. Here we present a phylogenetic hypothesis of *Myrcia* and close relatives comprising 253 species and based on two nuclear and seven plastid markers. We combine previously available sequence data with 234 new sequences of the genus *Myrcia* for this study. We use this phylogeny to investigate the evolution of selected morphological traits and to infer the biogeographic history of the genus. Our results yield a highly supported phylogenetic tree where the *Myrc Eugenia* group is sister to the *Myrcia* and *Plinia* groups. Five *Myrcia* sections previously considered unplaced emerge in a newly circumscribed clade. The monophyly of two *Myrcia* sections previously considered uncertain, *Aulomyrcia* and *Gomidesia*, are confirmed with strong support. Flowers with free calyx lobes, 2-locular ovaries, and anthers with symmetrical thecae are ancestral features of *Myrcia*. The *Myrcia* sect. *Gomidesia* is highly supported and recovered as monophyletic, with asymmetric anthers that retain their curvature after dehiscence as a morphological synapomorphy. The Atlantic Forest is the most likely ancestral area of the genus and most of its internal clades, from where multiple lineages colonized different regions of South and Central America, in particular the Brazilian Cerrado through multiple unidirectional range expansions. The southern Atlantic Forest is the ancestral area for *Myrcia* sect. *Gomidesia*, with lineages reaching the northern Atlantic Forest, Cerrado, Yungas, and other savanna vegetation of South America. Our results provide a solid backbone for further evolutionary and taxonomic work and clarify several previously uncertain relationships in this mega-diverse plant group, and shed light on its geographical range evolution.

1. Introduction

The plant family Myrtaceae comprises 142 genera, 17 tribes and 5500–5800 woody plant species of closed or open forests or woodlands (Wilson, 2011; WCSP [World Checklist of Selected Plant Families], 2017). The family includes many economically and widely known important relatives, such as eucalypts, *araçá-boi*, clove, myrtle, rose apple,

jabuticaba, guava, pineapple guava, *pitanga*, strawberry guava and tea tree (Kawasaki and Holst, 2004). Myrteae is the most species rich tribe with c. 2500 species, found mainly in the Neotropics but with few species in Australia and Asia (Wilson et al., 2005; Wilson, 2011). Following Vasconcelos et al. (2017a), tribe Myrteae is composed of ten main clades, eight of which comprise the Neotropical lineage (i.e. *Blepharocalyx*, *Eugenia*, *Myrc Eugenia*, *Myrcia*, *Myrteola*, *Pimenta*,

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Plinia, Psidium groups). *Myrcia* (*sensu* Lucas et al., 2018) is the second most species-rich genus in the tribe with c. 770 species, most of which are distributed in either the Atlantic Forest, the Cerrado, or the Amazon basin (Lucas et al., 2011; BFG [the Brazil Flora Group], 2015; WCSP, 2017).

Myrcia is one of the most taxonomically complex and morphologically homogenous genera of Myrtaceae. The taxon currently recognised as a single genus (*sensu* Lucas et al., 2018) was until recently recognized as four distinct genera: *Calyptranthes* Swartz, *Gomidesia* O. Berg, *Marlierea* Cambessèdes, and *Myrcia* DC. All four genera have been inferred to be either para- or polyphyletic by molecular analyses in the last 10 years (ie. *Calyptranthes* in Wilson et al., 2016; *Marlierea* in Staggemeier et al., 2015; Santos et al., 2016, 2017; and *Gomidesia* in Lucas et al., 2011). In place of the four traditionally recognized genera, *Myrcia* is now divided in nine sections, each representing highly supported clades (Lucas et al., 2011, 2018). All the nine sections are morphologically recognizable, and have been corroborated by multiple molecular phylogenetic studies (Staggemeier et al., 2015; Santos et al., 2016; Wilson et al., 2016; Vasconcelos et al., 2017a).

Despite recent efforts to infer the phylogenetic relationships within *Myrcia*, some phylogenetic relationships between the *Myrcia* clades remain unclear (Staggemeier et al., 2015; Santos et al., 2016, 2017; Wilson et al., 2016; Vasconcelos et al., 2017a). In particular, previous molecular phylogenetic studies included a limited representation of *Myrcia* sect. *Gomidesia*. Re-evaluation of that circumscription is desirable, particularly after inclusion of *Myrcia mischophylla* Kiaersk. (Lucas et al., 2007, 2011) a species not previously associated with *Gomidesia*. The monophyly of *Myrcia* sect. *Aulomyrcia* has also been questioned due to its low phylogenetic support (Staggemeier et al., 2015; Santos et al., 2016), with paraphyly also inferred (Santos et al., 2017). The uncertain relationships within *Myrcia* currently hinder monographic work, preventing revision of a single section without considering the whole genus.

To address these issues, here we: (1) Infer the phylogenetic relationships among *Myrcia* and related groups, expanding on and testing previous phylogenetic hypotheses. (2) Test the monophyly of *Myrcia* sections *Aulomyrcia* and *Gomidesia*. (3) Identify the phylogenetic position of previously unplaced *Myrcia* species. (4) Evaluate the evolution of morphological characters in *Myrcia* and *Myrcia* sect. *Gomidesia*; and (5) infer the geographical range evolution of *Myrcia* and *Myrcia* sect. *Gomidesia* within the Neotropics. To pursue these goals we compile the most comprehensively-sampled phylogeny of *Myrcia* to date, using a broad molecular matrix with existing and newly available sequences, and integrating it with both morphological characters and geographical distributions.

2. Material and methods

2.1. Taxon sampling and DNA sequencing

A total of 255 accessions of tribe Myrtleae were sampled, representing the Blepharocalyx, Myrceugenia, Myrcia, and Plinia groups (*sensu* Lucas et al., 2007; Vasconcelos et al., 2017a). Non-Myrtleae outgroups were represented by two accessions of tribes Syzygiaeae and Eucalypteae (*sensu* Wilson et al., 2005; see Appendix A for a complete list of sampled species and vouchers). The external transcribed spacer (ETS) and internal transcribed spacer (ITS) of the ribosomal nuclear region and seven plastid markers (*matK*, *ndhF*, *psbA-trnH*, *rpl16*, *rps16-trnQ*, *rpl32-trnL*, and *trnL-trnF*) were used, resulting in a dataset comprising 1418 sequences obtained from 253 species. A total of 234 sequences of the genus *Myrcia* were generated for this study and the remaining were obtained from previous studies (Systma et al., 2004;

Lucas et al., 2007, 2011; Murillo et al., 2012; Staggemeier et al., 2015; Santos et al., 2016; Wilson et al., 2016; Vasconcelos et al., 2017a) via GenBank (Benson et al., 2013) using the SUPERSMART platform (Antonelli et al., 2017).

Total DNA was extracted mainly from 0.3 g of silica-gel-dried leaf material (0.2 g from herbarium samples) using a modified CTAB (cetyltrimethylammonium bromide) protocol (Doyle and Doyle, 1987). Some samples were extracted using a DNeasy kit (Qiagen) according to the manufacturer's protocols. Amplification and purification of target DNA regions was executed according to protocols outlined in Lucas et al. (2007, 2011), Murillo et al. (2012) and Staggemeier et al. (2015). Amplified products were sent for Sanger sequencing at the Platform of sequencing-LABCEN/CCB at the Universidade Federal de Pernambuco in Brazil or the Jodrell Laboratory of the Royal Botanic Gardens Kew in the UK. DNA sequences were assembled and edited in Geneious v.7.1.9 (Kearse et al., 2012) and aligned using the MUSCLE (Edgar, 2004) plugin with subsequent manual adjustment.

2.2. Phylogenetic analyses

Phylogenetic relationships were reconstructed using both Maximum Likelihood (ML) and Bayesian Inference (BI). Analyses were performed separately on each dataset and combined afterwards. jModelTest v.2.1.6 (Darriba et al., 2012) was used to select the best model of DNA substitution for each individual marker in the combined dataset.

Maximum Likelihood (ML) analyses were performed with RAxML v8.2.8 (Stamatakis, 2006, 2014) using the rapid bootstrap algorithm with 1000 replicates to assess branch support, combined with a search of the best-scoring ML tree under default parameters. Bayesian Inference (BI) was performed using MrBayes v.3.2.6. (Ronquist et al., 2012). Four independent runs with four Markov Chain Monte Carlo (MCMC) runs were conducted, sampling every 1000 generations for 20 million generations. Each run was evaluated in Tracer v.1.6 (Rambaut et al., 2014) to determine that the estimated sample sizes (ESS) for each relevant parameter was higher than 200. The consensus tree was generated in MrBayes with a burn-in of 25%. The consensus tree and posterior probability (PP) were visualized and edited in FigTree v.1.4.2. (Rambaut, 2014). All analysis of ML, BI and jModelTest were performed in the CIPRES Science Gateway (Miller et al., 2010). Support values were considered high when bootstrapping (BS) was $\geq 70\%$ (Hillis and Bull, 1993) and posterior probability (PP) was ≥ 0.95 (Erixon et al., 2003; Pirie, 2015). Informal clade classification follows Lucas et al. (2007, 2011), and Staggemeier et al. (2015). Names and numbers of *Myrcia* sections refer to the circumscriptions proposed by Lucas et al. (2011, 2018), Staggemeier et al. (2015; subclades a-g in *Myrcia* sect. *Aulomyrcia* [9]) and by Lucas et al. (2007) and Vasconcelos et al. (2015, 2017a; informal groups in Myrtleae).

2.3. Ancestral reconstruction of morphological traits in *Myrcia*

In *Myrcia* systematics, calyx fusion, ovary locularity and anther specializations are traditionally used in infrageneric classification (Berg, 1855–1856; Legrand, 1958; McVaugh, 1968, 1969; Vasconcelos et al., 2017a; Lucas et al., 2018; Supplementary Material S1–S4). Evolution of these three morphological traits was reconstructed using ancestral character reconstruction based on the here inferred *Myrcia* phylogenetic hypothesis. For *Myrcia* sect. *Gomidesia*, three morphological traits were used to compile informal groups and infra-taxonomical classification: thecal displacement, presence/absence of anther glands and trichomes on abaxial leaf surface; S5–S8 were analyzed. Characters were scored on the basis of herbarium and field observations and data available in literature (Lucas et al., 2011; BFG, 2015; WCSP, 2017;

Amorim, 2017).

Bayesian analysis was used to infer ancestral state reconstructions. The evolution of selected morphological characters was reconstructed on the Bayesian Inference topology using the Bayesian Binary MCMC (BBM) tool implemented in RASP v.3.2. (Yu et al., 2015) using default parameters. For analyses of calyx fusion, ovary locularity and anther specializations, outgroup taxa and duplicate accessions of a single species were removed to avoid potential bias from over-representation. The tree was pruned to exclude the Blepharocalyx, Myrceugenia, Myrtus and Plinia groups, along with *Myrcia fenzliana* O. Berg (DF), *M. aff. hirtiflora* DC., *M. aff. racemosa* (O. Berg) Kiersk., *M. rorida* (O. Berg) Kiersk., *M. springiana* (O. Berg) Kiersk. (PE), and *M. sp. 2* (voucher: V. Staggemeier 792) using the *ape* package (Paradis et al., 2004) implemented in R (R Core Team, 2008).

2.4. Geographic range evolution of *Myrcia*

The geographical range evolution of *Myrcia* was reconstructed as a character in the phylogeny using the same methodology as above and departing from the current distribution of extant species. The geographic range was delimited following the biogeographic subregions of the Neotropics proposed by Morrone (2006, 2014), as follows: (A) Atlantic Forest. This area resembles the Parana sub-region (*sensu* Morrone, 2006) and includes the Atlantic, Parana Forest and Araucaria provinces (Morrone, 2014). In the case of *Myrcia* sect. *Gomidesia* analyses, a regionalization of this subregion was adopted, due to the influence of the Doce river flow, a putative barrier between the North and South portions, thought to shape species distribution (Prance, 1982; Carnaval and Moriz, 2008; Turchetto-Zolet et al., 2016; Zizka et al., 2017) and its relevance in sect. *Gomidesia* species distribution (Amorim, 2017). (B) South American Dry Diagonal. This area resembles the Chacoan subregion (*sensu* Morrone, 2006), that includes the Cerrado and Chacoan provinces (Morrone, 2014) plus *Campo Rupestre* vegetation of Central-eastern Brazil (Giulietti and Pirani, 1988). (C) Amazon basin. This area includes the Boreal Brazilian and South Brazilian domains (Morrone, 2014), represented by the Napo, Imeri, Pantepui, Guianan Lowlands, Roraima, Pará, Ucayali, Madeira, Rondônia and Yungas provinces (Morrone, 2014). (D) Andean highlands. This area corresponds to the South America transition zone (*sensu* Morrone, 2006), which includes the Paramo, Desert, Puna, Atacaman, Prepuna and Monte provinces (Morrone, 2014). (E) Caribbean. This area is similar to the Antillean subregion (Morrone, 2014). (F) Pacific dominion. This area includes Balsas Basin, Mosquito, Pacific Lowlands, Veracruz and Yucatan Peninsula provinces (*sensu* Morrone, 2014).

3. Results

The combined and aligned dataset comprises 8770 bp of two nuclear and seven plastid regions (Table 1). The combined nuclear regions (ETS and ITS) comprise 17.4% (1531 bp) of the total dataset length and contain 40.2% variable and 25.7 phylogenetically informative characters (against 23.6% of variable and 10% phylogenetically informative characters in the plastid regions). The combined plastid region (*matK*, *ndhF*, *psbA-trnH*, *rpl16*, *rps16-trnQ*, *rpl32-trnL*, and *trnL-trnF*) represent 82.5% (7239 bp) of the total dataset. Of the nuclear regions, ETS provided most variation and presence of phylogenetically informative characters (40.6% and 27%, respectively), followed by ITS (39.9% and 24.7%, respectively). Of the plastid markers, *psbA-trnH*, *rpl32-trnL* and *rps16-trnQ* provided most variable and phylogenetically informative characters (33.9% and 15%, 30.0% and 12.2%, 29.1 and 13.6%, respectively), while *matK* and *ndhF* were the least variable regions (11.8% and 3.9%, 19.4% and 9.4%, respectively). The best-fitting substitution models selected through the Akaike Information Criterion (AIC) (Akaike, 1974) were GTR+G for *matK*, *ndhF*, *rpl16* and *rpl32-trnL*, and GTR+I+G for ETS, ITS, *psbA-trnH*, *rps16-trnQ* and *trnL-trnF* (Table 1).

Table 1
Sequence statistics summary for the analysed markers used to infer phylogenetic relationships.

| | ETS | ITS | <i>matK</i> | <i>ndhF</i> | <i>psbA-trnH</i> | <i>rpl16</i> | <i>rpl32-trnL</i> | <i>rps16-trnQ</i> | <i>trnL-trnF</i> | Nuclear combined | Plastid combined | All data combined |
|---|-------------|-------------|--------------|-------------|------------------|--------------|-------------------|-------------------|------------------|------------------|------------------|-------------------|
| No. of taxa | 102 | 250 | 73 | 132 | 228 | 128 | 115 | 216 | 174 | 250 | 257 | 257 |
| Aligned length (bp) | 603 | 928 | 1350 | 780 | 869 (74.3%) | 936 (76.9%) | 914 (65.4%) | 1541 (60.2%) | 849 (71.0%) | 1531 (17.4%) | 7239 (82.5%) | 8770 |
| Conserved characters | 324 (53.7%) | 482 (51.9%) | 1173 (86.8%) | 580 (74.3%) | 389 (44.7%) | 720 (76.9%) | 598 (29.1%) | 928 (30.0%) | 603 (71.0%) | 806 (52.6%) | 4994 (68.9%) | 5800 (66.1%) |
| Variable characters | 245 (40.6%) | 371 (39.9%) | 160 (11.8%) | 152 (19.4%) | 295 (33.9%) | 189 (20.1%) | 275 (30.0%) | 449 (29.1%) | 184 (21.6%) | 616 (40.2%) | 1710 (23.6%) | 2326 (26.5%) |
| Phylogenetically informative characters | 163 (27%) | 230 (24.7%) | 53 (3.9%) | 73 (9.4%) | 131 (15%) | 73 (7.8%) | 112 (12.2%) | 209 (13.6%) | 80 (9.4%) | 393 (25.7%) | 731 (10%) | 1124 (12.3%) |
| Mean CG content | 49.0% | 55.9% | 33.6% | 28.4% | 26% | 30.3% | 28.6% | 26% | 34.9% | 54.3% | 28.8% | 32.3% |
| Substitution model | GTR + G | GTR + I + G | GTR + I + G | GTR + G | GTR + G | GTR + G | GTR + G | GTR + G | GTR + G | GTR + G | GTR + G | GTR + G |

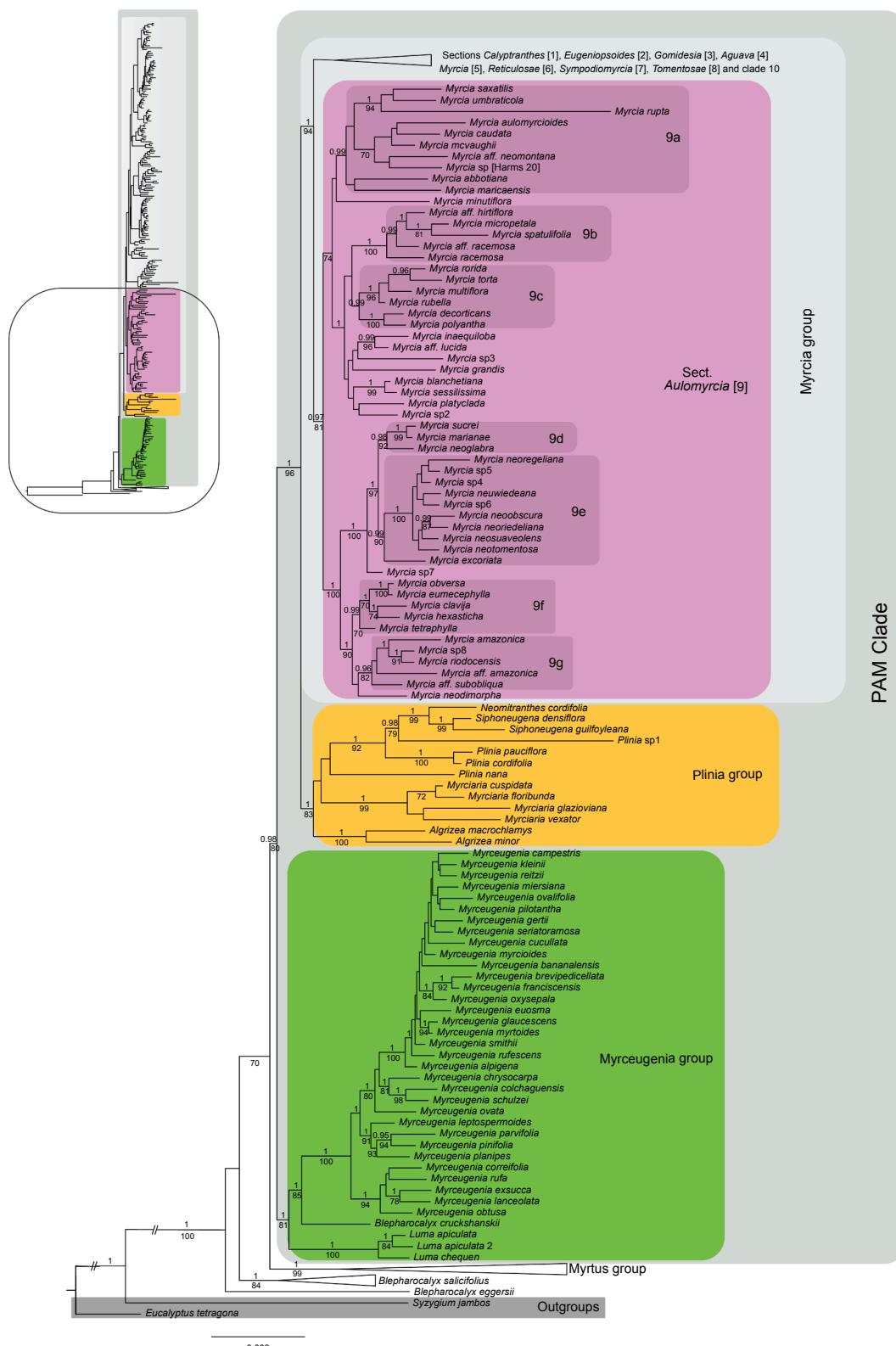


Fig. 1. Bayesian Inference (BI) majority rule consensus tree from the combined analysis of ITS (internal transcribed spacer), ETS (external transcribed spacer), *matK*, *ndhF*, *pasbA-trnH*, *rpl16*, *rps16-trnQ*, *rpl32-trnL*, and *trnL-trnF*. Posterior probabilities (from the BI analysis) greater than 0.95 are shown above branches; bootstrap percentages (from the ML analysis) greater than 70 are shown below branches. PE = state of Pernambuco (Brazil); BA = state of Bahia (Brazil); DF = Federal District (Brazil); REP = Dominican Republic. *Myrcia* sections follow Lucas et al., 2018; clades 1–9 follow Lucas et al., 2011; subclades 9a–9g follow Staggemeier et al., 2015. Clade 10, and subclades 1a, 1b, 3a, 3b, 5a, 5b, along with Springiana, Vittoriana, Pubescens and Cerqueiria subclades are newly used here. Scale bar: expected number of nucleotide substitutions per site.

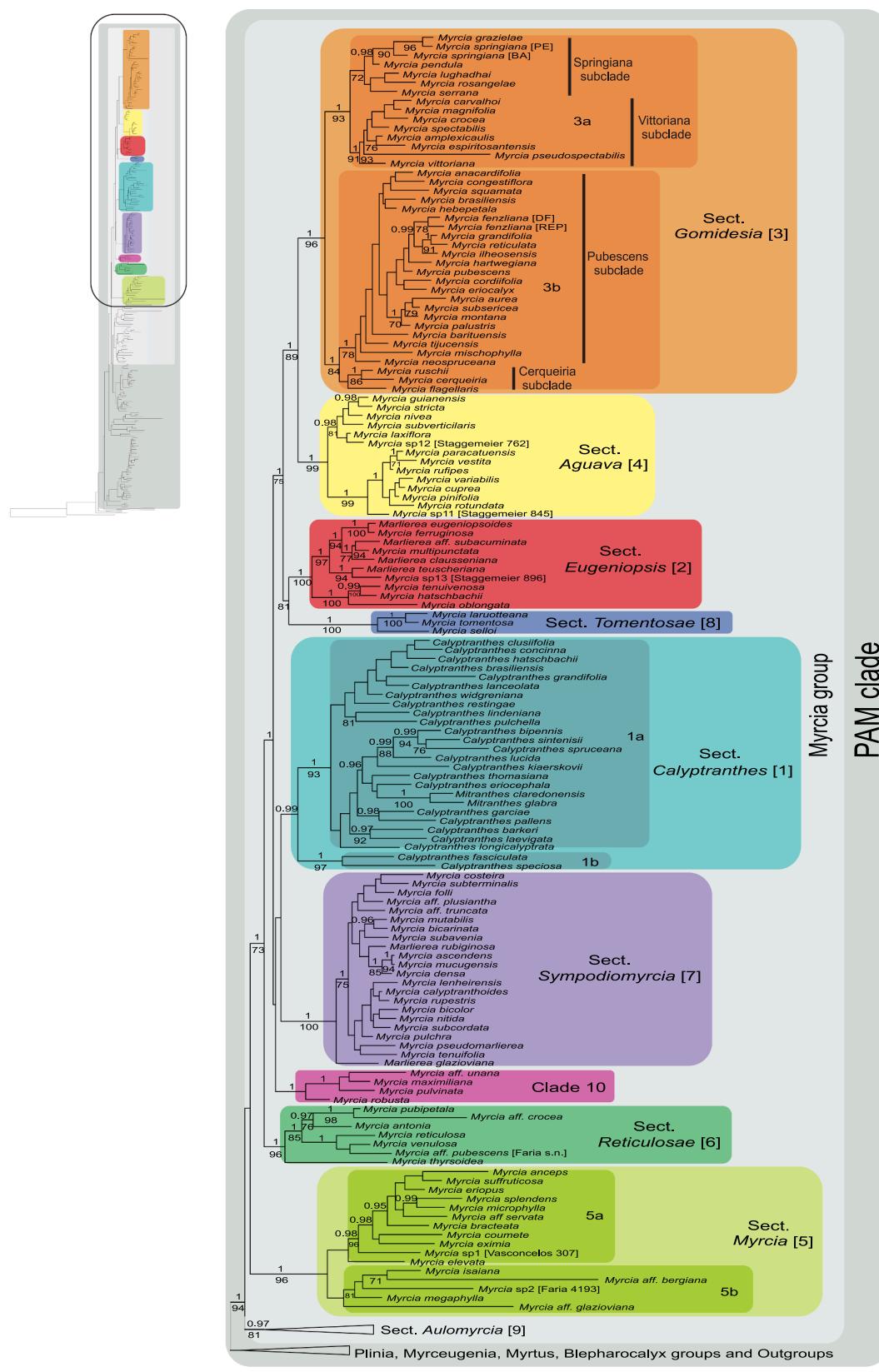


Fig. 1. (continued)

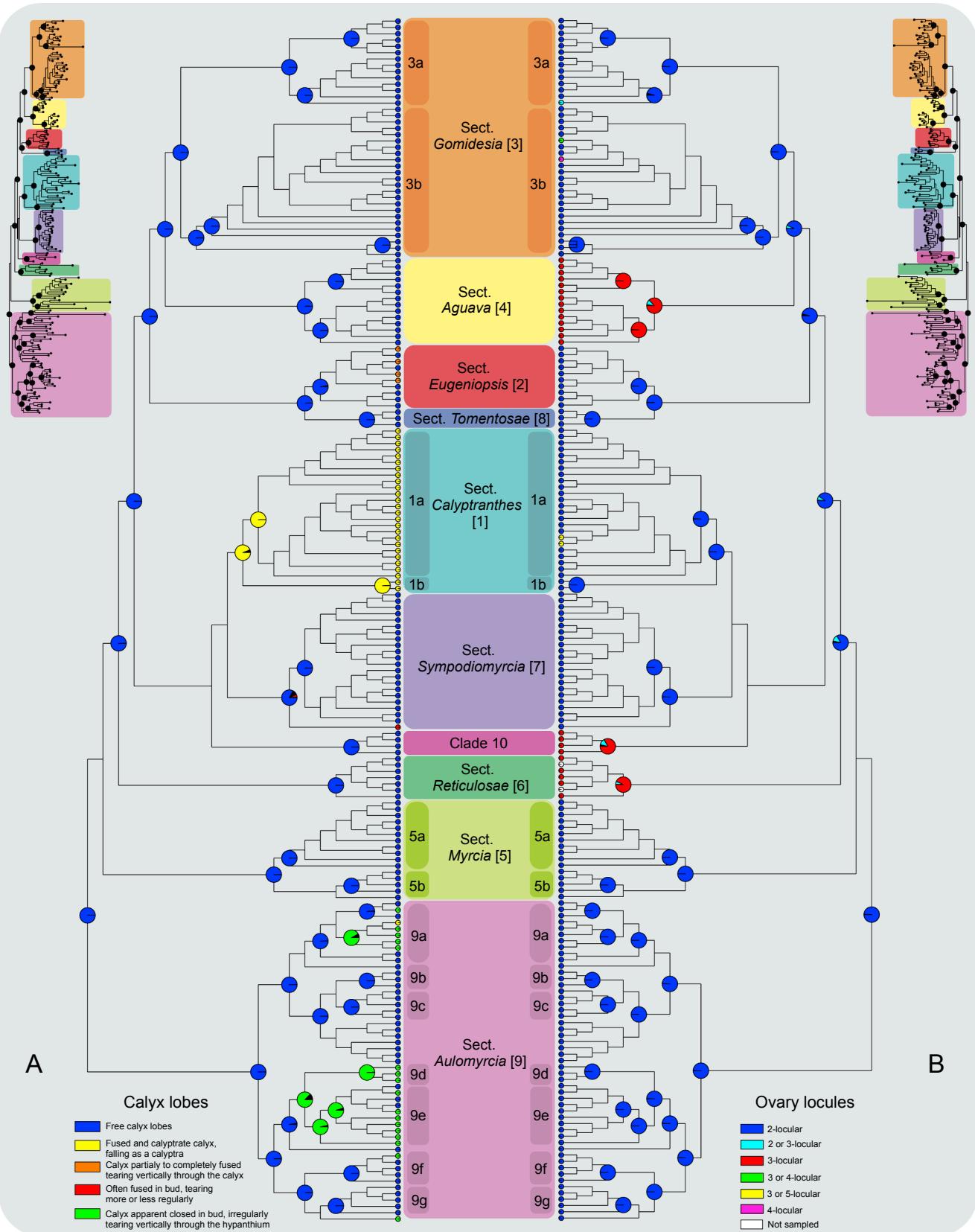


Fig. 2. Evolution of key morphological traits in *Myrcia* and relatives, showing the most likely ancestral character traits at all internal branches of the Bayesian Inference majority rule consensus tree from Fig. 1, inferred using Bayesian Binary MCMC. (A) Calyx lobes. (B) Ovary locules. Pie charts for each node indicate probabilities of character states. Colours indicate the proportional likelihood of the states reconstructed for each node (see text). Only ancestral states of strongly-supported clades are shown.

3.1. Phylogenetic reconstruction

Phylogenetic reconstructions of each individual partition resulted in generally low support values in both ML and BI analyses. Nevertheless, major clades were recovered with statistically significant bootstrap and posterior probabilities and no significant topological contradictions. Results and discussions presented here focus on the combined dataset as it provided greater resolution and statistical support, without contradicting the individual analyses (Fig. 1a, b). The consensus trees obtained under ML and BI were very similar (see S9 for ML topology), diverging only in the weakly supported phylogenetic position of *Blepharocalyx eggersii* (Kiaersk.) Landrum in relation to the rest of tribe Myrteae and the placement of clade 10 within *Myrcia*.

3.2. Phylogenetic relationships within tribe Myrteae

Fig. 1a shows the most probable relationships within tribe Myrteae, which emerges monophyletic (BS = 100; PP = 1) with *Blepharocalyx eggersii* as sister to the rest of the tribe. *Blepharocalyx salicifolius* (Kunth) O. Berg (BS = 84; PP = 1) emerges sister to a clade (BS = 70) comprising the Myrtus group (BS = 70; PP = 1), the Myrceugenia group and the PAM [*Plinia*, *Algrizea* and *Myrcia*] clade (*sensu* Vasconcelos et al., 2015). The Myrtus group (BS = 70; PP = 1) is sister to the Myrceugenia group plus the PAM clade (BS = 80; PP = 0.98). Within this clade, the Myrceugenia group (BS = 81; PP = 1) is sister to the PAM clade (BS = 96; PP = 1), which splits into two sister lineages comprised of the *Plinia* (BS = 83; PP = 1) and the *Myrcia* groups (BS = 94; PP = 1; Fig. 1a).

3.3. Phylogenetic relationships within *Myrcia*

Ten strongly supported clades are here recognized within *Myrcia* (Fig. 1a, b). These include the nine sections [1–9] described by Lucas et al. (2018) and a tenth clade, hereafter referred to as clade 10. *Myrcia* sect. *Aulomyrcia* (O. Berg) Griseb. [9] (BS = 81; PP = 0.97) is sister to a weakly supported clade composed of the rest of the *Myrcia* group. Within this clade, *Myrcia* sect. *Myrcia* [5] (BS = 96; PP = 1) is sister to the clade composed of the remaining *Myrcia* lineages (BS = 73; PP = 1). Within that latter clade, *Myrcia* sect. *Reticulosae* D.F. Lima & E. Lucas [6] (BS = 96; PP = 1) is sister to a clade (PP = 1) comprising the sections *Calyptranthes* (Sw.) A.R. Lourenço & E. Lucas [1], *Eugeniopsis* (O. Berg) M.F. Santos & E. Lucas [2], *Gomidesia* (O. Berg) B.S. Amorim & E. Lucas [3], *Aguava* D.F. Lima & E. Lucas [4], *Sympodiomyrcia* M.F. Santos & E. Lucas [7], *Tomentosae* E. Lucas & D.F. Lima [8] and the clade 10. *Myrcia* sects. *Calyptranthes* (PP = 0.99), *Sympodiomyrcia* (BS = 100; PP = 1) and clade 10 (BS = 93; PP = 1) are strongly supported as monophyletic but relationships among them receive weak support. That latter clade is sister to a strongly supported group composed of *Myrcia* sects. *Eugeniopsis*, *Gomidesia*, *Aguava*, and *Tomentosae* (BS = 75; PP = 1). Within this group, two main lineages are identified, the first (BS = 81) unites sections *Eugeniopsis* (BS = 100; PP = 1) and *Tomentosae* (BS = 100; PP = 1), while the second shows a strongly supported relationship (BS = 89; PP = 1) between sections *Gomidesia* (BS = 96; PP = 1) and *Aguava* (BS = 99; PP = 1). *Myrcia* sect. *Aulomyrcia* [9] also splits into two lineages. The first (BS = 74) comprises the strongly supported subclade 9a (*sensu* Staggemeier et al., 2015) including *Myrcia aulomyrcioides* E.Lucas & C.E.Wilson, *M. caudata* (McVaugh) E.Lucas & C.E.Wilson, *M. mcvaughii* (B. Holst) E.Lucas & C.E.Wilson, *M. abbotiana* (Urb.) Alain, and *M. maricaensis* Alain, with subclades 9b and 9c, along with eight unplaced species. The second main lineage (BS = 100; PP = 1) splits into two other strongly supported lineages. The first (BS = 100; PP = 1) is composed of *Myrcia* sp.

7 as highly supported as sister to subclades 9d and 9e, while the second lineage (BS = 90; PP = 1) is composed of subclades 9f and 9g. (Fig. 1a).

3.4. Phylogenetic relationships within *Myrcia* sect. *Gomidesia*

Our results corroborate *Myrcia* sect. *Gomidesia* (or clade 3) as monophyletic (BS = 84; PP = 1). This clade is composed of two highly supported lineages, the 3a (BS = 93; PP = 1) and 3b (BS = 84; PP = 1; Fig. 1b), each composed of two subclades. In 3a, *Springiana* subclade (BS = 72) is composed of a lineage in which *Myrcia grazielae* NicLugh., *M. springiana* (O. Berg) Kiaersk. and *M. pendula* Sobral are nested (PP = 0.98) and sister to a group of species which comprises *M. lugadhae* B.S. Amorim, *M. rosangelae* NicLugh. and *M. serrana* B.S. Amorim. *Vittoriana* subclade is highly supported (BS = 91 and PP = 1) and composed of *M. amplexicaulis* (Vell.) Hook.f., *M. carvalhoi* NicLugh., *M. crocea* Kiaersk., *M. espiritosantensis* B.S. Amorim, *M. magnifolia* (O. Berg) Kiaersk., *M. pseudospectabilis* Sobral, *M. spectabilis* DC. and *M. vittoriana* Kiaersk. In 3b, *Pubescens* subclade (BS = 78; PP = 1) is the most species rich clade and is composed of *Myrcia anacardiifolia* Gardner, *M. aurea* NicLugh., *M. barituensis* (Legmane) B. Holst, *M. brasiliensis* Kiaersk., *M. congestiflora* Calliari & V.C. Souza, *M. cordiifolia* DC., *M. eriocalyx* DC., *M. fenzliana* O. Berg, *M. grandifolia* Cambess., *M. hartzwegiana* (O. Berg) Kiaersk., *M. hebepepetala* DC., *M. ilheosensis* Kiaersk., *M. mischophylla* Kiaersk., *M. montana* Cambess., *M. neospruceana* E. Lucas & Sobral, *M. palustris* DC., *M. pubescens* DC., *M. reticulata* Cambess., *M. squamata* (Mattos & D. Legrand) Mattos, *M. subsericea* A. Gray and *M. tijucensis* Kiaersk.. *Cerqueiria* subclade is sister to *M. flagellaris* (D. Legrand) Sobral and composed of *Myrcia cerqueiria* (Nied.) E. Lucas & Sobral and *M. ruschii* B.S. Amorim.

3.5. Evolution of morphological traits within *Myrcia*

The state of free calyx lobes appears plesiomorphic in *Myrcia* (Bayesian posterior probability - BPP 0.99; Fig. 2a) with independent shifts to a fused calyx. *Myrcia* sect. *Aulomyrcia* [9] has species with free or apparently closed buds (see Vasconcelos et al., 2017b) but the ancestor of this group apparently had free calyx lobes (BPP 0.99), with bud closure events in subclades 9a, 9d, 9e, 9f. These events of bud closure occurred independently in multiple species within section *Aulomyrcia*; only subclades 9d, 9e, and the ancestor of *Myrcia aulomyrcioides*, *M. caudata*, *M. mcvaughii*, *M. aff montana* and *Marlierea* sp. (Harms 20) have an ancestral node with a closed bud (Fig. 2a). Species of *Myrcia* sects. *Calyptranthes* and *Sympodiomyrcia* can also possess closed buds, but these are morphologically distinct in other ways. *Myrcia* sect. *Calyptranthes* species have a closed bud with the calyx falling as a calyptra at anthesis, whereas section *Sympodiomyrcia* has species with closed buds and calyx lobes that tear regularly (Fig. 2a) at anthesis. The probability that the ancestor of section *Calyptranthes* had closed buds is 0.94, whereas the ancestor of section *Sympodiomyrcia* was likely to have had free calyx lobes (BPP 0.83). Closed buds are also found in *Myrcia* sect. *Eugeniopsis* where the calyx can be partially to completely fused (rarely free), tearing vertically through the calyx as in section *Aulomyrcia*. It is highly probable (BPP 0.97) that the ancestor of this clade had free calyx lobes.

A 2-locular ovary is the plesiomorphic character state for *Myrcia* (BPP 0.99). Independent shifts to 3 or more locular ovaries have occurred in *Myrcia* sects. *Calyptranthes*, *Gomidesia*, *Aguava*, *Reticulosae* and clade 10 (Fig. 2b). The most likely ancestral state of sections *Calyptranthes*, and *Gomidesia* is 2-locular (both BPP 0.99) with relatively common shifts to 3 or 4-locular species (Fig. 2b). Otherwise sections *Aguava*, *Reticulosae* and clade 10 appear to have had ancestors with 3-

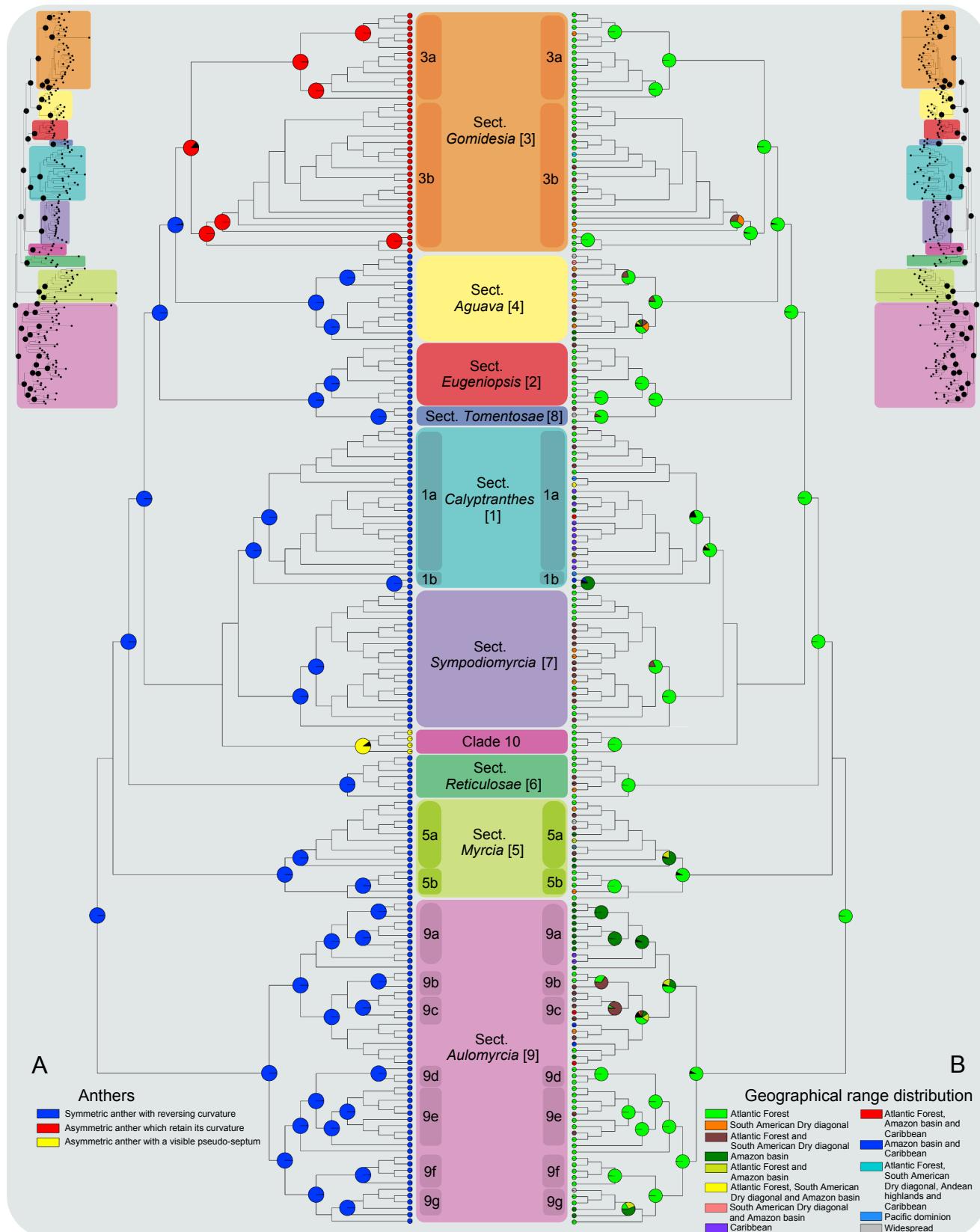


Fig. 3. Evolution of key morphological traits and Geographical range evolution in *Myrcia* and relatives, showing the most likely ancestral at all internal branches of the Bayesian Inference majority rule consensus tree from Fig. 1, inferred using Bayesian Binary MCMC. (A) Anthers. (B) Geographic range evolution. Pie charts for each node indicate probabilities of character states. Colours indicate the proportional likelihood of the states reconstructed for each node (see text). Only ancestral states of strongly-supported clades are shown.

locular ovaries (BPP 0.86, 0.93, and 0.82, respectively).

The symmetric anther with reversed curvature of the thecal wall on dehiscence is recovered as the ancestral state of *Myrcia* and all sections (BPP 0.99, each; Fig. 3a). The only variation to this is in the *Myrcia* sect. *Gomidesia* (BPP 0.86), where all species, to a lesser or greater extent, have asymmetric anthers in which the thecal walls retain curvature after dehiscence or have a visible septum (Fig. 8d), and clade 10 (BPP 0.89) in which anthers are also asymmetric with a visible pseudo-septum (Figs. 3a, 6a).

3.6. Evolution of morphological traits within *Myrcia* sect. *Gomidesia*

Two anther traits were used here: (1) proportion of thecal displacement and (2) presence or absence of glands (Fig. 7a–b). In species of the *Gomidesia* clade, the most common degree of thecal displacement is one quarter of the anther size (Fig. 8b). This character occurs in all subclades and is returned as the ancestral state of the clade (BPP 99%) and for all subclades proposed here (Cerqueiria, BPP 97%; Pubescens, BPP 93%; Springiana, BPP 99%; and Vittoriana, BPP 94%). Thecal displacement of one sixth to one eighth of total anther length occurs occasionally in Cerqueiria, Pubescens and Vittoriana subclades (Figs. 7a, 8c). *Gomidesia* clade species in which thecal displacement is one half of anther length, are found in most species of Pubescens sub-clade only; however, the ancestral state for thecal displacement in this clade is one quarter (Figs. 7a, 8a).

The presence of anther glands is recovered as the ancestral state of the *Gomidesia* clade (BPP 99%) and for all subclades proposed (Cerqueiria, Springiana and Vittoriana, BPP 99%, each; and Pubescens, BPP 95%; Fig. 7b). The absence of anther glands is restricted to a few lineages of Pubescens subclade and only *Myrcia brasiliensis* varies between both states.

The non-anther traits used was trichomes on abaxial leaf surface. The ancestral state of indument on the abaxial leaf surface of the *Gomidesia* clade is apressed trichomes (BPP 98%; Fig. 7c). This feature is also recovered for all subclades (Cerqueiria, BPP 91%; Springiana, BPP 93%; and Vittoriana, BPP 96%), except for Pubescens subclade, which is unresolved with states shared between apressed (BPP 37%)

and manicate (BPP 36%). Lineages with ascending to erect trichomes on the abaxial leaf surface evolved independently in the four subclades proposed. The state of manicate trichomes on the abaxial leaf surface occurred only in Pubescens subclade.

3.7. Geographical range evolution in *Myrcia*

The most likely ancestral area for *Myrcia* is the Atlantic Forest (BPP 0.98; Figs. 3b, 4). This pattern is shared by all *Myrcia* sections. *Myrcia* sects. *Eugenopsis* (BPP 0.99), *Gomidesia* (BPP 0.98), *Aguava* (BPP 0.82), *Reticulosae* (BPP 0.99), *Sympodiomyrcia* (BPP 0.98), and *Tomentosae* (BPP 0.92), appear to have subsequently and independently migrated from the Atlantic Forest to the Amazon basin (sect. *Aguava*), Cerrado (sects. *Eugenopsis*, *Gomidesia*, *Aguava*, *Reticulosae*, *Sympodiomyrcia* and *Tomentosae*), the Andean highlands and Yungas (sect. *Gomidesia*), or become widespread (sects. *Aguava*, *Myrcia* and *Tomentosae*). Although sections *Calyptranthes*, *Myrcia* and *Aulomyrcia* share the Atlantic Forest as their ancestor (BPP 0.82, 0.92, and 0.93, respectively), the Amazon basin and/or the Caribbean appears to be the most likely ancestral area of some of their main lineages. The main subclades of sect. *Calyptranthes* (1a and 1b) are inferred with the Atlantic Forest (BPP 0.81) and Amazon basin (BPP 0.84) as most likely ancestral areas, respectively. The most likely ancestral areas of subclades 5a and 5b of *Myrcia* sect. *Myrcia* have the Amazon basin (BPP 0.74) and Atlantic Forest (BPP 0.99) as their ancestors, respectively. The Amazon basin is the most likely ancestral area of subclade 9a plus its unplaced species (BPP 0.93), while the Atlantic Forest plus the Cerrado is the mostly likely ancestral area of subclades 9b (BPP 0.65) and 9c (BPP 0.91), respectively. The Atlantic Forest is the most likely ancestral area of subclades 9d, 9e, 9f (BPP 0.99, each), and the Amazon basin is the most likely ancestral area for subclade 9g (BPP 0.56). Clade 10 is composed entirely of Atlantic Forest species, where it originated (BPP 0.99).

3.8. Geographical range evolution in *Myrcia* sect. *Gomidesia*

The most likely ancestral recovered for the *Myrcia* sect. *Gomidesia* is the southern region of the Atlantic Forest (BPP 0.45; Fig. 7d). This same ancestral biome is recovered for clades 3b (BPP 0.62) and Cerqueiria clade (BPP 0.74; Fig. 7d). The ancestral of Pubescens subclade is unresolved with states shared between Caribbean (BPP 0.22) and Cerrado (BPP 0.22). This subclade apparently shifted into the highest number of different vegetation types with most of its lineages from southern Atlantic Forest, and others from southern Atlantic Forest plus Cerrado, endemic to Cerrado or widespread in Atlantic Forest. *Myrcia fenzliana* is the most widespread species, which in addition to the cited vegetation types also occurs in the savanna vegetations of South America, Lesser Antilles and West Indies. *Myrcia baritensis* is restricted to Yungas vegetation from northwestern Argentina and Bolivia. Cerqueiria subclade is also composed of Atlantic Forest species (Fig. 7d). The ancestor of clade 3a is the northern portion of the Atlantic Forest (BPP 0.76). The vegetation recovered for Springiana subclade is the northern Atlantic Forest (BPP 0.98), while the most likely vegetation of Vittoriana subclade is widespread in the Atlantic Forest (BPP 0.59; Fig. 7d).

4. Discussion

The phylogenetic results presented here corroborate the relationships within Myrteae proposed by previous phylogenetic studies (Lucas et al., 2007, 2011; Vasconcelos et al., 2017a), except for the *Blepharocalyx* group (*sensu* Vasconcelos et al., 2017a), composed of *B. egesii* and *B. salicifolius*, which is here recovered as paraphyletic. The whole genus *Blepharocalyx*, when also including *B. cruckshanskii* (placed in *Myrciogenia* group), is polyphyletic, a result already previously

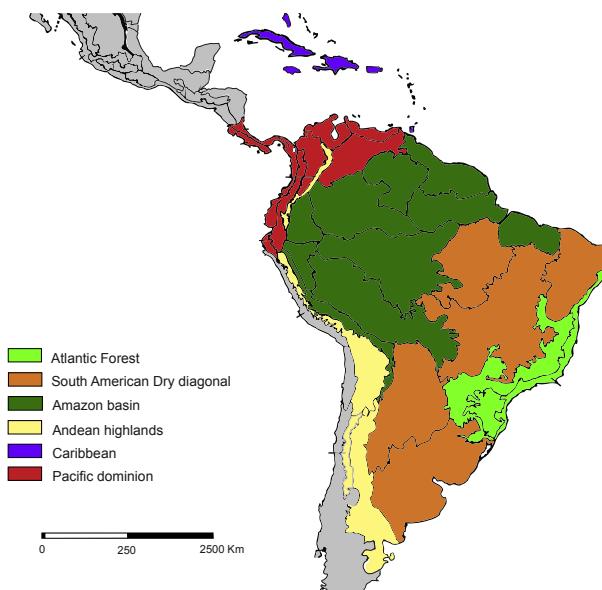


Fig. 4. Biogeographic areas used here for the analysis of geographical range evolution of *Myrcia* and relatives (based on Morrone, 2006, 2014).

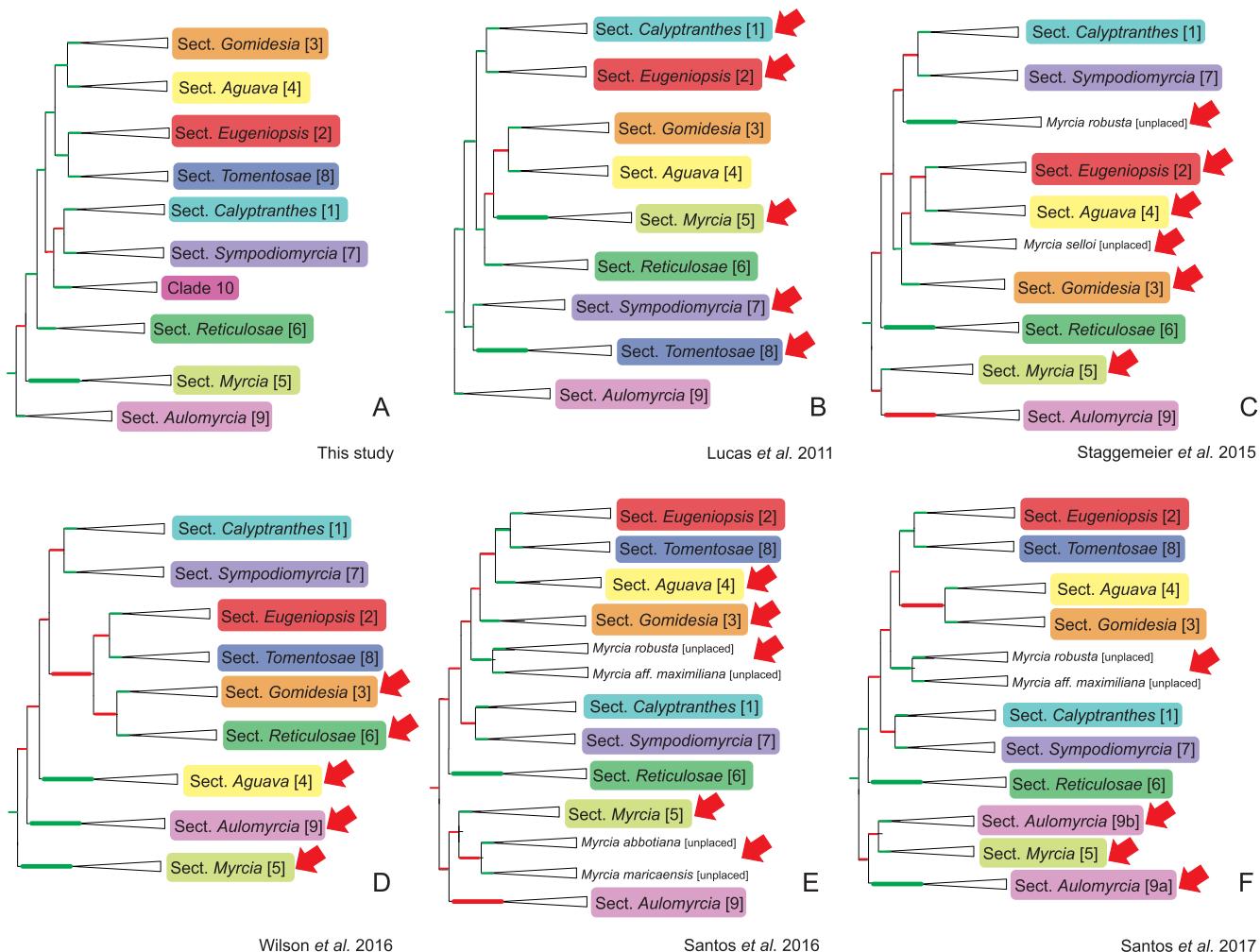


Fig. 5. Comparison of six published phylogenetic hypotheses for *Myrcia* based on nuclear and plastid sequences. Green branches indicate posterior probabilities (from BI) greater than 0.95 and/or bootstrap percentages (from ML) greater than 70. Red branches indicate poor supported phylogenetic relationships. Red arrows indicate the sections with most unstable positions in the phylogenetic relationships within *Myrcia*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recovered by studies cited above. Since we did not originally aim to test the monophyly of the Blepharocalyx group nor that of the genus *Blepharocalyx*, and our sampling is not sufficient to properly investigate it, we continue to adopt the circumscription of these groups as proposed by Vasconcelos et al. (2017a). The multi-locus analysis presented here strongly supports the PAM clade (*sensu* Vasconcelos et al., 2015) sister to Myrceugenia group.

The analyses presented there also confirm the monophyly of *Myrcia* and its nine sections (Lucas et al., 2011, 2018). Morphological trait reconstruction in *Myrcia* indicates that the floral characters of free calyx lobes, 2-locular ovaries, anthers with symmetrical thecae and reverse curvature are all ancestral states. *Myrcia* sects. *Aulomyrcia* and *Gomidesia* are recovered as monophyletic. The latter section has asymmetric anthers that retain their curvature after dehiscence, an apparently derived character. The Atlantic Forest is recovered as the most likely ancestral area of *Myrcia*, as well as all main lineages, with subsequent colonization of the Amazon basin, Cerrado, Andean highlands, and Caribbean. These frequent events of colonization across the Neotropics reflect a recent comparative analysis of plant and animal dispersals through time, showing the Atlantic Forest as the fourth major provider of Neotropical biodiversity (Antonelli et al., 2018).

4.1. Phylogenetic relationships within tribe Myrtleae

The monophyly of the Myrtleae group (*sensu* Lucas et al., 2007), including *Luma* A. Gray, sister to *Blepharocalyx cruckshanksii* (Hook. & Arn.) Nied. has been contested by previous phylogenetic studies (Murillo et al., 2012, 2013; Amorim, 2017) using a similar species sampling. Our results corroborate the monophyly of Myrtleae group, agreeing with other recent phylogenetic studies for the tribe (e.g. Vasconcelos et al., 2017a). Furthermore, the relationship between the PAM clade (*sensu* Vasconcelos et al., 2015) plus the Myrtleae group, receives strong statistical support. This corroborates their close relationship as inferred morphologically by similar stamen posture in the bud (Vasconcelos et al., 2015).

4.2. Phylogenetic relationships within *Myrcia*

The larger taxonomic sample and increased molecular data used produced higher statistical support between clades than previous phylogenetic studies (Staggemeier et al., 2015; Santos et al., 2016, 2017; Wilson et al., 2016), increasing our understanding of the infrageneric relationships in *Myrcia* (Fig. 5).

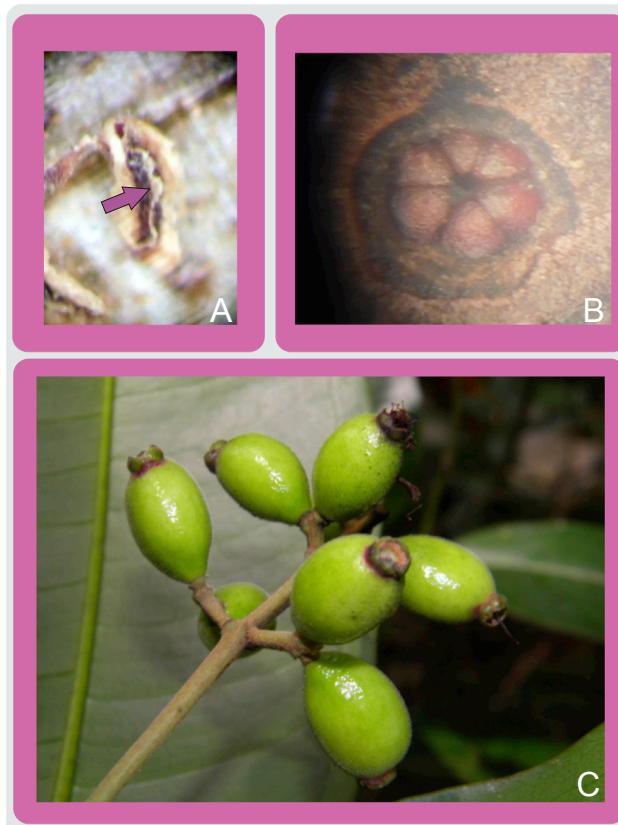


Fig. 6. Diagnostic features of Clade 10. (A) Detail of asymmetric anthers with a visible pseudo-septum (arrow); (B) Detail of 3-locular ovary with 2-ovules in each locule; (C) Fruits with distinct and imbricate calyx lobes and a glabrous staminal disc.

A tenth, previously undescribed clade is recognized and referred to here as ‘clade 10’ (Fig. 1b). The clade is composed of *M. maximiliana* O. Berg, *Myrcia pulvinata* B.S. Amorim, *M. robusta* Sobral and *Myrcia aff. unana* (voucher: B.S. Amorim 2024). All species are from a narrow region in the northern part of the Atlantic Forest. Other studies on *Myrcia* systematics additionally suggest that *Myrcia thomasi* B.S. Amorim & A.R. Lourenço belong in this clade (Lima, 2017). Previous studies concerning species implicated in clade 10 (Staggemeier et al., 2015, Fig. 5c; Santos et al., 2016, 2017, Figs. 5e, f) returned an unplaced *Myrcia robusta* and a clade composed of *M. maximiliana* and *M. robusta*, respectively (Fig. 5c, e, f), but never recognized as an entity in their own right. Clade 10 species share morphological features of large leaves, distinct and imbricate calyx lobes, a glabrous staminal disk, asymmetric anthers with a visible pseudo-septum (which do not divide the thecae in two parts) and a 3-locular ovary (Fig. 6; see anther septum of *Myrcia* sect. *Gomidesia*, which divide the thecae in two parts in Fig. 8d).

In the phylogenetic reconstruction of *Myrcia* presented here, section *Aulomyrcia* [9] is sister to the other *Myrcia* sections (Figs. 1, 5a) corroborating Lucas et al. (2011; Fig. 5b). The arrangement of the remaining sections resemble the topologies returned by Staggemeier et al. (2015; Fig. 5c) and Santos et al. (2016; Fig. 5e) except for *Myrcia* sect. *Myrcia*. Results presented here return sect. *Myrcia* as sister to all other sections except sect. *Reticulosae* [6] that is sister to all remaining clades. Within the clade of all other *Myrcia* clades, a weakly supported group comprises sections *Calyptranthes* [1], *Sympodiomyrcia* [7] and clade 10, sister to the rest. Sister to this lineage is the strongly supported

relationship between sections *Eugeniopsis* [2] plus *Tomentosae* [8], also returned by Santos et al. (2016, 2017). This clade is sister to a further strongly supported relationship between sections *Gomidesia* [3] and *Aguava* [4], never previously recovered with high support in previous phylogenetic hypothesis of *Myrcia* (Lucas et al., 2011; Staggemeier et al., 2015; Santos et al., 2016; Wilson et al., 2016; see Fig. 5b–f).

4.3. *Myrcia* sect. *Aulomyrcia* (O. Berg) Griseb.

Since the circumscription of *Myrcia* section *Aulomyrcia* [9] (Lucas et al., 2011, 2018), its monophyly has been questioned because of its low statistical support in some studies (Staggemeier et al., 2015; Santos et al., 2016, 2017; Wilson et al., 2016). Results presented here recover clade 9 as monophyletic with strong statistical support (Fig. 1a). Due to the inclusion of previously unplaced *Myrcia abbotiana* and *M. maricaensis* in this section and the unplaced species, the internal relationships of species within sect. *Aulomyrcia* (*sensu* Staggemeier et al., 2015) require re-examination.

4.4. *Myrcia* sect. *Gomidesia* (O. Berg) B.S. Amorim & E. Lucas

Myrcia section *Gomidesia* (Lucas et al., 2011, 2018) is predominantly composed of species previously described in the genus *Gomidesia* (*sensu* Berg, 1855–56). Lucas et al. (2011) highlighted the non-monophyly of this group after inclusion of *Myrcia mischophylla*, never before treated as *Gomidesia* (Berg, 1855–56, 1857; Legrand, 1958; NicLughadha, 1997). *Myrcia mischophylla* was published by Kjaerskou (1893), who did not accept *Gomidesia* as a distinct genus and treated it under *Myrcia*. Recently, a specimen with displaced anther thecae with evident septa was noted in *Myrcia mischophylla* (B.S. Amorim pers. observ.). The anther feature found in *Myrcia mischophylla* is not the most common in sect. *Gomidesia* species. This feature is only found in species which occur in the Cerrado, to where *M. mischophylla* is restricted (B.S. Amorim pers. observ.). Results presented here support the monophyly of the *Myrcia* sect. *Gomidesia* (or clade 3) and split it into two main lineages. A similar arrangement was found in Lucas et al. (2011), in which a lineage composed of *Myrcia spectabilis* and *M. vittoriana* was sister to the remaining *Gomidesia* clade species.

Within 3a clade of the *Myrcia* sect. *Gomidesia*, Springiana subclade is composed of two main lineages; *Myrcia grazielae*, *M. springiana* and *M. pendula*, are nested in a highly supported clade with species restricted to the North of the Atlantic Forest. The second group comprises *Myrcia lughadhae*, *M. rosangelae* and *M. serrana*. *Myrcia lughadhae* is restricted to *campos rupestres* (Cerrado vegetation) of northeastern Brazil (Amorim et al., 2014) with *Myrcia rosangelae* and *M. serrana* restricted to the North portion of the Atlantic Forest (Amorim and Alves, 2015; Amorim, 2017; Fig. 1b, 7d). The Vittoriana subclade is most composed of species from southern Atlantic Forest, but also has species exclusively from northern and wide distributed in Atlantic Forest. The 3b clade is composed of Pubescens subclade, the most species rich subclade represented by species from several geographic ranges such as the Atlantic Forest, Cerrado, Yungas, savanna vegetations of South America, the Lesser Antilles and West Indies (Fig. 1b, 7d). Cerqueiria subclade is composed of species restricted to the Atlantic Forest.

This strong evidence of geographical structuring found in *Gomidesia* clade species was already known for *Myrcia* s.l. (Staggemeier et al., 2015; Wilson et al., 2016), other neotropical tribe Myrtleae genera (Bünger et al., 2016; Murillo et al., 2012, 2016) and also in Myrtaceae (Michelangeli et al., 2013). It has been attributed to phylogenetic niche conservatism (Donoghue, 2008), which refers to the expectation that related species will tend to occupy the same sorts of environments (Harvey and Pagel, 1991). Even in *Myrcia* sect. *Gomidesia* species that shift to other geographic ranges (e.g. Pubescens and Springiana

subclades), they occur through similar forest habitats in open vegetation.

4.5. Evolution of morphological traits in *Myrcia*

Despite the evident homoplasy of those morphological characters relied on to distinguish the ten *Myrcia* clades discussed, the clades remain morphologically recognizable (Lucas et al., 2011, 2018; see discussion 4.2. for clade 10). Results presented here indicate that the ancestor of *Myrcia* possessed free calyx lobes and underwent independent shifts to a partial or complete closure of the bud. Staggemeier et al. (2015) and Vasconcelos et al. (2017b) proposed that the free calyx state was the ancestral condition in *Myrcia* sect. *Aulomyrcia*, as this is the state in lineages emerging from the deepest nodes and because most species possess this feature. Our results support the hypothesis of the ancestor of *Myrcia* sect. *Aulomyrcia* had free calyx lobes and suggest that this calyx feature is also ancestral for *Myrcia*, with independent shifts to bud closure (see results 3.5). Further description on different developmental modes of bud closure and how they relate to the phylogeny of *Myrcia* can be found in Vasconcelos et al. (2017b). Our results, with an extended sample, corroborate the conclusions found in the latter study.

The calyx is one of the most variable organs in the Myrtaceous flower, occurring in virtually every form from that of a completely closed calyx in bud to a free lobed calyx. Calyx morphology has been often used for taxonomic purposes (McVaugh, 1968), particularly to define generic limits (Landrum, 1984). Historically, multiple genera were described based entirely on the presence of fused calyx lobes (e.g. Britoa Berg (=Campomanesia), Calycorectes (=Eugenia), Calyptranthes (=Myrcia), Calyptrogenia (=Myrceugenia), Marlierea (=Myrcia) and Mitranches (=Myrcia; see McVaugh, 1968; Landrum, 1986; Lucas et al., 2011; Vasconcelos et al., 2017a)). However, recent molecular phylogenetic studies in tribe Myrtleae have demonstrated that in many cases genera that were described based only on the degree of closure of the calyx lobes are not natural groups (Lucas et al., 2011; Murillo et al., 2012; Mazine et al., 2014; Staggemeier et al., 2015; Santos et al., 2016; Wilson et al., 2016; Vasconcelos et al., 2017a).

Lucas et al. (2011) report the 3-locular ovary from sections *Gomidesia*, *Aguava* and *Reticulosae*, but that character state is here also reported from clade 10. All clades with this character state are strongly supported as distinct lineages (Fig. 2b), with ancestors of sections *Aguava*, *Reticulosae* and clade 10 sharing the 3-locular state. Within sections *Calyptranthes* and *Gomidesia*, cases of 3, 4 or 5-locular ovaries have been reported for some species (NicLughadha, 1997; Wilson, 2011; Vasconcelos et al., 2017a) although this is uncommon in ancestrally 2-locular groups in the family (McVaugh, 1968). The multi-locular ovary was hypothesized to be a primitive feature in tribe Myrtleae genus *Campomanesia*, *Myrceugenia* and *Psidium* demonstrating this state, and the 2-locular ovary was considered a specialized state (McVaugh, 1968). In *Myrcia*, the 2-locular ovary is the ancestral state thereby countering the pattern in tribe Myrtleae, with shifts to a 3, 4 or 5 locular ovary.

The typical symmetrical anther with reversing curvature during dehiscence is the most common anther state in *Myrcia* (Lucas et al., 2011) and is here recovered as the ancestral state for the genus. A combination of asymmetric anthers that retain curvature after dehiscence, and asymmetric anthers with visible pseudo-septa (see Figs. 6, 8 for more details), is recovered as the most likely ancestral combination of states for both the section *Gomidesia* and clade 10 and provide the character with which *Gomidesia* was distinguished as a separate genus by Berg (1855–1856). The shared possession of asymmetric anthers by section *Gomidesia* and by clade 10 species was the reason that species of clade 10 were mis-placed in sect. *Gomidesia* (Amorim and Alves, 2015).

The specialised asymmetric anther appears to be derived in *Myrcia* and are diagnostic for the two clades in which they occur. This anther feature is associated with buzz pollination (Nic Lughadha, 1997) and may represent an adaptation to specialist bees.

4.6. Evolution of morphological traits in *Myrcia* sect. *Gomidesia*

An infrageneric classification of the *Myrcia* sect. *Gomidesia* species was published by Legrand (1958) who proposed sections of the genus *Gomidesia* (*sensu* Berg 1955–1956) based on anther features. That morphology-based classification does not reflect the clades recovered in the phylogenetic hypothesis presented here, where all sections proposed by Legrand (1958) emerge as para- or polyphyletic (Fig. 9a). Legrand's section *Eytroteca* subsect. *Subaequales* is best represented in this study with species emerging in Springiana, Vittoriana and Pubescens subclades. Section *Eytroteca* subsect. *Oppositae* species were found only in Pubescens subclade (Fig. 9a). Section *Tetraspora* is represented by a single species, *Myrcia cerqueiria*, placed here in Cerqueiria subclade. Section *Platitecae* subsect. *Auriculatae* emerged in six separate lineages of Pubescens subclade while subsect. *Collaterales*, here represented by *M. brasiliensis* and *M. ilheosensis* are recovered in separate clades within Pubescens subclade (Fig. 6). *Myrcia pubescens* (Pubescens subclade) was also cited to sect. *Platitecae*, subsect. *Auriculatae*, and to sect. *Eytroteca* subsect. *Oppositae* (under the synonym *Gomidesia aubletiana* O. Berg).

An informal *Gomidesia* species grouping based on morphological similarity proposed by Nic Lughadha (1997) is a better fit to the molecular phylogenetic arrangement presented here. Nic Lughadha (1997) recognized nine morphological groups (Fig. 9b). Group 1 comprises large-leaved species from the Atlantic Forest with particularly long anthers with hidden septa. *Myrcia amplexicaulis*, *M. carvalhoi*, *M. crocea*, *M. grazielae*, *M. magnifolia*, *M. rosangelae*, *M. springiana*, and *M. vittoriana* belong to this group, forming the 3a clade (Fig. 9b), along with *M. espiritosantensis*, *M. lughadhae*, *M. pendula*, and *M. serrana* that were published later (Sobral, 2010; Amorim et al., 2014; Amorim and Alves, 2015, 2016). The morphological characters used by Nic Lughadha (1997) are useful to recognise group 1 species (*sensu* Nic Lughadha, 1997), however they can not be considered diagnostic for the 3a clade as they are also found in species from the 3b clade (e.g. *Myrcia cordifolia*, *M. grandifolia*, and *M. ruschii*). *Gomidesia* species placed in groups 2–9 (*sensu* Nic Lughadha (1997)) all emerge in the 3b clade (Fig. 9b). This clade includes the majority of species sampled here as well as high morphological variation and geographical range occurrence (Fig. 7a–d, 9b). Morphological characters exclusive to the 3b clade are aglandular anthers, thecae displacement comprising c. half of the total anther length and manicate trichomes on abaxial leaf surfaces (Fig. 7a–c). Species that occur in the Atlantic Forest and Cerrado (e.g. *Myrcia eriocalyx*, *M. montana* and *M. pubescens*) (Fig. 7d), endemic to Cerrado (e.g. *M. mischophylla* and *M. neospruceana*), endemic to Yungas (e.g. *M. baritensis*), and widely distributed in Atlantic Forest, Cerrado, and savanna biomes of South America, Lesser Antilles and West Indies (e.g. *M. fenzliana*), are also restricted to the 3b clade.

4.7. Geographical range evolution in *Myrcia*

Lucas et al. (2011) propose eastern South America as the ancestral area of *Myrcia*, a suggestion based on elevated species richness in the Cerrado and Atlantic Forest. In accordance to their proposal and corroborating the biogeographic studies of Santos et al. (2017), we recovered the most likely ancestral area of *Myrcia* in the Atlantic Forest. This region is also the likely ancestral area of all ten main *Myrcia* lineages.

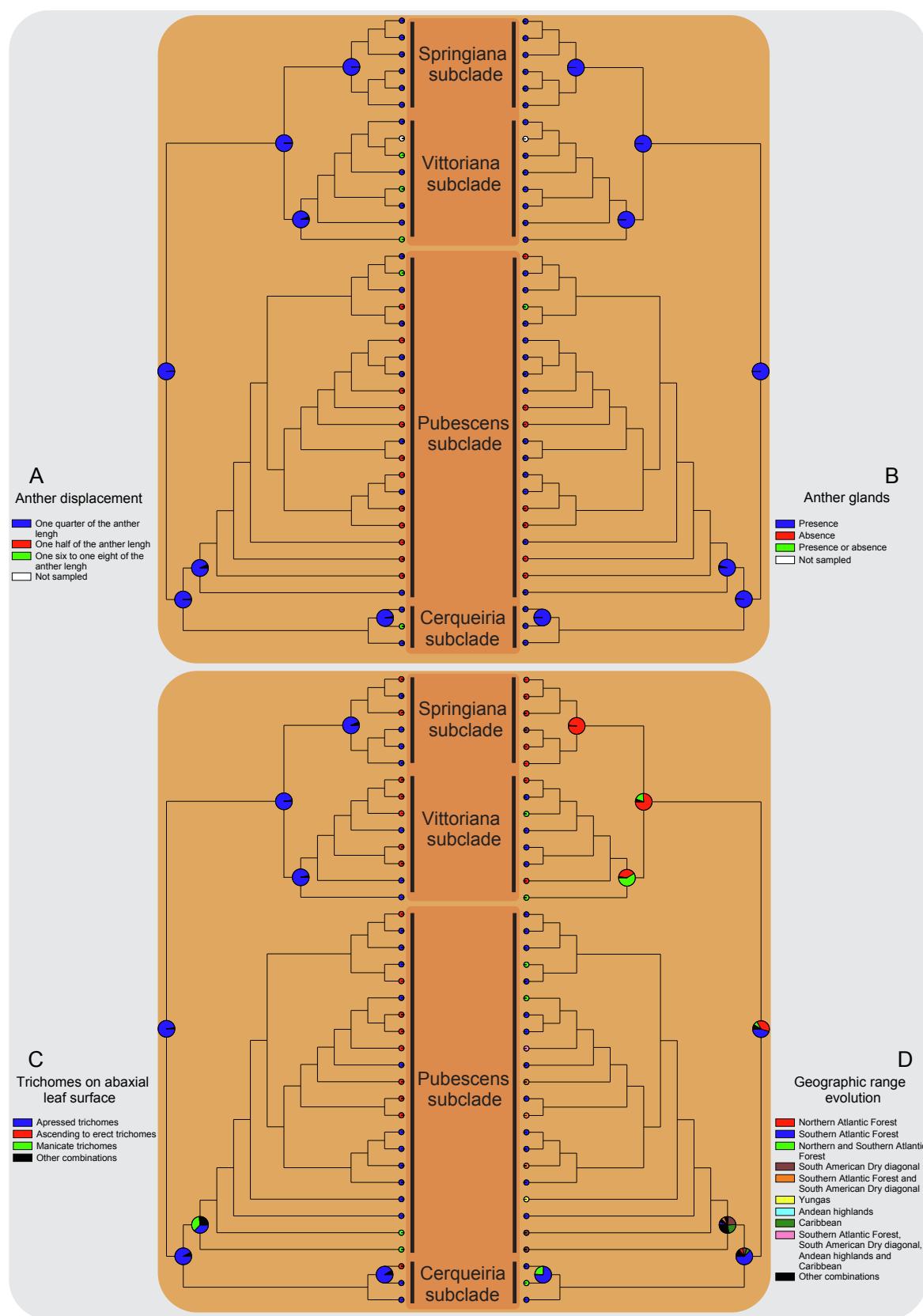


Fig. 7. Inference of *Myrcia* section *Gomidesia* (clade 3) ancestral reconstruction using BMM. (A) Anther displacement. (B) Anther glands. (C) Trichomes on abaxial leaf surface. (D) Geographic range evolution. Pie charts for each node indicate probabilities for each alternative ancestral character. Colors represented in the nodes indicate the proportional likelihood of the states reconstructed for each node (see text). Only the ancestors of the supported clades are shown.

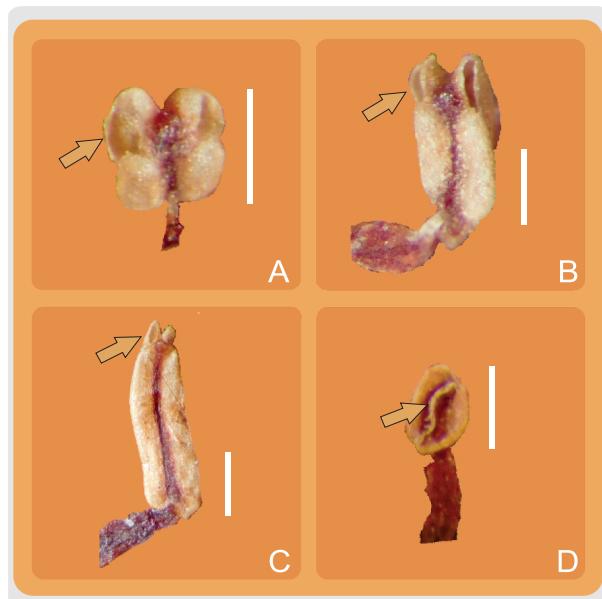


Fig. 8. *Myrcia* section *Gomidesia* (clade 3). A–C, Anther displacement; (A) one half of anther length (arrow); (B) one quarter of the anther length (arrow); (C) one sixth to one eighth of anther length (arrow). (D) Detail of the anther septum (arrow). Scale bar 0.5 mm long.

4.8. Atlantic Forest lineages

The Atlantic Forest has been recovered as most likely ancestral area for other species rich genera of neotropical Myrtaceae (e.g. *Eugenia*; Bünger et al., 2016). Stable areas in the Atlantic Forest appear to have acted as forest refuges for the family during Pleistocene glaciation, responsible for maintaining high species richness and endemism in these genera (Staggemeier et al., 2015; Bünger et al., 2016). The Atlantic Forest is one of the largest rainforest areas of the Americas, with highly heterogeneous environmental conditions due to its wide latitudinal and high altitudinal ranges, along with variation in rainfall (Galindo-Leal and Câmara, 2003). The Atlantic Forest is also incomparably rich in *Myrcia* species (264 species), followed by the Caribbean, Amazon basin (as circumscribed here) and Cerrado with 231, 228 and 93 spp., respectively (BFG, 2015; WCSP, 2017; *Myrcia* in Flora do Brasil 2020, in preparation). When considering species endemism to particular regions, the Atlantic Forest is the third richest in *Myrcia* species (ca. 80%), after the Caribbean and Amazon basin (ca. 93%, and 90%, respectively; WCSP, 2017).

Migration of *Myrcia* ancestral lineages towards northern South America is supported by evidence of colonization routes between the Atlantic Forest and Amazonia (inferred for birds and bromeliads; Batalha-Filho et al., 2013; Maciel et al., 2017). These routes cross southern portions of the Cerrado in Central-Western Brazil, through the Caatinga, or along the coastal areas of Northeastern Brazil. The connection route through southern portions of the Cerrado proposed by Batalha-Filho et al. (2013) existed during the main period of diversification of several *Myrcia* sections (e.g. *Calyptanthes*, *Myrcia* and *Aulomyrcia*), as well as Amazonian and Caribbean lineages that diversified during the Miocene (Staggemeier et al., 2015; Santos et al., 2017). It is therefore possible that *Myrcia* Atlantic Forest ancestors used this route to colonize the Amazon basin, reaching the southern fringe of the Caribbean.

The colonization of the Cerrado by *Myrcia* species is relatively recent, between 7.7 and 1.0 Mya (Santos et al., 2017). This period agrees

with earlier dates of Cerrado colonization by other Angiosperm families (Simon et al., 2009; Antonelli et al., 2010), in contrast with older Cerrado lineages reported for *Eugenia* (16.7–9.2 Mya; Bünger et al., 2016).

4.9. Caribbean lineages

The Caribbean is known to boast high species diversity in *Myrcia* (Wilson et al., 2016; WCSP, 2017). However, this area was not recovered as ancestral for any of the main lineages of *Myrcia*. The highest numbers of species and endemic species in this region are found in *Myrcia* sect. *Calyptanthes* (Sw.) A.R. Lourenço & E. Lucas (Acevedo-Rodríguez and Strong, 2017; WCSP, 2017; Lucas et al., 2018). The Caribbean subregion is recovered as most likely ancestral area of a weakly supported lineage within subclade 1a (Fig. 4b); independent colonization of this area occurred in sections *Gomidesia*, *Aguava*, *Myrcia*, *Tomentosae* and *Aulomyrcia* (see results Section 3.7). Thornhill et al. (2015) reported independent dispersal events of *Myrcia* sect. *Calyptanthes* and sect. *Myrcia* species from South to Central America in a period congruent with the closure of the Isthmus of Panama, starting in the Miocene (Montes et al., 2015; Bacon et al., 2015).

Santos et al. (2017) hypothesized that at the initial diversification of *Calyptanthes* (16.7–9.2 Mya), the Lesser Antilles and Isthmus of Panama had emerged allowing *Myrcia* species to use these routes to colonize the Caribbean. This is also hypothesized as possible migration routes by other angiosperm groups with probable origins in continental mainland (e.g. Santiago-Valentín and Olmstead, 2004; Hansen et al., 2006; Roncal et al., 2008; Bacon et al., 2013; Franck et al., 2013; Fine et al., 2014). This provides a scenario where island taxa gave rise to continental species also being possible (Roncal et al., 2008; Nieto-Blázquez et al. 2017; Antonelli et al., 2018).

4.10. Amazon basin lineages

The Amazon basin, as delimited for this study, has not been considered a main center of endemism of Myrtaceae (McVaugh, 1968, 1969). In contrast, it has played an important role in the diversification of *Myrcia*, by boasting high numbers of species and endemics (WCSP, 2017). The oldest lineage of *Myrcia* sect. *Aulomyrcia* is composed exclusively of species from the Amazonia, an area that was suggested as the area of origin of that section (Staggemeier et al., 2015). Our results do not corroborate this hypothesis. Mainly Amazonian lineages are found in sections *Myrcia* and *Aulomyrcia*, along with lineages in sects. *Calyptanthes* (e.g. *Calyptanthes speciosa* Sagot and *C. spruceana*), *Aguava* (e.g. *Myrcia cuprea* (O. Berg) Kiaersk. and *M. rotundata* (Amshoff) McVaugh), *Tomentosae* (e.g. *M. tomentosa*) and in sect. *Aulomyrcia* (e.g. *M. platyclada* and *M. grandis*). Subclade 9a of this section (*sensu* Staggemeier et al., 2015) appears to originate in the Amazonia and is also the lineage with most Amazonian species; only a lineage composed of Caribbean species is nested within it. The second main lineage is found in sect. *Myrcia*, which also has the Amazon basin inferred as its ancestral area, but unlike the previous case, this clade is composed of several lineages that reached the Caribbean (e.g. *Myrcia coumata*), Cerrado (e.g. *Myrcia suffruticosa*), Atlantic Forest and Cerrado (e.g. *Myrcia eriopus*, *M. eximia*, *M. microphylla*), Atlantic Forest (*Myrcia anceps* and *M. bracteata*) and the widespread *Myrcia splendens*. These two Amazonian clades are the oldest in *Myrcia* (Staggemeier et al., 2015; Santos et al., 2017) and their crown age coincides with a high diversification suggested during this period in Amazonian angiosperms (see Santos et al., 2017).

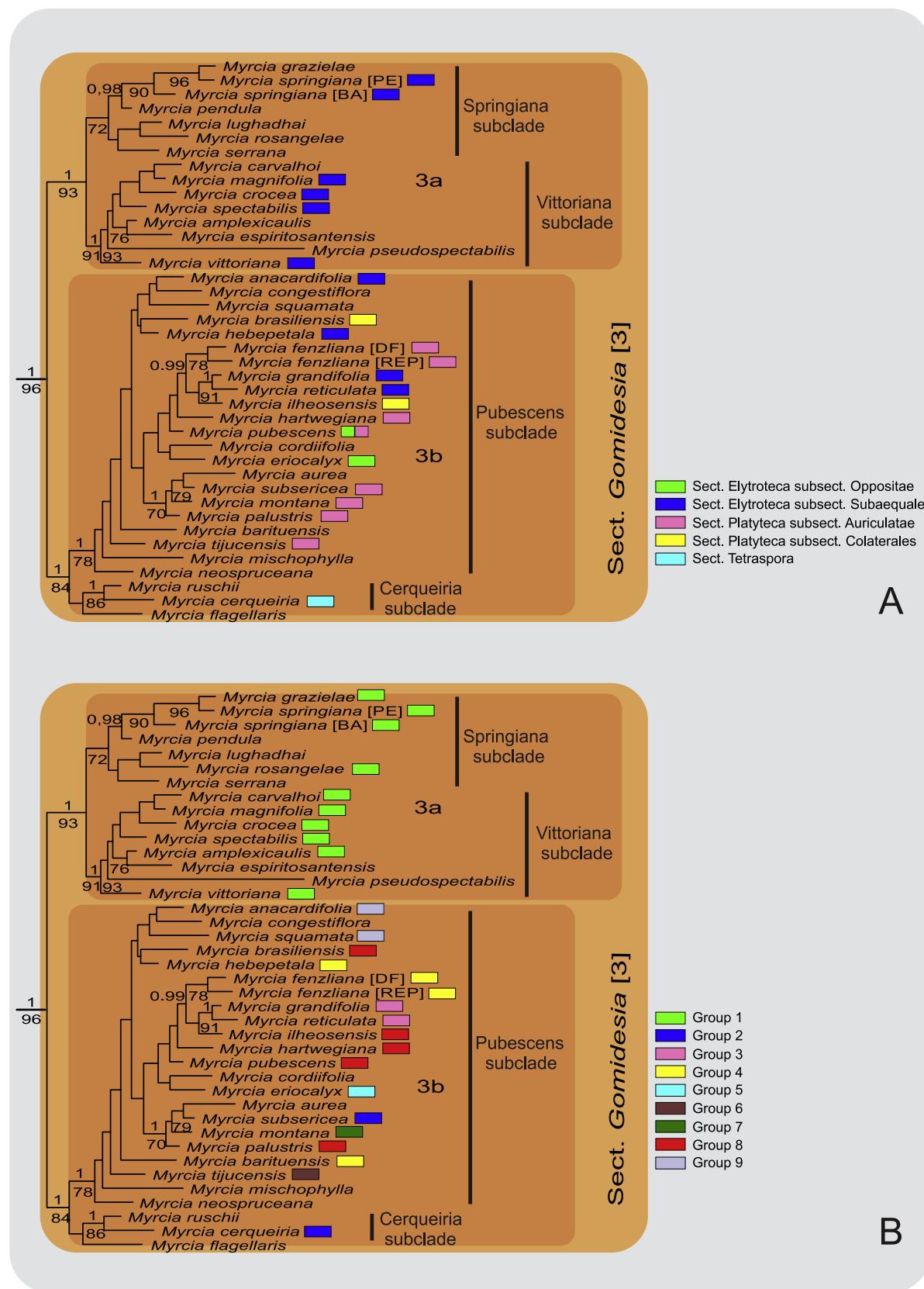


Fig. 9. *Myrcia* section *Gomidesia* (clade 3) Bayesian Inference (BI) majority rule consensus tree from analysis of the combined markers. (A) Infrageneric classification (Legrand, 1958) of the genus *Gomidesia* (*sensu* 1855–1856). (B) Informal classification (Lughadha, 1997) of the genus *Gomidesia* (*sensu* 1855–1856). Posterior probabilities (from BI analysis) greater than 0.95 are shown above branches; bootstrap percentages (from ML analysis) greater than 70 are shown below branches. PE = state of Pernambuco; BA = state of Bahia; DF = Federal District; REP = Dominican Republic. Springiana, Vittoriana, Pubescens and Cerqueiria clades are proposed here. Scale bar: substitutions per site.

4.11. Cerrado lineages

Based on the Cerrado diversity, high levels of endemism, and elevated human threats, the Cerrado is considered a global biodiversity “hotspot” and the most diverse tropical savanna in the world (Myers, 2003). Despite the presence of a relatively large number of *Myrcia* species, of which almost half are endemic (BFG, 2015), the Cerrado appears not to have played a major role in the evolution of *Myrcia* (Santos et al., 2017). Independent Cerrado colonizations were recovered in most main lineages of *Myrcia* (except clade 10, comprised only of Atlantic Forest species; see Results 3.7). Similarly, multiple, independent lineages of Cerrado species with ancestral areas in wet forests are also found in other Myrtaceae genera (e.g. *Eugenia* sect. *Phyllocalyx* and *E.* sect. *Speciosae*; Bünger et al., 2016 and *Myrceugenia*; Murillo et al., 2016), and other angiosperm families (Simon et al., 2009; Simon and Pennington, 2012), supporting a general pattern of shifts from forest to savanna vegetation (Crisp et al., 2009; Antonelli et al., 2018).

Despite its high endemism, the Cerrado shares more than 40% of its species with the Atlantic Forest (Françoso et al. 2016), suggesting bi-directional exchange of floristic elements between these vegetations after the origin of the Cerrado (Forni-Martins and Martins, 2000). Contrary to this hypothesis, all *Myrcia* species found in both the Cerrado and the Atlantic Forest (sects. *Calyptranthes*, *Eugeniopsis*, *Gomidesia*, *Aguava*, *Reticulosae*, *Sympodiomyrcia*, *Tomentosae*, and *Aulomyrcia*) or endemic to Cerrado (e.g. sects. *Gomidesia*, *Aguava*, *Sympodiomyrcia*, and *Aulomyrcia*) have the Atlantic Forest as their most probable ancestral area; no opposite migration was recovered in our analysis. A further pattern is found in sect. *Myrcia*, where species moved to the Cerrado and Atlantic Forest from the Amazonia occurred (e.g. *Myrcia eriopus* DC., *M. microphylla* O. Berg and *M. suffruticosa* O. Berg).

The proportion of Cerrado species shared with the Atlantic Forest is known to be three times higher than the proportion shared with the Amazonia (Françoso et al., 2016). This is corroborated by our data, in which except for the widely distributed *Myrcia amazonica*, *M. guianensis*, *M. laruotteana*, *M. multiflora*, *M. splendens* and *M. tomentosa*, only *Myrcia stricta* (O. Berg) Kiaersk. (sect. *Aguava*) occurs in both areas (based on our sampled species). This scenario also reflects the distribution pattern of *Myrcia*, in which only 12% of Cerrado species are shared with the Amazonia, while 46% are shared with the Atlantic Forest (BFG, 2015).

4.12. Geographical range evolution in *Myrcia* sect. *Gomidesia*

The Atlantic Forest is a center of species diversity for *Myrcia* s.l. (Murray-Smith et al., 2009; Lucas et al., 2011) and the ancestor of the genus (Santos et al., 2017). A majority of *Gomidesia* clade species occur in the Atlantic Forest (BFG, 2015; Amorim, 2017), and due to the importance of this area, it was subdivided allowing the part of the Atlantic Forest from which the ancestral lineages of the sect. *Gomidesia* originated to be identified. The ancestral region of the section *Gomidesia* is the southern Atlantic Forest, corroborating the hypothesis of Santos et al. (2017). This region is the richest in sect. *Gomidesia* species and has the highest number of endemics (BFG, 2015; Amorim, 2017). From the southern Atlantic Forest, multiple lineages reached the northern Atlantic Forest, in which Springiana subclade species, along with *Myrcia cavalhoi* and *M. pseudospectabilis* (Vittoriana subclade) are restricted (Fig. 7d). Most shifts to Cerrado (e.g. *M. eriocalyx*, *M. montana*, *M. mischophylla* and *M. pubescens*), Yungas (e.g. *M. baritensis*), and savanna vegetation of South America, Lesser Antilles and West Indies

(e.g. *M. fenziana*), have their ancestors in the southern Atlantic Forest (e.g. Pubescens subclade; Fig. 5b). This pattern is in accordance with the general distribution pattern of *Myrcia* s.l. species (Santos et al., 2017) and agrees with the tendency of neotropical tribe Myrtleae from Savanna having their ancestors in forest areas, which independently colonized open area vegetation (Bünger et al., 2016; Murillo et al., 2016; discussion 4.11). The exception is *M. lughadhae* (Springiana subclade), which is endemic to Cerrado and has its ancestral in northern Atlantic Forest. Within section *Gomidesia*, a strong evidence of geographical structuring was found. This same pattern is also found in *Myrcia* s.l. and other neotropical tribe Myrtleae genera (Murillo et al., 2012, 2016; Staggemeier et al., 2015; Bünger et al., 2016; Wilson et al., 2016; see discussion 4.4).

5. Conclusions

The multilocus analysis presented here strongly supports the phylogenetic placement of the *Myrceugenia* group as sister to the *Myrcia* and *Plinia* groups. Our inclusion of previously available molecular data with novel sequences of *Myrcia* and relatives significantly improved our phylogenetic estimates as compared to previous studies. The biogeographic analysis performed indicate a major role of the Atlantic Forest for the diversification of the group, from which multiple transitions took place to other Neotropical regions, in particular from forests to savannas. Further studies could make use of a more thorough genome sampling as well as aim for complete species level sampling in the *Myrcia* group. Particularly desirable foci for further investigation are the phylogenetic relationships within Clade 10. It would also be important to further study the morphological and geographical range evolution within the poorly sampled sections *Aguava*, *Myrcia*, *Reticulosae* and *Tomentosae*.

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Appendix A

Sample list, collection localities and GenBank accession numbers for the species used in the phylogenetic analysis. Blank spaces represent missing data. Asterisks (*) indicate the new sequences generated in this study.

| Species | Voucher | Collection locality | ITS | <i>matK</i> | <i>ndhF</i> | <i>psbA-tmH</i> | <i>rpl16</i> | <i>rpl32-trnL</i> | <i>rps16-trnQ</i> | <i>trnL-trnF</i> |
|--|--------------------|-------------------------|----------|-------------|-------------|-----------------|--------------|-------------------|-------------------|------------------|
| <i>Accra elegans</i> (DC.) Landrum | Vasconcelos 485 | Brazil (Minas Gerais) | MF954013 | MF954518 | MF954431 | MF954309 | MF954197 | KP722283 | JN091320 | |
| <i>Algizria macrochlamys</i> (DC.) Proença & NicLugh. | Giulietti 1648 | Brazil (Bahia) | AM489890 | AM234126 | MF954432 | AM489809 | MF954310 | MF954198 | MF954078 | |
| <i>Algizria minor</i> Sobral, Faría & Proença | Faria 4157 | Brazil (Bahia) | MF954014 | AM234070 | MF954433 | MF954272 | MF954311 | MF954199 | JN661055a | |
| <i>Blepharocalyx cruckshanksii</i> (Hook. & Arn.) Nied. in H.G.A.E.-ngler & K.A. E. Prantl | Murillo 4219 | Edinburgh (cultivated) | | | MF954437 | AM489814 | JN660956a | JN661055a | | |
| <i>Blepharocalyx eggersii</i> (Kiersk.) Landrum | Vasconcelos 458 | Brazil (Bahia) | MF954017 | MF954519 | MF954438 | MF954274 | MF954313 | MF954202 | MF954081 | |
| <i>Blepharocalyx salicifolius</i> (Kunth) O. Berg [1] | Lucas 78 | Brazil (São Paulo) | AM234084 | AM489979 | MF954440 | AM489815 | JN660984 | JN661133 | MF954139 | |
| <i>Blepharocalyx salicifolius</i> (Kunth) O. Berg [2] | Vasconcelos 482 | Brazil (Minas Gerais) | MF954314 | MF954520 | MF954439 | MF954275 | MF954314 | MF954082 | MF954138 | |
| <i>Calycopus goetheanus</i> (Mart. ex DC.) O. Berh | Vasconcelos 332 | Brazil (Amazonas) | MF954019 | MF954521 | MF954441 | MF954276 | MF954315 | MF954203 | MF954083 | |
| <i>Calycopus moritzianus</i> (O.Berg) Burret | (all from GenBank) | Colombia | KU945986 | KU945991 | KU945999 | | | | MF954140 | |
| <i>Calyptranthes Barkeri</i> Elmán & Urb. | Lucas 1116 | Dominican Republic | KU164811 | | | KU164837 | | KU171284 | KU164862 | |
| <i>Calyptranthes bipinnis</i> O. Berg | Holst 8054 | Ecuador | KU164817 | | | KU164843 | | KU164868 | KU164856 | |
| <i>Calyptranthes brasiliensis</i> Spreng. | Lucas 930 | Brazil (Espírito Santo) | MF954020 | | MF954443 | MF954278 | | | | |
| <i>Calyptranthes clasifolia</i> O. Berg | Lucas 253 | Brazil | JN091251 | JN091200 | AM489980 | KP722454 | JN091391 | JK182467* | KP722231 | |
| <i>Calyptranthes concinna</i> DC. | Lucas 74 | Brazil | AM489898 | AM234103 | KU164809 | KU164835 | KU164835 | KU171282 | KU164860 | |
| <i>Calyptranthes eriocephala</i> Urb. | Araujo 1803 | Dominican Republic | | KU164798 | | KU164824 | | | KU164849 | |
| <i>Calyptranthes fasciculata</i> O. Berg | Bhiki 285 | Suriname | | KU164812 | | KU164838 | | KU171285 | KU164863 | |
| <i>Calyptranthes garciae</i> Alain & M. M. Mejía | Araujo 1802 | Dominican Republic | | | | | | | | |
| Species | Voucher | Collection locality | ITS | <i>matK</i> | <i>ndhF</i> | <i>psbA-tmH</i> | <i>rpl16</i> | <i>rpl32-trnL</i> | <i>rps16-trnQ</i> | <i>trnL-trnF</i> |
| <i>Calyptranthes grandifolia</i> O. Berg, | Lucas 122 | Brazil (Paraná) | JN091252 | JN091201 | JN091302 | JN091392 | JK182468* | KU188502 | JN091322 | |
| <i>Calyptranthes hirsutibachii</i> D. Legrand | Lucas 171 | Brazil (Parana) | KU164801 | | KU164827 | KU164827 | KU171278. | KU164852 | JN091323 | |
| <i>Calyptranthes kierskovi</i> Krug & Urb. | Pollard 1194 | British Virgin Islands | AM489900 | AM234105 | AM489981 | AM489819 | KU164830 | KU171279. | KU164855 | |
| <i>Calyptranthes laevigata</i> Urb. & Ekman | Araujo 1793 | Dominican Republic | KU164804 | | | | | KU171279. | | |
| <i>Calyptranthes lanceolata</i> O. Berg, | Lucas 84 | Brazil (Bahia) | AM489899 | AM234104 | KU164816 | KU164842 | JK182469* | KU171288 | KU164866 | |
| <i>Calyptranthes lindeniana</i> O. Berg | Harley 54,077 | Brazil (Bahia) | | | | | | | | |
| <i>Calyptranthes longicalyptrata</i> B. Holst & M.I. Kawas. | Vasconcelos 523 | Costa Rica | | | | | | | | |
| <i>Calyptranthes lucida</i> Mart. ex DC. | Sasaki 2448 | Brazil (Mato Grosso) | KU164815 | | | | | | | |
| <i>Calyptranthes pallens</i> Griseb. | Vasconcelos 534 | Costa Rica | MF954021 | AF368201 | MF954445 | MF954279 | MF954319 | | | |
| <i>Calyptranthes pulchella</i> DC. | Zappi 2496 | Brazil (Minas Gerais) | KU164808 | | KU164834 | | | KU171281 | KU164859 | |
| <i>Calyptranthes restitae</i> Sobral | Lucas 990 | Brazil (Bahia) | KU164813 | | KU164839 | | | KU171286 | KU164864 | |
| <i>Calyptranthes sintenisii</i> Kiersk. | Araujo 1785 | Dominican Republic | KU164810 | | KU164836 | | | KU171283 | KU164861 | |
| <i>Calyptranthes speciosa</i> Sagot | Holst 9399 | Frech Guiana | KU164818 | | KU164844 | | | KU171289 | KU164869 | |
| <i>Calyptranthes spruceana</i> O. Berg | Araujo 1874 | Brazil (Rondônia) | KU164799 | | KU164825 | | | KU171277 | KU164850 | |
| <i>Calyptranthes thomasiana</i> O. Berg. | Pollard 1195 | British Virgin Islands | AM489901 | AM234106 | KP722434 | AM489820 | | KP722211 | JN091325 | |
| <i>Calyptranthes weddigeniana</i> O. Berg | Lucas 467 | Brazil (São Paulo) | KU164806 | | KU164832 | | | | KU164857 | |
| <i>Changua schippii</i> (Standl.) Landrum | Aguilar 9833 | Costa Rica | MF954523 | MF954451 | MF954285 | MF954325 | MF954211 | MF954091 | MF954149 | |
| Species | Voucher | Collection locality | ITS | <i>matK</i> | <i>ndhF</i> | <i>psbA-tmH</i> | <i>rpl16</i> | <i>rpl32-trnL</i> | <i>rps16-trnQ</i> | <i>trnL-trnF</i> |
| <i>Eucalyptus teretiformis</i> (R. Br.) Muell. | Udovicic 177 | Australia | AM489906 | AF190364 | AF190381 | | | | | |
| <i>Luma apiculata</i> (DC.) Burret | Murillo 4205 | Chile | JN660860 | JN660910 | JN661009 | AM489995 | JN660959 | JN661108 | | |
| <i>Luma apiculata</i> (DC.) Burret [T] | Lucas 208 | RBG Kew (cultivated) | | | | | | KP722209 | KP722231 | |
| <i>Luma chequen</i> (Molina) A. Gray | Landrum 7873 | Chile | JN660861 | JN660911 | JN661010 | KU898344 | AM489844 | | | |
| <i>Marlierea clausentiana</i> (O. Berg) Kiersk. | Matsumoto 752 | Brazil (Minas Gerais) | JN091202 | AM234107 | AM489996 | KP722429 | JN091393 | KU88504 | JN091326 | |
| <i>Myrcia euonymoides</i> (D. Legrand & Kausel) Mazine | Lucas 61 | Brazil (São Paulo) | JN091255 | JN091204 | KP722451 | JN091395 | JK182468* | KP722205 | JN091327 | |
| <i>Marlierea glazioviana</i> Kiersk. | Matsumoto 799 | Brazil (São Paulo) | | | | | | KP722275 | JN091329 | |
| <i>Marlierea rubiginosa</i> (Cambess.) D. Legrand | Santos 600 | Brazil (Minas Gerais) | | | | | | KU898507 | KU898451 | |

| | | | | | | | |
|--|---------------------------|----------------------------|-----------|-----------|-----------|-----------|-----------|
| <i>Marietea aff. subacuminata</i> Kiersch. | | | KD722397 | KD722305 | KD722475 | KD722252 | KD722355 |
| <i>Marietea teuscheriana</i> (O. Berg.) D. Legrand | Brazil (Espírito Santo) | Brazil (Minas Gerais) | KU898332 | KU898390 | KU898440 | KP722280 | KU898495 |
| <i>Miranthes clarendonensis</i> (Proctor) Proctor | Jamaica | Jamaica | MF954049 | MF954307 | MF954352 | MF954110 | MF954170 |
| <i>Miranthes glabra</i> DC. | Brazil (Minas Gerais) | Brazil (Minas Gerais) | AM234098 | MF954308 | MF954353 | MF954111 | MF954171 |
| <i>Myrcengetia campestris</i> (DC.) Landrum | Brazil (Distrito Federal) | Brazil (São Paulo) | MF954052 | JN660991 | KP722441 | JN661040 | KP722376 |
| <i>Myrcengetia brevipedicellata</i> (Burret) D. Legrand & Kausel | Landrum 2830 | Brazil (Paraná) | JN660844 | JN660993 | JN660943 | JN661042 | JN661092 |
| <i>Myrcengetia campestris</i> (DC.) D. Legrand & Kausel Species | Kummirow 2940 | Collection locality | JN660845 | JN660994 | JN660944 | JN661043 | JN661093 |
| <i>Myrcengetia euosma</i> (O. Berg) D. Legrand | Voucher | ITS | ndhf | psbA-trnH | rp16 | rp32-trnL | rp32-trnF |
| <i>Myrcengetia exsucca</i> (DC.) O. Berg | Murilo 4217 | Brazil (São Paulo) | JN660850 | JN660999 | JN660945 | JN661044 | JN661094 |
| <i>Myrcengetia franciscensis</i> (O. Berg) Landrum | Miyagi 357 | Brazil (São Paulo) | JN660852 | JN660902 | JN660996 | JN661045 | JN661095 |
| <i>Myrcengetia gertii</i> Landrum | Barbosa 948 | Brazil (São Paulo) | JN660854 | JN660904 | JN661003 | JN660953 | JN661052 |
| <i>Myrcengetia glaucescens</i> (Cambess.) D. Legrand & Kausel | Landrum 11.231 | Brazil | JN660855 | JN660905 | JN661004 | JN660954 | JN661053 |
| <i>Myrcengetia klemii</i> D. Legrand | Cordeiro 734 | Brazil (São Paulo) | JN660856 | JN660906 | JN661005 | JN660955 | JN661054 |
| <i>Myrcengetia lanceolata</i> (Juss. Ex J. St.-Hil.) Kausel | Mihoc 6220 | Brazil | JN660858 | JN660908 | JN661007 | AM48949 | JN661056 |
| <i>Myrcengetia leptospermoidea</i> (DC.) Kausel | Murilo 4214 | Chile | JN660859 | JN660909 | JN661008 | AM489850 | JN660958 |
| <i>Myrcengetia miersiana</i> (Gardner) D. Legrand & Kausel | Lucas 164 | Brazil (Paraná) | JN660862 | JN660912 | JN661011 | JN660961 | JN661060 |
| <i>Myrcengetia myrtoides</i> (Cambess.) O. Berg | Lucas 503 | Brazil (Rio de Janeiro) | JN660865 | JN660915 | JN661014 | JN660953 | JN661103 |
| <i>Myrcengetia myrtoides</i> O. Berg | Rossato 47 | Brazil (Rio Grande do Sul) | JN660919 | JN660869 | JN661018 | JN660968 | JN661113 |
| <i>Myrcengetia obtusa</i> (DC.) O. Berg | Brownless 1227 | Chile | JN660866 | JN660916 | JN661015 | JN660965 | JN661114 |
| <i>Myrcengetia ovalifolia</i> (O. Berg) Landrum Species | Lucas 259 | Collection locality | JN660867 | JN660917 | JN661016 | ndhf | JN661065 |
| <i>Myrcengetia ovata</i> (Hook. & Arn.) O. Berg | Voucher | ITS | matK | psbA-trnH | rp16 | rp32-trnL | rp32-trnF |
| <i>Myrcengetia oxysepala</i> (Burret) D. Legrand & Kausel | Gardner 19 | Chile | AM489935 | AM234096 | JN661022 | KU898334 | KU898442 |
| <i>Myrcengetia parvifolia</i> (DC.) Kausel | Ribas 2234 | Brazil (Paraná) | JN660873 | JN660923 | JN661023 | AM489852 | JN660971 |
| <i>Myrcengetia pilanthia</i> (Kiersch.) Landrum | Landrum 5916 | Chile | JN660924 | JN660974 | JN661024 | JN660973 | JN661120 |
| <i>Myrcengetia planipes</i> (Hook. & Arn.) O. Berg | Lucas 230 | Brazil | JN660875 | JN660925 | JN661025 | JN660974 | JN661123 |
| <i>Myrcengetia reitzii</i> D. Legrand & Kausel | Gardner 164 | Chile | JN660877 | JN660927 | JN661026 | JN660976 | JN661125 |
| <i>Myrcengetia rufa</i> (Colla) Skottsberg | Aedo 7378 | Chile | JN660878 | JN660928 | JN661027 | MF954486 | JN660977 |
| <i>Myrcengetia rufescens</i> (DC.) D. Legrand & Kausel | Barbosa 945 | Brazil (São Paulo) | JN660937 | JN660987 | JN661036 | MF954390 | JN660986 |
| <i>Myrcengetia schulzei</i> Johow | Tellier 150,795 | Chile | JN660879 | JN660929 | JN661028 | JN660973 | JN661121 |
| <i>Myrcengetia serotaromosa</i> (Kiersch.) D. Legrand & Kausel | Lucas 469 | Brazil (São Paulo) | JN660880 | JN660930 | JN661029 | JN660974 | JN661122 |
| <i>Myrcengetia smithii</i> Landrum | Ruiz 8266 | Juan Fernández | JN660888 | JN660938 | JN661031 | JN660981 | JN661080 |
| <i>Myrcia abbotiana</i> (Ur.) Alain | Silva 2358 | Brazil (Paraná) | JN660882 | JN660932 | JN661030 | JN660980 | JN661129 |
| <i>Myrcia amplexicaulis</i> (O. Berg) Hook. f. | Garcia 533 | Brazilian Republic | JN660881 | KU898328 | KU898386 | MF954357 | KU898544 |
| <i>Myrcia amplexicaulis</i> (O. Berg) Hook. f. | Lucas 1108 | Brazil (Paraná) | JN091263 | JN091212 | KP722437 | JN091403 | JN091337 |
| <i>Myrcia antonina</i> DC. | Neto 3007 | Brazil (Mato Grosso) | KP722417 | KP722495 | KP722325 | KP722272 | KP722375 |
| <i>Myrcia antonina</i> DC. | Amorim 1940 | Brazil (Espírito Santo) | MH880933* | JN091212 | KP722419 | MK157002* | MK182476* |
| <i>Myrcia antonina</i> DC. | Nadruz 999 | Brazil (Rio de Janeiro) | JN091267 | JN091212 | JN091407 | MK175003* | MK182477* |
| <i>Myrcia antonina</i> DC. | Voucher | Collection locality | JN091268 | JN091217 | ndhf | psbA-trnH | rp32-trnL |
| <i>Myrcia antonina</i> DC. | Lucas 236 | Brazil (São Paulo) | KU898301 | KU898358 | JN091408 | MK175004* | MK182478* |
| <i>Myrcia ascendens</i> M.F.Santos | Santos 840 | Brazil (Bahia) | KU898300 | KU898357 | KU898405 | KP722277 | KU898460 |
| <i>Myrcia aulomyrtoides</i> E.Lucas & C.E.Wilson | Santos 829 | Brazil (Rondônia) | KU164807 | KU164833 | KU898404 | KU171280 | KU164859 |
| <i>Myrcia aurea</i> Niclugh. | Araujo 1885 | Brazil (Espírito Santo) | MH880934* | MK157093* | MK157005* | MK202486* | MK202487* |
| <i>Myrcia baritiensis</i> (Legname) B. Holst. | Serrano 5327 | Argentina | MH880935* | MK175094* | MK175006* | MK182479* | MK202487* |

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|---|---------------------------|---------------------------|-----------|------------------|-----------------------|---------------------|
| <i>Myrcia aff. bergiana</i> O. Berg | Brazil (Ceará) | MH880929* | KU898418 | MK174996* | MK182471* | MK202482* |
| <i>Myrcia bicarinata</i> (O. Berg) D. Legrand | Brazil (São Paulo) | KU898313 | KU898370 | KU898528 | KU898473 | |
| <i>Myrcia bicolor</i> Kiersk. | Brazil (Rio de Janeiro) | KU898331 | KU898439 | KU898546 | KU898494 | |
| <i>Myrcia blanchetiana</i> (O. Berg) Mattos | Brazil (Bahia) | KU898321 | KU898379 | KU898428 | KU898538 | KU898483 |
| <i>Myrcia bracteata</i> (Rich.) DC. | French Guyana | JN091269 | JN091218 | JN091409 | JN091344 | |
| <i>Myrcia brasiliensis</i> Kiersk. | Brazil (São Paulo) | AM489917 | AM234112 | AM489935 | MK175007* | MK202488* |
| <i>Myrcia calyptanthoides</i> (O. Berg) Mattos | Brazil (Bahia) | KU898310 | KU898367 | KU898415 | KU898470 | JN091345 |
| <i>Myrcia carvalhoi</i> Niclugh. | Brazil (Bahia) | MH880936* | | MK157095* | MK182481* | MK202489* |
| <i>Myrcia caudata</i> (McVaugh) E. Lucas & C.E. Wilson | Brazil (Mato Grosso) | KU164819 | KU164845 | KU164845 | KP722232 | KU164870 |
| <i>Myrcia cerqueira</i> (Nied.) E. Lucas & Sobral | Brazil (Espírito Santo) | MH880937* | | MK157096* | MK182482* | MK202490* |
| <i>Myrcia clavigia</i> Sobral | Brazil | JN091271 | JN091220 | KD722442 | JN091411 | KP722217 |
| Species | Collection locality | ITS | matK | psBA-tmH ndhF | tpL16 MK157097* | KP722332 tmL-tmF |
| <i>Myrcia congestiflora</i> Caliari & V.C. Souza | Brazil (São Paulo) | MH880938* | | MK157098* | MK182483* | |
| <i>Myrcia cordifolia</i> DC. | Brazil (Minas Gerais) | MH880929* | | MK175011* | MK182484* | |
| <i>Myrcia costeira</i> M.F.Santos | Brazil (São Paulo) | AM489945 | AM234121 | KU898336 | AM489864 | KU898499 |
| <i>Myrcia couamée</i> (Aubl.) DC. | French Guyana | AM489947 | AM234123 | MK175012* | MK182485* | JN091346 |
| <i>Myrcia crocea</i> Kiersk. | Brazil (Espírito Santo) | MH880940* | | MK175013* | MK182486* | MK202491* |
| <i>Myrcia aff. crocea</i> Kiersk. | Brazil (São Paulo) | KP722394 | JN091308 | KP722472 | KP722302 | MK202483* |
| <i>Myrcia cuprea</i> (O. Berg) Kiersk. | Brazil (Pará) | KP722383 | KU898351 | KP722460 | KP722237 | KP722352 |
| <i>Myrcia decorticans</i> DC. | Brazil (Sergipe) | KU898294 | | KU898398 | KU898509 | KU898453 |
| <i>Myrcia densa</i> (DC.) Sobral | Brazil (Minas Gerais) | MH880941* | | KU898413 | KU898468 | KU898523 |
| <i>Myrcia elevata</i> M.F.Santos | Brazil (Amazonas) | JN091222 | | MK157100* | MK182487* | MK202492* |
| <i>Myrcia eriocalyx</i> DC. | Brazil (Minas Gerais) | MH880942* | | JN091413 | MK175015* | MK202493* |
| <i>Myrcia eriopus</i> DC. | Brazil (São Paulo) | JN091273 | | MK157101* | MK175016* | MK202494* |
| <i>Myrcia espiritosantensis</i> B.S. Amorim | Brazil (Espírito Santo) | KU898315 | | KD722446 | JN091414 | KP722223 |
| <i>Myrcia espiritosantensis</i> B.S. Amorim | Brazil (Espírito Santo) | JN091274 | JN091223 | KP722449 | JN091394 | KP722226 |
| <i>Myrcia euinecaphylla</i> (O. Berg) Nied. | Brazil (Espírito Santo) | JN091254 | JN091203 | KU898373 | KU898422 | JN091348 |
| <i>Myrcia excoridata</i> (Mart.) E. Lucas & C.E. Wilson | Brazil (Espírito Santo) | KU898310* | | KU898422 | KU898532. | KU898477 |
| <i>Myrcia eximia</i> DC. | Brazil (Distrito Federal) | ITS | matK | ndhF | psBA-tmH MK157102* | KP722223 |
| Species | Collection locality | ITS | MH880943* | ndhF | tpL16 MK157101* | KP722249* |
| <i>Myrcia fenzliana</i> [DF] | Voucher Santos 622 | Brazil (Distrito Federal) | KU898315 | KU898422 | KU898532. | KU898477 |
| <i>Myrcia fenzliana</i> [REP] | Vasconcelos 592 | Dominican Republic | MH880944* | KU898353 | MK157103* | KP722226 |
| <i>Myrcia ferruginea</i> Marzine | Santos 689 | Brazil (Rio de Janeiro) | KU898296 | KU898353 | KU898400 | JN091328 |
| <i>Myrcia flagellaris</i> (D. Legrand) Sobral | Lucas 83 | Brazil (São Paulo) | AM489918 | AM234113 | MK175019* | MK182489* |
| <i>Myrcia follii</i> G.M.Barroso & Peixoto | Stagemeier 907 | Brazil (Espírito Santo) | KP722384 | KP722461 | KP722291 | KP722238 |
| <i>Myrcia aff. glazioviana</i> Kiersk. | Nadruz 1007 | Brazil (Rio de Janeiro) | MH880930* | MK157090* | MK174998* | KP7222340 |
| <i>Myrcia grandifolia</i> Cambess. | Faria 2073 | Brazil (Rio de Janeiro) | MH880945* | MK157104* | MK175021* | MK202497* |
| <i>Myrcia grandis</i> McVaugh | Stagemeier 850 | Brazil (Amazonas) | KP722385 | KP722462 | KP722292 | KP698772 |
| <i>Myrcia graziae</i> Niclugh. | Amorim 2016 | Brazil (Amazonas) | MH880946* | MK157105* | MK175022* | KP722341a |
| <i>Myrcia guianensis</i> (Aubl.) DC. | Harter 50,307 | Brazil (Bahia) | JN091276 | JN091225 | JN091416 | JN091351 |
| <i>Myrcia hantwegiana</i> (O. Berg) Kiersk. | Amorim 1925 | Brazil (São Paulo) | JN091277 | MH880947* | MK157106* | JN091352 |
| <i>Myrcia hastibachii</i> D. Legrand | Santos 661 | Brazil (Paraná) | KU898304 | KU898361 | KU898408 | KU898463 |
| <i>Myrcia helpepetala</i> DC. | Lucas 64 | Brazil (São Paulo) | AM489916 | AM234111 | AM48934 | MK157024* |
| <i>Myrcia hexasticha</i> Kiersk. | Lucas 194 | Brazil (Paraná) | JN091227 | JN091309 | KP722438 | JN091353 |
| <i>Myrcia hirtiflora</i> DC. | Lucas 1181 | Brazil (Bahia) | KP722409 | KP722487 | KP722317 | KP722264 |
| <i>Myrcia ilheocensis</i> Kiersk. | Amorim 2037 | Brazil (Espírito Santo) | MH880948* | MK157107* | MK175025* | KP202500* |

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|--|--|----------------------------|-----------|-----------|-----------|-----------|-----------|-----------|------------|-----------|-----------|----------|
| Species | | Collection locality | ITS | | | | | | | | | |
| <i>Myrcia inaequiloba</i> (DC.) Lemée | | Brazil | JN091279 | JN091228 | matK | ndhF | psbA-trnH | rpl16 | tp132-trnL | tp16-trnQ | tpL-trnF | JN091355 |
| <i>Myrcia isatiana</i> G.M.Barroso & Peixoto | | Brazil (São Paulo) | JN091280 | JN091229 | JN091310 | KP722428 | JN091419 | KP722204 | KP722249 | KU71297 | JN091356 | JN091357 |
| <i>Myrcia lanotteeana</i> Cambess., | | Brazil (Minas Gerais) | AM489939 | AM234115 | JN091311 | KP722423 | JN091420 | AM489856 | KP722257 | KP722257 | | |
| <i>Myrcia laxiflora</i> Cambess. | | Brazil (Espírito Santo) | KP722403 | KP722481 | KP722311 | KU898380 | KU898429 | KU898342 | JN091421 | KU898503 | JN091358 | KU898484 |
| <i>Myrcia leneirensis</i> Kiersk. | | Brazil (Amazonas) | JN091281 | JN091230 | JN091312 | KU898380 | KU898380 | KU157108* | MK157109* | MK182495* | | |
| <i>Myrcia aff. lucida</i> McVaugh | | Brazil (Bahia) | MH880949* | MH880950* | | | | | | | | |
| <i>Myrcia lighdhaea</i> B.S. Amorim | | Brazil (Rio de Janeiro) | | | | | | | | | | |
| <i>Myrcia magnifolia</i> (O. Berg) Kiersk. | | Brazil (Bahia) | KP722381 | KU898388 | KU898438 | KP722458 | KP722288 | KU898545 | KP722337 | KU898493 | | |
| <i>Myrcia marianae</i> Stagemeier & Lucas | | Puerto Rico | KU8983230 | | | | | | | | | |
| <i>Myrcia maricaensis</i> Alain | | Brazil (Amazonas) | KU8983233 | KU898317 | JN091231 | KU898391 | KU898441 | KU898547 | KU898496 | | | |
| <i>Myrcia mcaughii</i> (B. Holst) E. Lucas & C.E. Wilson | | Brazil (Minas Gerais) | KU898317 | KU8983225 | KU898325 | KU898384 | KU898442 | KU898534 | KU898479 | | | |
| <i>Myrcia megaphylla</i> M.F.Santos & Sobral | | Brazil (Bahia) | JN091282 | KP722399 | KP722477 | KP722307 | KU898433 | KU898542 | KU898488 | | | |
| <i>Myrcia micropetala</i> (Mart.) Ned. | | Brazil (Goiás) | KP722399 | KP722307 | KU157110* | MK175027* | MK175028* | MK182496* | MK202501* | | | |
| <i>Myrcia microphylla</i> O. Berg, | | Brazil (Mato Grosso) | JN091283 | MH880951* | MH880952* | KU898376 | KU898425 | KU898535 | KU898480 | | | |
| <i>Myrcia minutiflora</i> Sagot | | Brazil (Minas Gerais) | JN091283 | KU8983233 | KU898317 | KU898384 | KU898441 | KU898547 | KU898496 | | | |
| <i>Myrcia mischophylla</i> Kiersk. | | Brazil (Mato Grosso) | JN091283 | KU8983225 | KU898325 | KU898384 | KU898442 | KU898534 | KU898479 | | | |
| <i>Myrcia montana</i> DC. | | Brazil (Minas Gerais) | JN091283 | KU8983225 | KU898325 | KU898384 | KU898442 | KU898534 | KU898479 | | | |
| Species | | Brazil (Bahia) | JN091282 | KU8983225 | KU898325 | KU898384 | KU898442 | KU898534 | KU898479 | | | |
| <i>Myrcia mucugensis</i> Sobral | | Brazil (Mato Grosso) | JN091284 | JN091233 | JN091313 | KU8983233 | KU898368 | KU898416 | KU898526 | KU898471 | | |
| <i>Myrcia multiflora</i> (Lam.) DC. | | Brazil (Minas Gerais) | JN091284 | MH880953* | KP722416 | KP722494 | KP722324 | JN091424 | KP722241 | KP722344 | | |
| <i>Myrcia mutabilis</i> (O. Berg) N.Silveira | | Brazil (Minas Gerais) | JN091284 | KP722416 | KP722494 | KP722324 | KP722307* | MK182497* | MK202502* | KP722271 | KP722374 | |
| <i>Myrcia myrtinifolia</i> DC. | | Brazil (Espírito Santo) | JN091284 | KP722391 | KP722469 | KP722299 | KU157111* | MK182496* | MK182497* | KP722245 | KP722349 | |
| <i>Myrcia neoglabra</i> E.Lucas & C.E.Wilson | | Brazil (Rio de Janeiro) | JN091284 | KP722377 | KP722453 | KP722285 | KU898441 | KU898458 | KU898514 | KP722229 | KP722333 | |
| <i>Myrcia neomontana</i> (Aubl.) E.Lucas & C.E.Wilson | | Brazil | JN091256 | JN091205 | JN091205 | KP722452 | JN091396 | KU898458 | KU898514 | KP722228 | JN091330 | |
| <i>Myrcia neoboscara</i> (O. Berg) E.Lucas & C.E.Wilson | | Brazil (Minas Gerais) | JN091256 | JN091259 | JN091208 | KP722448 | JN091399 | KU898458 | KU898514 | KP722225 | JN091333 | |
| <i>Myrcia neoregularis</i> E.Lucas & C.E.Wilson | | Brazil (Espírito Santo) | JN091259 | | | | | | | | | |
| <i>Myrcia neoriedeliana</i> E.Lucas & C.E.Wilson | | Brazil (São Paulo) | AM489930 | AM234109 | AM489997 | KP722432 | AM489847 | KP722208 | KP722330 | | | |
| <i>Myrcia neopruzeana</i> E. Lucas & Sobral | | Brazil (Minas Gerais) | AM489929 | KU898324 | KU898383 | KU898432 | KU898446 | KU898541 | KU898487 | | | |
| <i>Myrcia neostavroedens</i> E.Lucas & C.E.Wilson | | Brazil (São Paulo) | AM234108 | JN091261 | JN091261 | KP722431 | JN091410 | KP722207 | KP722329 | | | |
| <i>Myrcia neuwiediana</i> E.Lucas & C.E.Wilson | | Brazil (Sergipe) | KP722402 | KU898363 | KU898363 | KU898410 | KP722310 | JN091224 | JN091336 | | | |
| <i>Myrcia nitida</i> Cambess. | | Brazil (Minas Gerais) | KU898306 | MH880954* | MH880954* | KU157113* | MK175031* | MK182500* | MK202503* | KP638774 | KP722336 | |
| Species | | Brazil (Santa Catarina) | JN091206 | KP722450 | KP722450 | KU898399 | KU898352 | KP722307* | KU898510 | KU898454 | KU898465 | |
| <i>Myrcia nobilis</i> DC. | | Brazil (Espírito Santo) | JN091206 | MH880955* | MH880955* | KU157114* | MK175032* | MK182501* | MK202504* | KP722227 | JN091331 | |
| <i>Myrcia oblongata</i> DC. | | Brazil (Rio Grande do Sul) | JN091206 | KP722418 | KP722421 | AM489942 | MK157115* | MK175033* | MK182502* | KP722230 | KP722328a | |
| <i>Myrcia paracatuensis</i> Kiersk. | | Brazil (Minas Gerais) | MH880956* | | | | | | | | | |
| <i>Myrcia pendula</i> Sobral | | Brazil (Bahia) | | | | | | | | | | |
| <i>Myrcia pinitifolia</i> Cambess. | | Brazil (Goiás) | | | | | | | | | | |
| <i>Myrcia platyclada</i> DC. | | Grenade | | | | | | | | | | |
| <i>Myrcia aff. plusiantha</i> Kiersk. | | Hawthorne 502 | | | | | | | | | | |
| <i>Myrcia polyantha</i> DC. | | Brazil (Espírito Santo) | | | | | | | | | | |
| <i>Myrcia pseudomarliacea</i> Sobral | | Souza 1139 | | | | | | | | | | |

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|--|---------------------------|-------------------------|-------------------------|-------------|--------------|-------------------|
| <i>Myrcia pseudospectabilis</i> Sobral | Brazil (Bahia) | JN091285 | MH880957* | MK175035* | MK202506* | JN091363 |
| <i>Myrcia pubescens</i> DC. | Brazil (Distrito Federal) | JN091234 | MK175036* | MK182505* | MK202507* | JN091365 |
| <i>Myrcia aff. pubescens</i> DC. | Faria s.n. (28.11.2014) | MH880931* | MK175000* | MK182474* | MK182474* | JN091364 |
| <i>Myrcia pubipetala</i> Miq. | Brazil (São Paulo) | AM489938 | AM234114 | KP722426 | AM489855 | KP722273 |
| <i>Myrcia pulchra</i> (O. Berg) Kiersk. | Brazil (Paraná) | JN091286 | JN091235 | JN091314 | JN091426 | KU898501 |
| <i>Myrcia pulvinata</i> B.S. Amorim | Brazil (Bahia) | MH880958* | MK157117* | MK175037* | MK202508* | JN091366 |
| Species | Collection locality | ETs | ITS | <i>matK</i> | <i>rpl16</i> | <i>tps16-trnQ</i> |
| <i>Myrcia racemosa</i> (O. Berg) Kiersk. | Brazil (São Paulo) | AM489944 | AM234120 | AM490005 | KP722424 | KP722259 |
| <i>Myrcia aff. racemosa</i> (O. Berg) Kiersk. | Brazil (Bahia) | KP722380 | KP722457 | KP722287 | KP722234 | KP722336 |
| <i>Myrcia reticulata</i> Cambess. | Brazil (Rio de Janeiro) | MH880959* | MK157118* | MK175038* | MK182507* | MK202509* |
| <i>Myrcia reticulosa</i> Miq. | Brazil | JN091287 | JN091236 | KP722466 | JN091427 | MK182508* |
| <i>Myrcia riedocensis</i> G.M.Barroso & Peixoto | Harley 50.309 | Santo | Brazil (Espírito Santo) | KU898346 | KU898393 | MK175039* |
| <i>Myrcia robusta</i> Sobral | Staggemeier 917 | Brazil (Espírito Santo) | KU898289 | JN091238 | KP722296 | KP722243 |
| <i>Myrcia rufa</i> (O. Berg) Liaersk. | Lucas 727 | Brazil (Espírito Santo) | KU898289 | MH880960* | KP722243 | KP722346 |
| <i>Myrcia rosangae</i> Niclugh. | Bridgewater 1076 | Brazil (Tocantins) | JN091289 | JN091429 | KU898448 | KU898448 |
| <i>Myrcia rotundata</i> (Amshoff) McVaugh | Amorim 1459 | Brazil (Sergipe) | MH880961* | MK175119* | MK202510* | JN091368 |
| <i>Myrcia russchii</i> B.S. Amorim | Caddah 555 | Brazil (Amazonas) | JN091289 | KU898419 | KU898529 | KU898474 |
| <i>Myrcia rufipes</i> DC. | Amorim 1941 | Brazil (Espírito Santo) | MH880961* | MK175042* | MK182510* | JN091369 |
| <i>Myrcia rupestris</i> M.F.Santos | Lucas 280 | Brazil | JN091290 | JN091239 | JN091430 | KU898452 |
| <i>Myrcia rupifolia</i> M.I.Kawas. & B.Holst | Santos 640 | Brazil (Minas Gerais) | KU898293 | KU898350 | KU898508 | KU898508 |
| <i>Myrcia sacatilis</i> (Amshoff) McVaugh | Vasconcelos 311 | Brazil (Amazonas) | MT954055 | MT954487 | MF954256 | MF954113 |
| <i>Myrcia selloi</i> (Spreng.) N.Silveira | Lucas 98 | Brazil | AM234119 | KP722427 | KP722203 | JN091370 |
| <i>Myrcia serrana</i> B.S. Amorim | Lucas 110 | Brazil (Bahia) | JN091240 | JN091315 | KU898600 | KU898600 |
| Species | Collection locality | ETs | ITS | <i>matK</i> | MK175043* | MK175043* |
| <i>Myrcia aff. servata</i> McVaugh | Amorim 2013 | Brazil (Amazonas) | MH880962* | KP722436 | MK157121* | MK202511* |
| <i>Myrcia sessilissima</i> M.F.Santos | Voucher | Brazil (Amazonas) | KU898319 | KU898377 | KU898426 | <i>tps16-trnQ</i> |
| <i>Myrcia spathulifolia</i> Proenca | Santos 777 | Brazil (Minas Gerais) | KU898316 | KU898374 | KU898423 | <i>rpl16</i> |
| <i>Myrcia speciosibilis</i> DC. | Santos 641 | Brazil (Bahia) | MT954058 | MT954394 | MF954263 | <i>tp132-trnL</i> |
| <i>Myrcia splendens</i> (Sw.) DC. | Faria 214 | Brazil (Rio de Janeiro) | MH880963* | MK175122* | MK182512* | <i>tp132-trnL</i> |
| <i>Myrcia springiana</i> O. Berg [BA] | Amorim 1989 | Brazil (Rio de Janeiro) | JN091292 | MK175044* | MK175044* | <i>tp132-trnL</i> |
| <i>Myrcia springiana</i> O. Berg [PE] | Lucas 73 | Brazil (Minas Gerais) | AM489946 | AM234122 | KP722425 | <i>tp132-trnL</i> |
| <i>Myrcia squamata</i> (Mattos & D. Legrand) Matos | Amorim 2007 | Brazil (Pernambuco) | MH880964* | MH880965* | MK157123* | <i>tp132-trnL</i> |
| <i>Myrcia stricta</i> (O. Berg) Kiersk. | Amorim 1985 | Brazil (Paraná) | MH880965* | MH880965* | MK157124* | <i>tp132-trnL</i> |
| <i>Myrcia subavenia</i> (O. Berg) N.Silveira | Vieira 800 | Brazil (Goiás) | KU898314 | KU898371 | KU898420 | <i>tp132-trnL</i> |
| <i>Myrcia subcordata</i> DC. | Santos 608 | Brazil (Minas Gerais) | KU898291 | KU898348 | KU898395 | <i>tp132-trnL</i> |
| <i>Myrcia aff. subobliqua</i> (Benth.) Nied. | Santos 585 | Brazil (Minas Gerais) | KU898302 | KU898359 | KU898406 | <i>tp132-trnL</i> |
| <i>Myrcia subserricea</i> A. Gray | Staggemeier 839 | Brazil (Amazonas) | KP722396 | KP722474 | KP722304 | <i>tp132-trnL</i> |
| <i>Myrcia subterminalis</i> M.F.Santos | Santos 797 | Brazil (Rio de Janeiro) | MH880967* | MK175126* | MK175048* | <i>tp132-trnL</i> |
| <i>Myrcia subverticillaris</i> (O. Berg) Kiersk. | Santos 733 | Brazil (Espírito Santo) | KU898307 | KU898364 | KU898411 | <i>tp132-trnL</i> |
| <i>Myrcia succulenta</i> Sobral | Lucas 251 | Brazil (Minas Gerais) | JN091295 | JN091244 | JN091435 | <i>tp132-trnL</i> |
| <i>Myrcia succulenta</i> Sobral | Matsumoto 824 | Brazil (Espírito Santo) | JN091260 | JN091209 | KP722445 | KP722222 |
| Species | Collection locality | ETs | ITS | <i>matK</i> | <i>ndhF</i> | <i>psbA-trnH</i> |
| <i>Myrcia suffruticosa</i> O. Berg | Voucher | Brazil (Minas Gerais) | JN091296 | JN091245 | KU898446 | <i>psbA-trnH</i> |
| <i>Myrcia tenuifolia</i> (O. Berg) Sobral | Mello-Silva 1690 | Brazil (Espírito Santo) | KU898308 | KU898365 | KU898412 | <i>psbA-trnH</i> |
| <i>Myrcia tenuivenosa</i> Kiersk. | Santos 747 | Santo | KU898307 | KU898364 | KU898521 | <i>psbA-trnH</i> |
| <i>Myrcia tenuivenosa</i> Kiersk. | Lucas 87 | Brazil (São Paulo) | JN091297 | JN091246 | KU898500 | JN091335 |
| <i>Myrcia terraphylla</i> Sobral | Staggemeier 926 | Brazil (Bahia) | KP722389 | KP722467 | KP698873 | KP722347 |
| <i>Myrcia throssoides</i> O. Berg | Amorim 2019 | Brazil (Bahia) | MH880968* | MK175049* | MK182516* | MK202516* |

| | | | | | | | | | |
|--|----------------------|---------------------------|-----------|-----------|-----------|-----------|------------|-----------|-----------|
| <i>Myrcia tijucensis</i> Kiersk. | | Brazil (Santa Catarina) | AM489915 | MH880969* | MK157128* | MK175050* | MK182516* | MK202517* | JN091379 |
| <i>Myrcia tomentosa</i> (Aubl.) DC. | | Brazil (Distrito Federal) | AM489940 | AM234116 | AM489857 | | | | JN091380 |
| <i>Myrcia torta</i> DC. | | Soares 751 | JN091298 | JN091247 | JN091318 | JN091438 | | | JN091381 |
| <i>Myrcia aff. truncata</i> Sobral | Lucas 1189 | Brazil (Bahia) | KP722412 | KP722320 | KP722320 | KP722267 | KP722246 | KP7222370 | |
| <i>Myrcia umbraticola</i> (Kunth) E.Lucas & C.E.Wilson | Souza s.n. | Brazil (Amazonas) | KP722392 | KP722300 | KP722300 | KP722267 | KP722246 | KP7222350 | |
| <i>Myrcia aff. unana</i> Sobral | Amorim 2024 | Brazil (Bahia) | MH880932* | MK157091* | MK157091* | MK182475* | MK202484* | | JN091382 |
| <i>Myrcia variabilis</i> DC. | Lucas 277 | Brazil | JN091299 | JN091248 | JN091319 | JN091439 | MK175051* | MK182517* | JN091383 |
| <i>Myrcia venulosa</i> DC. | Cruz 195 | Brazil (Paraná) | AM489949 | AM234125 | JN091249 | JN091440 | AM489866 | KU898537 | JN091384 |
| <i>Myrcia vestita</i> DC. | Lucas 93 | Brazil (São Paulo) | JN091300 | JN091249 | JN091301 | MH880970* | MK157129* | MK182518* | JN091385 |
| <i>Myrcia vitoriana</i> Kiersk. | Amorim 2008 | Brazil (Amazonas) | KU898323 | KU898323 | KU898382 | KU898431 | KU898540 | KU898486 | |
| <i>Myrcia</i> sp. [Harms 20] | Harms 20 | Brazil (Amazonas) | MF954056 | MF954392 | MF954488 | MF954362 | MF954260 | MF954114 | MF954174 |
| <i>Myrcia</i> sp1 [T] | Vasconcelos 307 | Collection locality | ITS | matK | ndhF | rp16 | rp32-rnL | rp16-rnQ | rp16-rnL |
| Species | Voucher | Brazil (Sergipe) | KP722382 | KP722382 | KP722459 | KP72289a | KP722236 | KP722236 | KP722238 |
| <i>Myrcia</i> sp2 | 792 | Brazil (Bahia) | MF954057 | MF954489 | MF954364 | MF954262 | KP722265 | KP722265 | KP7222368 |
| <i>Myrcia</i> sp2 [T] | Faria 4193 | Brazil (Bahia) | KP722410 | KP722488 | KP722318 | KP722318 | KP722468 | KP722468 | KP722348 |
| <i>Myrcia</i> sp3 | Lucas 1169 | Brazil (Bahia) | KP722390 | KP722468 | KP722298 | KP722298 | KP722492 | KP722322 | KP722372 |
| <i>Myrcia</i> sp4 | Stagemeier 927 | Brazil (Bahia) | KP722414 | KP722405 | KP722405 | KP722483 | KP722313 | KP722360 | KP722363 |
| <i>Myrcia</i> sp5 | Lucas 1192 | Brazil | KP722405 | KP722491 | KP722321 | KP722321 | KP722479 | KP722359 | KP722371 |
| <i>Myrcia</i> sp6 | Souza 1131 | Brazil (Bahia) | KP722413 | KP722401 | KP722309 | KP722309 | KP722356 | KP722359 | KP722359 |
| <i>Myrcia</i> sp7 | Lucas 1190 | Brazil (Espírito Santo) | KP722398 | KP722306 | KP722476 | KP722476 | KP722353 | KP722356 | |
| <i>Myrcia</i> sp8 | Stagemeier 901 | Brazil (Espírito Santo) | KP722393 | KP722301 | KP722471 | KP722471 | KP722247 | KP722247 | KP722351 |
| <i>Myrcia</i> sp9 | Stagemeier 845 | Brazil (Amazonas) | KP722407 | KP722315 | KP722485 | KP722315 | KP722262 | KP722262 | KP722365a |
| <i>Myrcia</i> sp10 | Stagemeier 762 | Brazil (Bahia) | | | | | | | |
| <i>Myrcia</i> sp11 | Stagemeier 896 | Brazil (Espírito Santo) | | | | | | | |
| <i>Myrcia</i> sp12 | ICN 167,445 | Brazil | JQ033316 | JQ033345 | JQ033345 | JQ033345 | KP722282 | KP722282 | |
| <i>Myrcia</i> sp13 | Mazine, F. 796 | Brazil | AM234094 | AM489870 | MF954369 | MF954267 | MF954266 | MF954117 | MF954177 |
| <i>Myrcia</i> sp14 | Vasconcelos 413 | Brazil (Bahia) | MT954061 | MF954397 | MF954368 | MF954266 | MF954117 | MF954119 | MF954119 |
| <i>Myrcia</i> sp15 | Vasconcelos 709 | Singapore BG (cultivated) | MT954063 | AY521544 | MF954495 | MF954414 | MF954268 | | |
| <i>Myrtus communis</i> L. | RBG Kew (cultivated) | AM234149 | AM490009 | KP722420, | AM489872 | JN660939 | MF954420 | KP722221 | KP7222327 |
| <i>Neomitrannes cordifolia</i> (D.Legrand) D.Legrand | Lucas 211 | Brazil (Minas Gerais) | AM489413 | AM489410 | AM489569 | MF954418 | MF954421 | JN091386 | MF954123 |
| <i>Pinia cordifolia</i> (D.Legrand) Sobral | Foster 1011 | Brazil (Minas Gerais) | AM489411 | AM489411 | AM489570 | AM489570 | This study | KP722219 | |
| Species | Mazine 957a | Collection locality | ITS | matK | ndhF | rp16 | rp16-rnL | KP722276 | MF954187 |
| <i>Pinia nana</i> Sobral | Voucher | Brazil (Minas Gerais) | MT954068 | MF954504 | MF954404 | MF954375 | MF954237 | JN091388 | |
| <i>Pinia pauciflora</i> M.I.Kawas. & B.Holst | Mazine 662 | Brazil (Minas Gerais) | AM489411 | AM489411 | AM489570 | MF954405 | MF954405 | MF954188 | |
| <i>Pinia</i> sp1 | Mazine 957b | French Guiana | MT954069 | MF954505 | MF954376 | MF954383 | MF954383 | KP722220 | JN091389 |
| <i>Siphoneugena densiflora</i> O. Berg | Mazine 1050 | Brazil (Minas Gerais) | AM489572 | AM489412 | AM489571 | AM490638 | AM490638 | | |
| <i>Siphoneugena galloyleana</i> C.Poerane | Lucas 70 | Brazil (São Paulo) | AM489966 | AM490016 | AM490016 | AM489882 | | | |
| <i>Syzygium lombos</i> (L.) Alston in H. Trimen | Lucas 214 | RBG Kew (cultivated) | AM234135 | AM234135 | | | | | |

Appendix B. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ympev.2019.05.014>.

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