



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 Myrceugenia group is sister to the *Myrcia* and *Plinia* groups. Five *Myrcia* species 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, Myrceugenia, *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; WCSF, 2017).

Myrcia is one of the most taxonomically complex and morphologically homogenous genera of Myrteaceae. The taxon currently recognised as a single genus (*sensu* Lucas et al., 2018) was until recently recognized as four distinct genera: *Calyptanthes* 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. *Calyptanthes* 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 Myrteae were sampled, representing the Blepharocalyx, Myrceugenia, *Myrcia*, and *Plinia* groups (*sensu* Lucas et al., 2007; Vasconcelos et al., 2017a). Non-Myrteae outgroups were represented by two accessions of tribes Syzygieae 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 Fig-Tree 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 Myrteae).

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; WCSF, 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, Myrceogenia, Myrtus and Plinia groups, along with *Myrcia fenziiana* O. Berg (DF), *M. aff. hirtiflora* DC., *M. aff. racemosa* (O. Berg) Kiaersk., *M. rorida* (O. Berg) Kiaersk., *M. springiana* (O. Berg) Kiaersk. (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	936	914	1541	849	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 (65.4%)	928 (60.2%)	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 (12.8%)
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 + I + G			

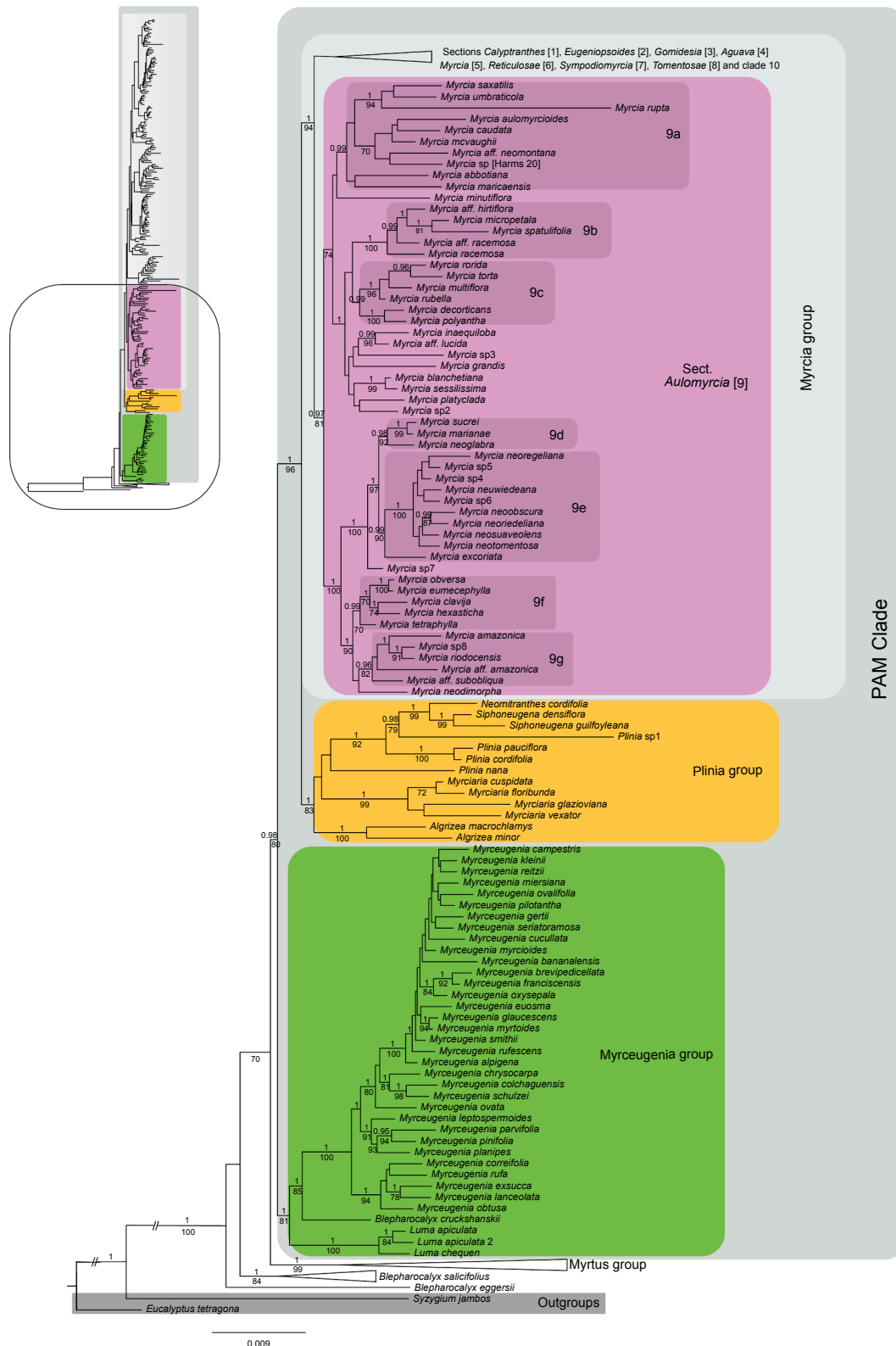


Fig. 1. Bayesian Inference (BI) majority rule consensus tree from the combined analysis of ITS (internal transcribed spacer), ETS (external transcribed spacer), *matK*, *ndhF*, *pasbA-trnH*, *rpl16*, *rps16-trnQ*, *rpl32-trnL*, and *trnL-trnF*. Posterior probabilities (from the BI analysis) greater than 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 Cerqueiraia subclades are newly used here. Scale bar: expected number of nucleotide substitutions per site.

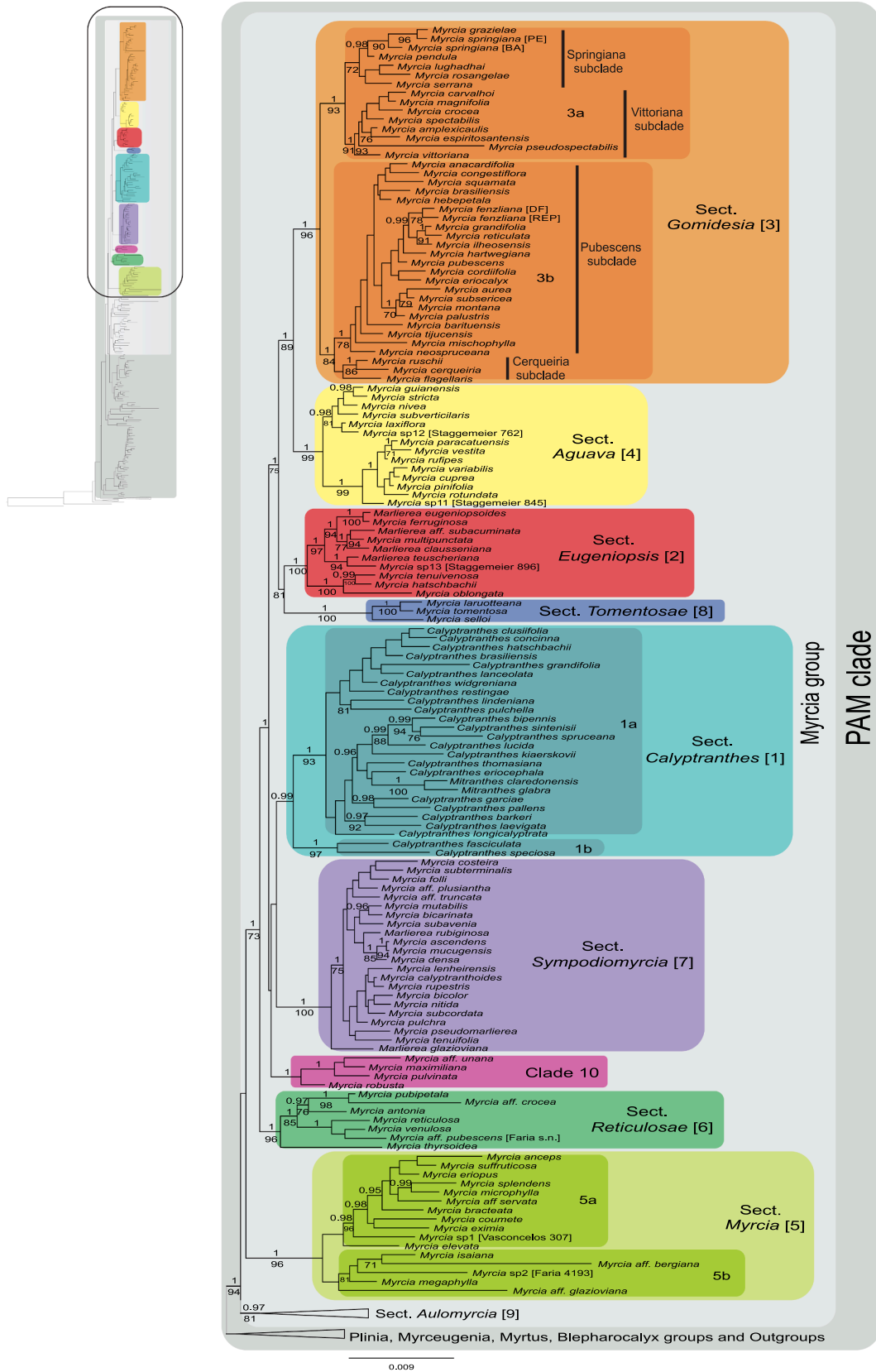


Fig. 1. (continued)

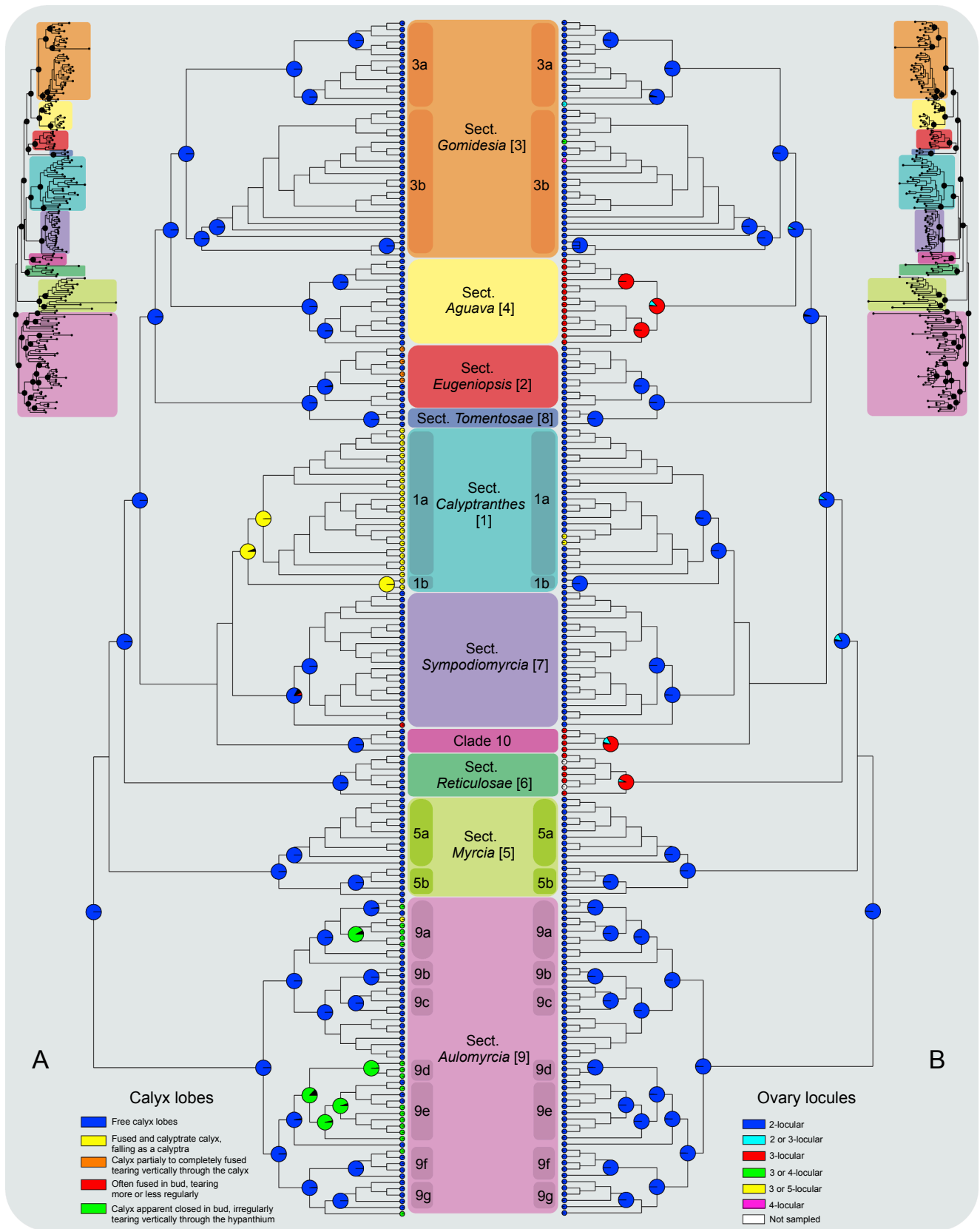


Fig. 2. Evolution of key morphological traits in *Myrcia* and relatives, showing the most likely ancestral character traits at all internal branches of the Bayesian Inference majority rule consensus tree from Fig. 1, inferred using Bayesian Binary MCMC. (A) Calyx lobes. (B) Ovary locules. Pie charts 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 *Calyptanthes* (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. *Calyptanthes* (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 eighth 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. lughadhae* 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. pseudospectralibis* 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. hartwegiana* (O. Berg) Kiaersk., *M. hebetata* 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. tijuacensis* Kiaersk.. Cerqueiraia subclade is sister to *M. flagellaris* (D. Legrand) Sobral and composed of *Myrcia cerqueiraia* (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. *Calyptanthes* and *Sympodiomyrcia* can also possess closed buds, but these are morphologically distinct in other ways. *Myrcia* sect. *Calyptanthes* 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 *Calyptanthes* 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. *Calyptanthes*, *Gomidesia*, *Aguava*, *Reticulosae* and clade 10 (Fig. 2b). The most likely ancestral state of sections *Calyptanthes*, 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-

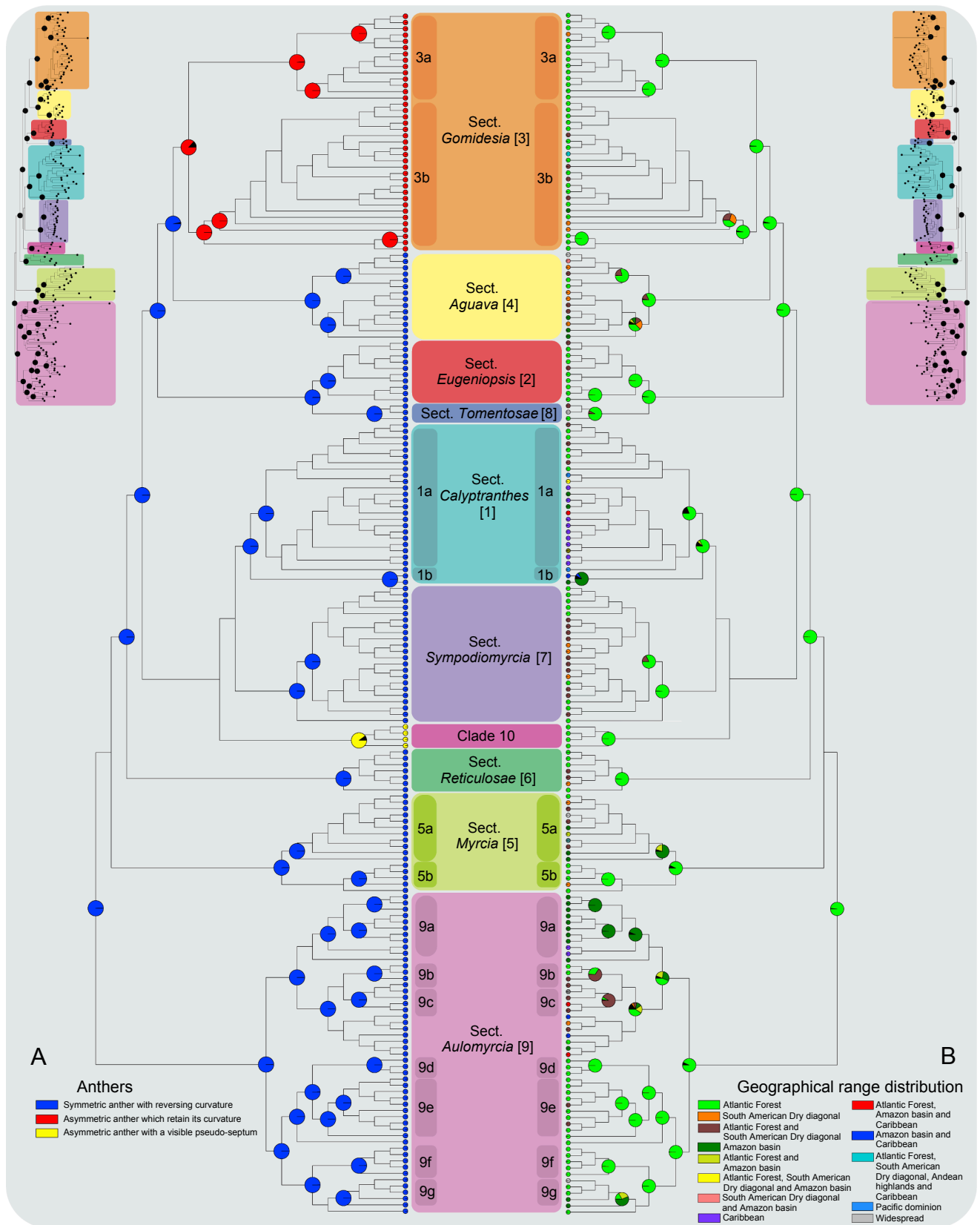


Fig. 3. Evolution of key morphological traits and Geographical range evolution in *Myrcia* and relatives, showing the most likely ancestral at all internal branches of the Bayesian Inference majority rule consensus tree from Fig. 1, inferred using Bayesian Binary MCMC. (A) Anthers. (B) Geographical range 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 subclade 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 appressed 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 appressed (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. *Eugeniopsis* (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. *Eugeniopsis*, *Gomidesia*, *Aguava*, *Reticulosae*, *Sympodiomyrcia* and *Tomentosae*), the Andean highlands and Yungas (sect. *Gomidesia*), or become widespread (sects. *Aguava*, *Myrcia* and *Tomentosae*). Although sections *Calypttranthes*, *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. *Calypttranthes* (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 most 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 ancestor 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 barituensis* 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 Myrceugenia 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).

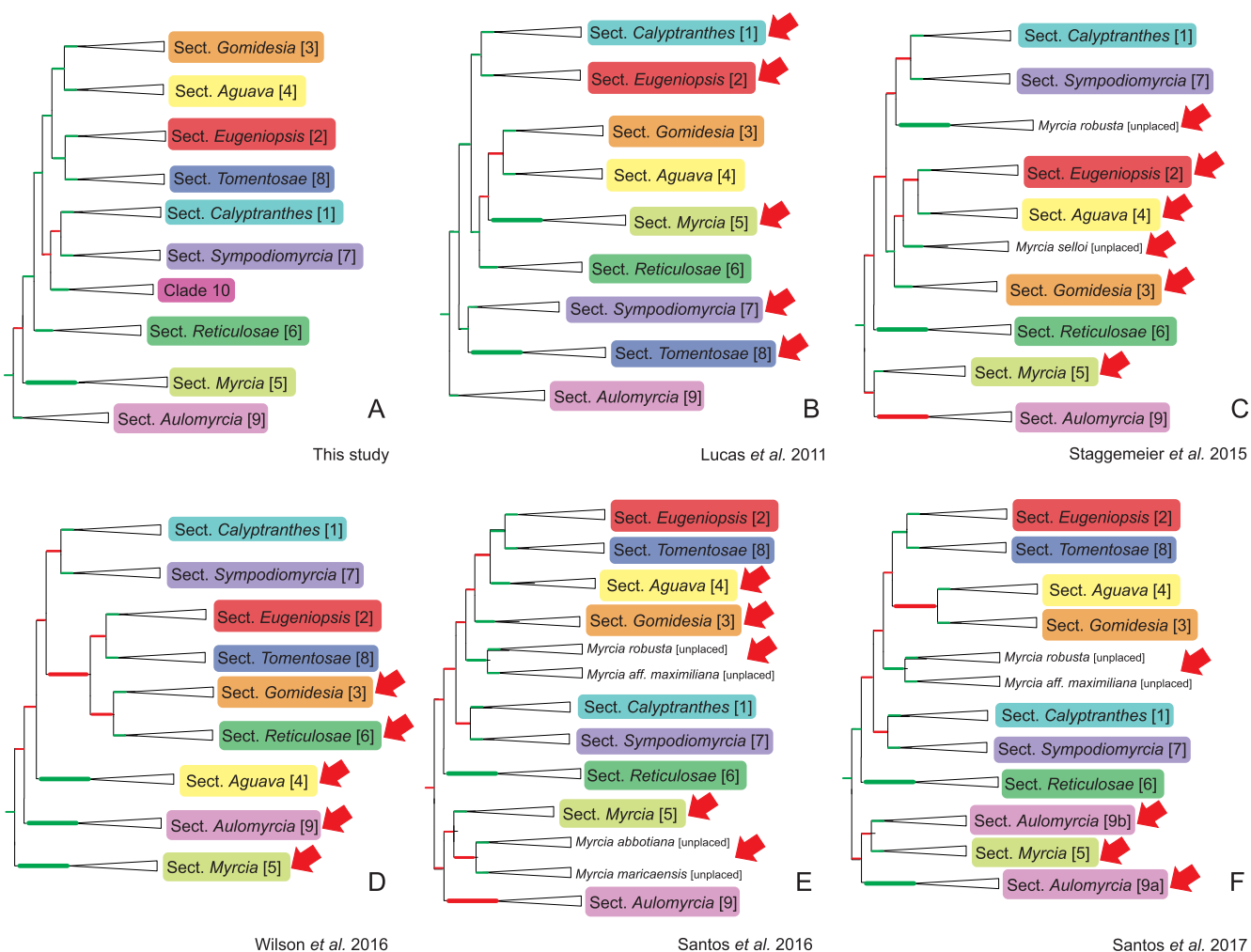


Fig. 5. Comparison of six published phylogenetic hypotheses for *Myrcia* based on nuclear and plastid sequences. Green branches indicate posterior probabilities (from BI) greater than 0.95 and/or bootstrap percentages (from ML) greater than 70. Red branches indicate poor supported phylogenetic relationships. 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 here 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 Myrteae

The monophyly of the Myrceugenia 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 Myrceugenia 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 Myrceugenia 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).

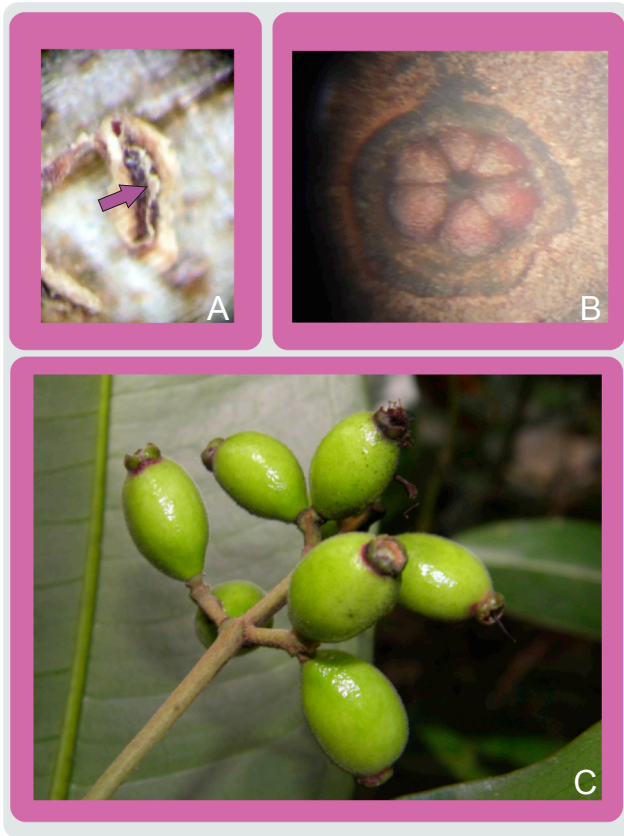


Fig. 6. Diagnostic features of Clade 10. (A) Detail of asymmetric anthers with a visible pseudo-septum (arrow); (B) Detail of 3-locular ovary with 2-ovules in each locule; (C) Fruits with distinct and imbricate calyx lobes and a glabrous staminal disc.

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 *Calyptanthus* [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 Kiaerskou (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). Cerqueiriana 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 Myrteae genera (Bünger et al., 2016; Murillo et al., 2012, 2016) and also in Myrtales (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*), *Calyptanthes* (= *Myrcia*), *Calyptrogenia* (= *Myrceugenia*), *Marlierea* (= *Myrcia*) and *Mitranthes* (= *Myrcia*; see McVaugh, 1968; Landrum, 1986; Lucas et al., 2011; Vasconcelos et al., 2017a). However, recent molecular phylogenetic studies in tribe Myrteae 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 *Calyptanthes* 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 Myrteae 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 Myrteae, 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 cordiiifolia*, *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. barituensis*), and wide 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.

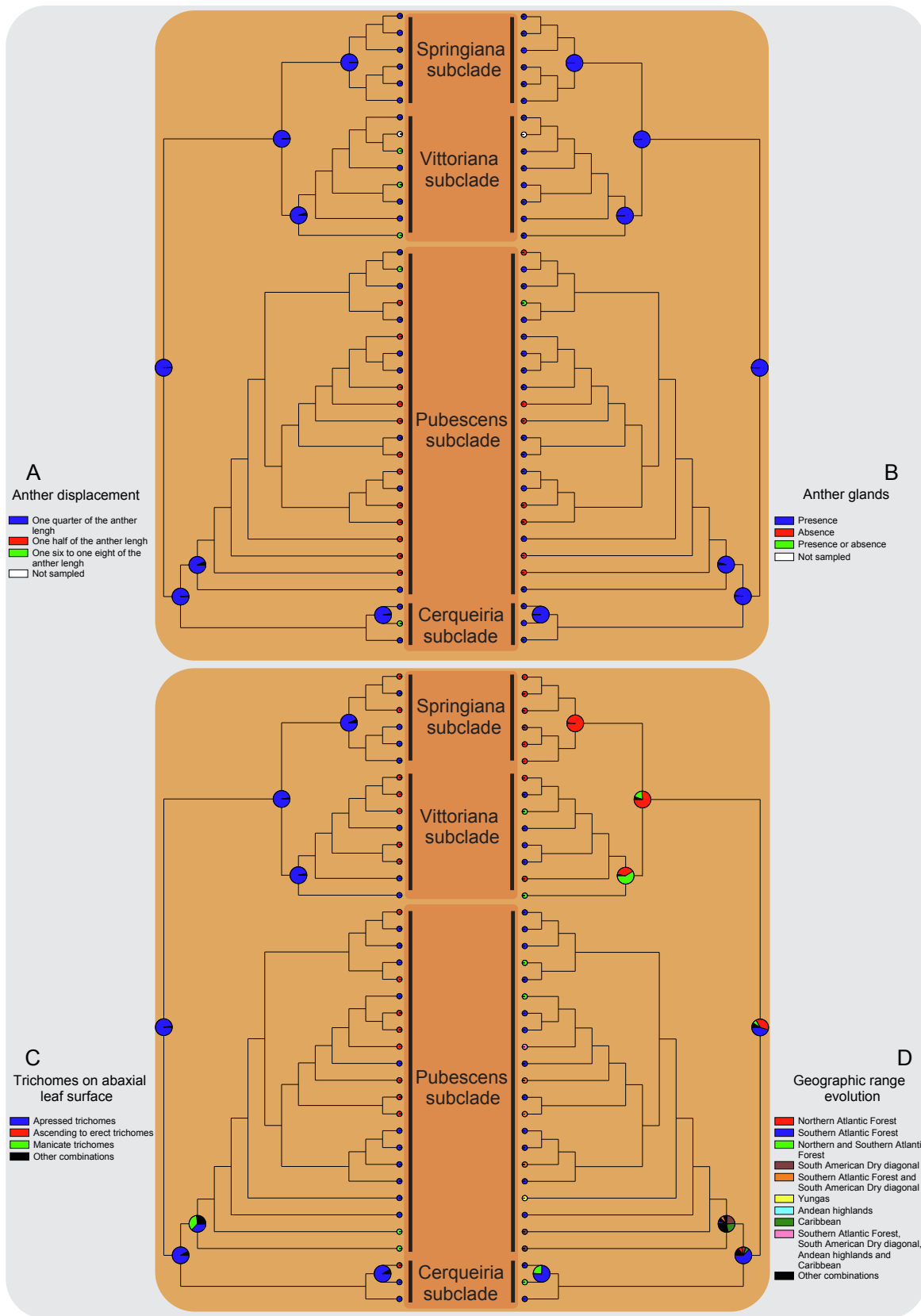


Fig. 7. Inference of *Myrcia* section *Gomidesia* (clade 3) ancestral reconstruction using BMM. (A) Anther displacement. (B). Anther glands. (C) Trichomes on abaxial leaf surface. (D) Geographic range evolution. Pie charts for each node indicate probabilities for each alternative ancestral character. 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.

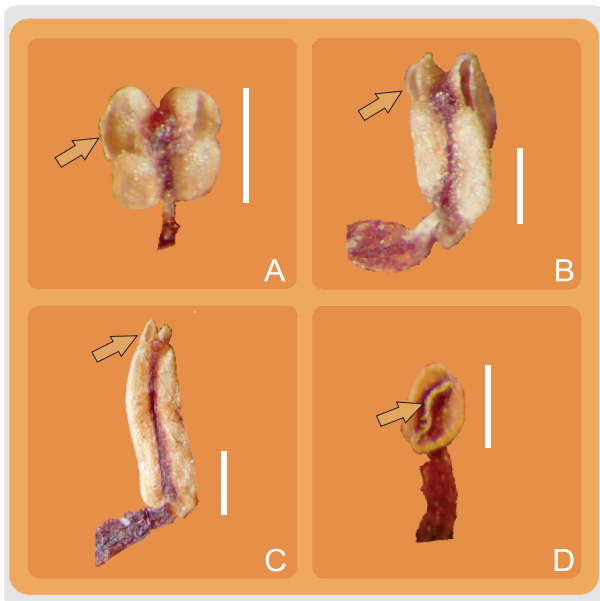


Fig. 8. *Myrcia* section *Gomidesia* (clade 3). A-C, Anther displacement; (A) one half of anther length (arrow); (B) one quarter of the anther length (arrow); (C) one sixth to one eighth of anther length (arrow). (D) Detail of the anther septum (arrow). Scale bar 0.5 mm long.

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-Rodriguez 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*, *Tommentosae* 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), *Tommentosae* (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 coumete*), Cerrado (e.g. *Myrcia suffruticosa*), Atlantic Forest and Cerrado (e.g. *Myrcia eriopus*, *M. eximia*, *M. microphyla*), 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).

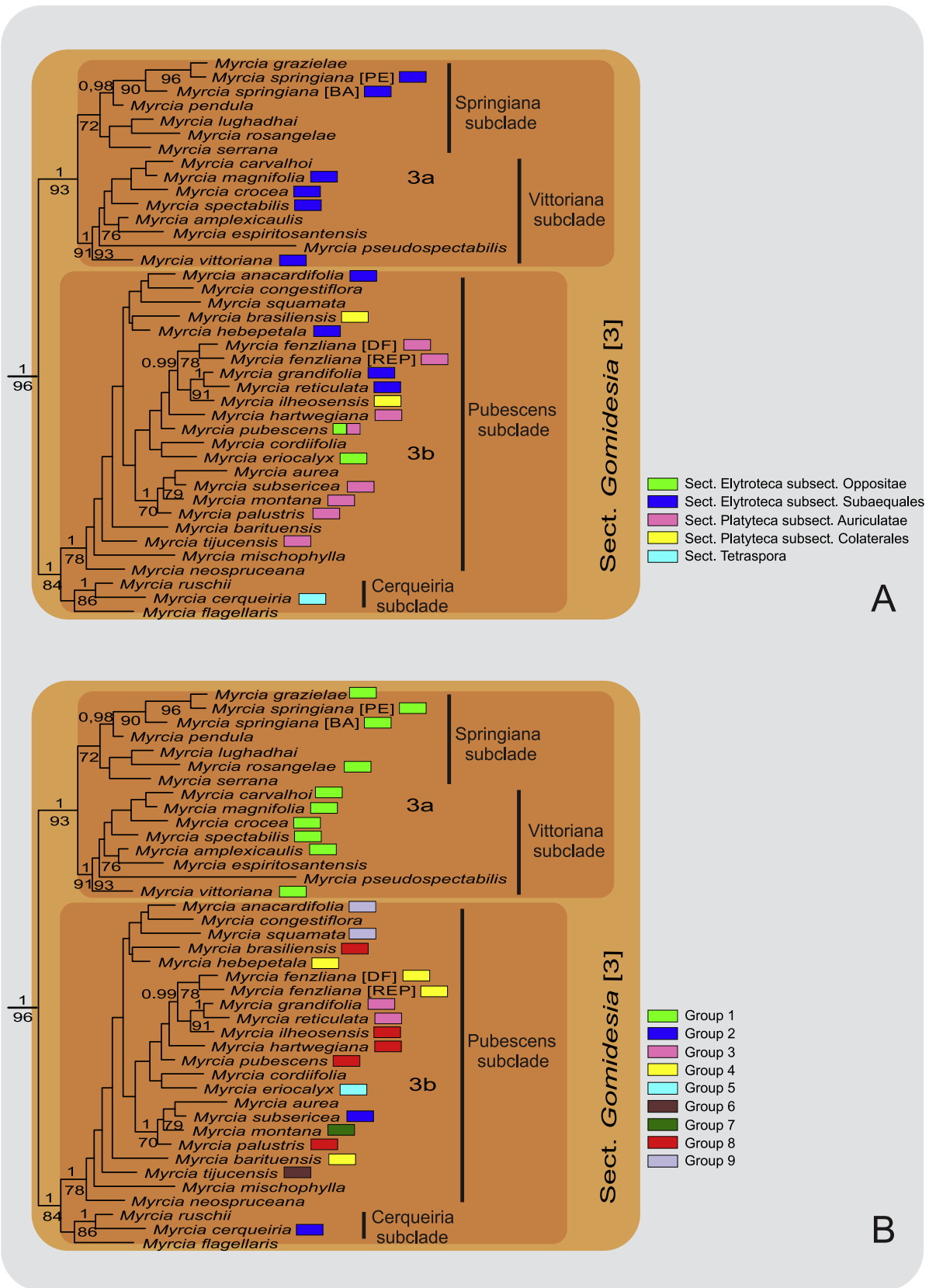


Fig. 9. *Myrcia* section *Gomidesia* (clade 3) Bayesian Inference (BI) majority rule consensus tree from analysis of the combined markers. (A) Infrageneric classification (Legrand, 1958) of the genus *Gomidesia* (*sensu* 1855–1856). (B) Informal classification (Lughadha, 1997) of the genus *Gomidesia* (*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 Cerqueiraia 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 Myrteaceae 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 bidirectional 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. *Calyptanthes*, *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 cavallhoi* 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. barituensis*), and savanna vegetation of South America, Lesser Antiles and West Indies

(e.g. *M. fenziiana*), 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 Myrteae 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 Myrteae 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	ETS	ITS	matK	ndhF	psbA-trnH	rpl16	rpl32-trnL	rps16-trnQ	rnl-tmf
<i>Accara elegans</i> (DC.) Landrum	Vasconcelos 485	Brazil (Minas Gerais)		MF954013	MF954518	MF954431	MF954271	MF954309	MF954197		
<i>Algrizea macrochlamys</i> (DC.) Proença & Niclugh.	Giulietti 1648	Brazil (Bahia)	AM489890	AM234126	AM489975	AM489809	AM489809	MF954310	MF954198	KP722283	JN091320
<i>Algrizea minor</i> Sobral, Faria & Proença	Faria 4157	Brazil (Bahia)		MF954014	MF954433	MF954272	MF954272	MF954311	MF954199	MF954078	
<i>Blepharocalyx cruckshankii</i> (Hook. & Arn.) Nied. in H.G.A.E.-ngler & K.A. E-Prantl	Murillo 4219	Edinburgh (cultivated)		AM234070	AM489978	AM489814	AM489814	JN661055a	JN661055a	JN661105a	
<i>Blepharocalyx egerisii</i> (Kiaersk.) Landrum	Vasconcelos 458	Brazil (Bahia)		MF954017	MF954519	MF954438	MF954274	MF954313	MF954202	MF954081	MF954137
<i>Blepharocalyx salicifolius</i> (Kunth) O. Berg [1]	Lucas 78	Brazil (São Paulo)		AM234084	AM489979	MF954440	AM489815	JN660984	JN661133	JN661133	MF954139
<i>Blepharocalyx salicifolius</i> (Kunth) O. Berg [2]	Vasconcelos 482	Brazil (Minas Gerais)		MF954314	MF954520	MF954439	MF954275	MF954314	MF954082	MF954082	MF954138
<i>Calycolpus goethanus</i> (Mart. ex DC.) O. Berh	Vasconcelos 332	Brazil (Amazonas)		MF954019	MF954521	MF954441	MF954276	MF954315	MF954203	MF954083	MF954140
<i>Calycolpus mortizianus</i> (O.Berg) Burret	(all from GenBank)	Colombia		KU945986	KU945991	KU945991	KU945999				
<i>Calypranthes barkeri</i> Ekman & Urb.	Lucas 1116	Dominican Republic		KU164811							KU164862
<i>Calypranthes bipennis</i> O. Berg	Holst 8054	Ecuador		KU164817							KU164868
<i>Calypranthes brasiliensis</i> Spreng.	Lucas 930	Brazil (Espírito Santo)		MF954020		MF954443	MF954278				KU164856
<i>Calypranthes clusifolia</i> O. Berg	Lucas 253	Brazil	JN091251	JN091200							
<i>Calypranthes concinna</i> DC.	Lucas 74	Brazil	AM489898	AM234103	AM489980	KP722454	AM489817		MK182467*	KP722231	JN091321
<i>Calypranthes eriocphala</i> Urb.	Araujo 1803	Dominican Republic		KU164809						KU171282	KU164860
<i>Calypranthes fasciculata</i> O. Berg	Bhiki 285	Suriname		KU164798							KU164849
<i>Calypranthes garciae</i> Alain & M. M. Mejia	Araujo 1802	Dominican Republic		KU164812							KU164863
Species	Voucher	Collection locality	ETS	ITS	matK	ndhF	psbA-trnH	rpl16	rpl32-trnL	rps16-trnQ	rnl-tmf
<i>Calypranthes grandifolia</i> O. Berg,	Lucas 122	Brazil	JN091252	JN091302							
<i>Calypranthes hatschbachii</i> D. Legrand	Lucas 171	Brazil (Paraná)		KU164801							
<i>Calypranthes kiaerskovii</i> Krug & Urb.	Pollard 1194	British Virgin Islands	AM489900	AM234105	AM489819						
<i>Calypranthes laevigata</i> Urb. & Ekman	Araujo 1793	Dominican Republic		KU164804							
<i>Calypranthes lanceolata</i> O. Berg,	Lucas 84	Brazil		AM234104							
<i>Calypranthes lindeniana</i> O. Berg	Hartley 54,077	Brazil (Bahia)	AM489899	KU164816							
<i>Calypranthes longicalyptrata</i> B. Holst & M.I. Kawas.	Vasconcelos 523	Costa Rica		KU164815							
<i>Calypranthes lucida</i> Mart. ex DC.	Sasaki 2448	Brazil (Mato Grosso)		MF954021							
<i>Calypranthes pallens</i> Griseb.	Vasconcelos 534	Costa Rica		KU164815							
<i>Calypranthes pulchella</i> DC.	Zappi 2496	Costa Rica		MF954021	AF368201	MF954444	MF954279	MF954319			
<i>Calypranthes restingae</i> Sobral	Lucas 990	Brazil (Minas Gerais)		KU164808							
<i>Calypranthes sintenisii</i> Kiaersk.	Araujo 1785	Brazil (Bahia)		KU164813							
<i>Calypranthes speciosa</i> Sagot	Holst 9399	Dominican Republic,		KU164818							
<i>Calypranthes spruceana</i> O. Berg	Araujo 1874	French Guiana		KU164810							
<i>Calypranthes thomasi</i> O. Berg	Pollard 1195	British Virgin Islands	AM489901	AM234106							
<i>Calypranthes widgeriana</i> O. Berg	Lucas 467	Brazil (São Paulo)		KU164806							
<i>Changuava schippii</i> (Standl.) Landrum	Aguiar 9833	Costa Rica		MF954027	MF954523	MF954451	MF954285	MF954325	MF954211	MF954091	KU164857
Species	Voucher	Collection locality	ETS	ITS	matK	ndhF	psbA-trnH	rpl16	rpl32-trnL	rps16-trnQ	rnl-tmf
<i>Eucalyptus tetragona</i> (R. Br.) F. Muell.	Udovicic 177	Australia	AM489906	AF190364							
<i>Luma apiculata</i> (DC.) Burret	Murillo 4205	Chile	JN660860	JN660910	JN661009						
<i>Luma apiculata</i> (DC.) Burret [T]	Lucas 208	RBG Kew (cultivated)		AM234101	AM489995	AY498795	AM489843	JN660959	JN661058	JN661108	KP722209
<i>Luma apiculata</i> (DC.) Burret [T]	Lucas 208	RBG Kew (cultivated)		AM234101	AM489995	AY498795	AM489843	KX789340	MF954229	KP722209	KP722331
<i>Luma chequen</i> (Molina) A. Gray	Landrum 7873	Chile	JN660861	JN660911	JN661010						
<i>Martiera clauseniana</i> (O. Berg) Kiaersk.	Matsumoto 752	Brazil (Minas Gerais)		JN091202							
<i>Myrcia eugenioioides</i> (D.Legrand & Kausel) Mazine	Lucas 61	Brazil (São Paulo)	AM489928	AM234107	AM489996	KP722429	AM489845	MF954359	MF954257	KP722205	JN091327
<i>Martiera glazioviana</i> Kiaersk.	Matsumoto 799	Brazil (São Paulo)	JN091255	JN091204							
<i>Martiera rubiginosa</i> (Cambess.) D. Legrand	Santos 600	Brazil (Minas Gerais)		KU898292							

<i>Martiera aff. subacuminata</i> Kiaersk.	Staggemeier 742	Brazil (Espírito Santo)	KP722397	KP722475	KP722305	KP722355
<i>Martiera teucheriana</i> (O. Berg.) D. Legrand	Lucas 633	Brazil (Minas Gerais)	KU898332	KU898390	KU898440	KU898495
<i>Mitranthes clarendonensis</i> (Proctor) Proctor	Vasconcelos 511	Jamaica	MF954049	MF954482	MF954307	MF954170
<i>Mitranthes glabra</i> Proctor	Lucas 1224	Jamaica	MF954050	MF954483	MF954308	MF954171
<i>Myrcogenia albigena</i> (DC.) Landrum	Lucas 167	Brazil (Minas Gerais)	AM234098	KP722441	AM489854	KP722376
<i>Myrcogenia bananalis</i> Bezzera & Landrum	Faria 4049	Brazil (Distrito Federal)	MF954052	MF954485	MF954389	MF954173
<i>Myrcogenia brevipedicellata</i> (Burret) D. Legrand & Kausel	Landrum 2830	Brazil (São Paulo)	JN660894	JN660893	JN660943	JN661092
<i>Myrcogenia campestris</i> (DC.) D. Legrand & Kausel	Kummrow 2940	Brazil (Paraná)	JN660895	JN660994	JN661043	JN661093
Species	Voucher	Collection locality	ITS	<i>matK</i>	<i>rpl16</i>	<i>rps16-trnQ</i>
<i>Myrcogenia chrysoarpa</i> (O. Berg) Kausel	Landrum 8166	Chile	JN660896	JN660995	JN661044	JN661094
<i>Myrcogenia colchaguensis</i> (Phil.) L.E. Navas	Landrum 8033	Chile	JN660847	JN660996	JN661045	JN661095
<i>Myrcogenia correfolia</i> (Hook. & Arn.) O. Berg	Tellier 5360	Chile	JN660901	JN661000	JN661049	JN661099
<i>Myrcogenia cucullata</i> D. Legrand	Wasum 105	Brazil (Rio Grande do Sul)	JN660898	JN660997	JN661046	JN661096
<i>Myrcogenia euosma</i> (O. Berg) D. Legrand	Soares 715	Brazil (Paraná)	JN660899	JN660998	JN661047	JN661097
<i>Myrcogenia exsucca</i> (DC.) O. Berg	Murillo 4217	Chile	JN660900	JN660999	JN661048	JN661098
<i>Myrcogenia franciscensis</i> (O. Berg) Landrum	Miyagi 357	Brazil (São Paulo)	JN660902	JN661001	JN661050	JN661100
<i>Myrcogenia gerritii</i> Landrum	Barbosa 948	Brazil (São Paulo)	JN660854	JN661003	JN661052	JN661102
<i>Myrcogenia glaucescens</i> (Cambess.) D. Legrand & Kausel	Landrum 11,231	Brazil	JN660905	JN661004	JN661053	JN661103
<i>Myrcogenia kleinii</i> D. Legrand	Cordeiro 734	Brazil (São Paulo)	JN660906	JN661005	JN661054	JN661104
<i>Myrcogenia lanceolata</i> (Juss. Ex J. St.-Hil.) Kausel	Mihoc 6220	Brazil	JN660908	AM489849	JN661056	JN661106
<i>Myrcogenia leptospermaides</i> (DC.) Kausel	Murillo 4214	Chile	JN660909	AM489850	JN661057	JN661107
<i>Myrcogenia miersiana</i> (Gardner) D. Legrand & Kausel	Lucas 164	Brazil (Paraná)	JN660912	JN661008	JN661058	JN661107
<i>Myrcogenia myrcioides</i> (Cambess.) O. Berg	Lucas 503	Brazil (Rio de Janeiro)	JN660862	JN661011	JN661060	JN661110
<i>Myrcogenia myrcioides</i> O. Berg	Rossato 47	Brazil (Rio Grande do Sul)	JN660915	JN661014	JN661063	JN661113
<i>Myrcogenia myrcioides</i> O. Berg			JN660869	JN661018	JN661067	JN661117
<i>Myrcogenia obtusa</i> (DC.) O. Berg	Brownless 1227	Chile	JN660916	JN661015	JN661064	JN661114
<i>Myrcogenia ovalifolia</i> (O. Berg) Landrum	Lucas 259	Chile	JN660917	JN661016	JN661065	JN661115
Species	Voucher	Collection locality	ITS	<i>matK</i>	<i>rpl16</i>	<i>rps16-trnQ</i>
<i>Myrcogenia ovata</i> (Hook. & Arn.) O. Berg	Gardner 19	Chile	AM489935	JN66102	JN661070	JN661120
<i>Myrcogenia oxysepala</i> (Burret) D. Legrand & Kausel	Ribas 2234	Brazil (Paraná)	JN660923	JN661022	JN661071	JN661121
<i>Myrcogenia parvifolia</i> (DC.) Kausel	Landrum 5916	Chile	JN660924	JN661023	JN661072	JN661122
<i>Myrcogenia pilotantha</i> (Kiaersk.) Landrum	Lucas 230	Brazil	JN660875	JN661024	JN661073	JN661123
<i>Myrcogenia pinifolia</i> (Phil.) Kausel	Gardner 164	Chile	JN660877	JN661026	JN661075	JN661125
<i>Myrcogenia planipes</i> (Hook. & Arn.) O. Berg	Aedo 7378	Chile	JN660928	JN661027	JN661076	JN661126
<i>Myrcogenia reitzii</i> D. Legrand & Kausel	Barbosa 945	Brazil (São Paulo)	JN660887	JN661036	JN661085	JN661135
<i>Myrcogenia rufo</i> (Colla) Skottsbo.	Tellier 150,795	Chile	JN660937	JN661036	JN661085	JN661135
<i>Myrcogenia schulzii</i> Johow	Ruiz 8266	Brazil (São Paulo)	JN660929	JN661028	JN661077	JN661127
<i>Myrcogenia seriatomosa</i> (Kiaersk.) D. Legrand & Kausel	Silva 2358	Brazil (Paraná)	JN660930	JN661029	JN661078	JN661128
<i>Myrcogenia smithii</i> Landrum	García 533	Brazil (São Paulo)	JN660888	JN661030	JN661086	JN661136
<i>Myrcia amazonica</i> DC.	Lucas 1108	Brazil (São Paulo)	JN660881	JN661030	JN661080	JN661130
<i>Myrcia aff. amazonica</i> DC.	Lucas 189	Dominican Republic	KU898328	JN091304	JN661129	JN661129
<i>Myrcia amplexicaulis</i> (O. Berg) Hook. f.	Neto 3007	Brazil (Mato Grosso)	KP722417	KP722325	MF954357	KU898544
<i>Myrcia anacardifolia</i> Gardner	Amorim 1940	Brazil (Espírito Santo)	MH880933*	MK157092*	MF954255	KU898544
	Nadrux 999	Brazil (Rio de Janeiro)	JN091267	JN091407	MF954255	KP722272
Species	Voucher	Collection locality	ITS	<i>matK</i>	MK175002*	KP722272
<i>Myrcia anceps</i> (Spreng.) O. Berg	Lucas 236	Brazil	ETS	<i>psbA-trnH</i>	MK175003*	KP722272
<i>Myrcia antonia</i> (O. Berg) Mazzini	Santos 840	Brazil (São Paulo)	JN091268	JN091408	MK175004*	rp16-trnQ
<i>Myrcia ascendens</i> M.F. Santos	Santos 829	Brazil (Bahia)	KU898300	KU898405	MK175004*	MK202485*
<i>Myrcia aulomyrcioides</i> F. Lucas & C.E. Wilson	Araujo 1885	Brazil (Rondônia)	KU164807	KU898404	KU898460	KP722277
<i>Myrcia aurea</i> NicLugh.	Lucas 729	Brazil (Espírito Santo)	MH880934*	KU164833	KU171280	KU898515
				MK157093*	MK202486*	KU164858
<i>Myrcia barttuensis</i> (Legname) B. Holst.	Serrano 5327	Argentina	MH880935*	MK157094*	MK182479*	MK202487*

<i>Myrcia aff. bergiana</i> O. Berg	Amorim 1810	Brazil (Ceará)	MH880929*	KU898370	MK157088*	MK174996*	MK182471*	MK202482*	KU898473
<i>Myrcia bicarinata</i> (O. Berg) D.Legrand	Santos 849	Brazil (São Paulo)	KU898313	KU898389	KU898418		KU898528	KU898528	KU898473
<i>Myrcia bicolor</i> Kiaersk.	Lucas 219	Brazil (Rio de Janeiro)	KU898331		KU898439		KU898546	KU898546	KU898494
<i>Myrcia blanchetiana</i> (O. Berg) Mattos	Santos 834	Brazil (Bahia)	JN091271	KU898379	KU898428		KU898538	KU898538	KU898483
<i>Myrcia bracteata</i> (Rich.) DC.	Prévost 4712	Brazil (Bahia)	JN091269		JN091409		JN091344	JN091344	JN091344
<i>Myrcia brasiliensis</i> Kiaersk.	Lucas 62	Brazil (São Paulo)	AM489917		AM489835		MK182480*	MK202488*	JN091345
<i>Myrcia calyptroanthoides</i> (O. Berg) Mattos	Santos 833	Brazil (Bahia)	KU898310	KU898367	KU898415		MK182481*	KU898470	KU898525
<i>Myrcia carvalhoi</i> NicLough.	Amorim 2026	Brazil (Bahia)	MH880936*		MK157095*		MK182481*	MK202489*	KU898470
<i>Myrcia caudata</i> (McVaugh) E.Lucas & C.E.Wilson	Zappi 1506	Brazil (Mato Grosso)	KU164819		KU164845		MK182482*	KU164870	KU164870
<i>Myrcia clauquetia</i> (Nied.) E.Lucas & Sobral	Amorim 2028	Brazil (Espírito Santo)	MH880937*		MK157096*		MK182482*	MK202490*	KU164870
<i>Myrcia clavelja</i> Sobral	Lucas 244	Brazil	JN091220	KP722442	JN091411		KP722217	KP722332	KP722332
Species	Voucher	Collection locality	ITS	<i>ndhF</i>	<i>psbA-trnH</i>	<i>rpl16</i>	<i>rpl32-trnL</i>	<i>rps16-trnQ</i>	<i>trnL-trnF</i>
<i>Myrcia congestiflora</i> Calliari & V.C. Souza	Torres 1673	Brazil (São Paulo)	MH880938*		MK157097*	MK175010*	MK182483*		KP722352
<i>Myrcia cordifolia</i> DC.	Faria 2470	Brazil (São Paulo)	MH880939*		MK157098*	MK175011*	MK182484*		KP722339
<i>Myrcia costera</i> M.F.Santos	Lucas 71	Brazil (São Paulo)	AM489945	KU898336	AM489862				KU898453
<i>Myrcia coumiete</i> (Aubl.) DC.	Lucas 107	French Guiana	AM234123		AM489864				KU898468
<i>Myrcia crocea</i> Kiaersk.	Amorim 1942	Brazil (Espírito Santo)	MH880940*		MK157099*	MK175013*	MK182486*		KU898523
<i>Myrcia aff. crocea</i> Kiaersk.	Amorim 1919	Brazil (São Paulo)			MK157089*	MK174997*			JN091343
<i>Myrcia cuprea</i> (O. Berg) Kiaersk.	Staggemeier 862	Brazil (Pará)	KP722394	KP722472	KP722302				JN091346
<i>Myrcia decorticans</i> DC.	Staggemeier 799	Brazil (Sergipe)	KP722383		KP722290				MK202491*
<i>Myrcia densa</i> (DC.) Sobral	Santos 643	Brazil (Minas Gerais)	KU898294	KU898351	KU898398				MK202483*
<i>Myrcia elevata</i> M.F.Santos	Santos 763	Brazil (Amazonas)			KU898413				KP722248
<i>Myrcia eriocalyx</i> DC.	Faria 1446	Brazil (Minas Gerais)	MH880941*		MK157100*	MK175014*	MK182487*		KP722237
<i>Myrcia eriopus</i> DC.	Lucas 258	Brazil	JN091222		JN091413	MK175015*			KU898509
<i>Myrcia espiritosantensis</i> B.S. Amorim	Amorim 2033	Brazil (Espírito Santo)	MH880942*		MK157101*	MK175016*			KU898468
<i>Myrcia eumecephylla</i> (O. Berg) Nied.	Matsumoto 803	Brazil (Espírito Santo)	JN091274	KP722446	JN091414				KU898477
<i>Myrcia excoriata</i> (Mart.) E.Lucas & C.E.Wilson	Matsumoto 825	Brazil (Espírito Santo)	JN091254	KP722449	JN091394				JN091328
<i>Myrcia eximita</i> DC.	Santos 625	Brazil (Distrito Federal)	KU898315	KU898373	KU898422				KU898532.
Species	Voucher	Collection locality	ITS	<i>ndhF</i>	<i>psbA-trnH</i>	<i>rpl16</i>	<i>rpl32-trnL</i>	<i>rps16-trnQ</i>	<i>trnL-trnF</i>
<i>Myrcia fenzliana</i> [DF]	Santos 622	Brazil (Distrito Federal)	MH880943*		MK157102*	MK175017*			MK202495*
<i>Myrcia fenzliana</i> [REP]	Vasconcelos 592	Dominican Republic	MH880944*		MK157103*	MK175018*	MK182488*		MK202496*
<i>Myrcia ferruginosa</i> Mazine	Santos 689	Brazil (Rio de Janeiro)	KU898296	KU898353	KU898400				KU898511.
<i>Myrcia flagellaris</i> (D.Legrand) Sobral	Lucas 83	Brazil (São Paulo)	AM234113	KP722430	AM489836				JN091350
<i>Myrcia follii</i> G.M.Barroso & Peixoto	Staggemeier 907	Brazil (Espírito Santo)	KP722384	KP722461	KP722291				KP722238
<i>Myrcia aff. glazioviana</i> Kiaersk.	Nadrux 1007	Brazil (Rio de Janeiro)	MH880950*		MK157090*	MK174998*	MK182472*		KU898455
<i>Myrcia grandifolia</i> Cambess.	Faria 2073	Brazil (Rio de Janeiro)	MH880945*		MK157104*	MK175021*	MK182491*		MK202497*
<i>Myrcia grandis</i> McVaugh	Staggemeier 850	Brazil (Amazonas)	KP722385	KP722462	KP722292				KP698772
<i>Myrcia graziae</i> NicLough.	Amorim 2016	Brazil (Bahia)	MH880946*		MK157105*	MK175022*			KP722341a
<i>Myrcia guianensis</i> (Aubl.) DC.	Harley 50,307	Brazil	JN091225	KU898361	JN091416				JN091351
<i>Myrcia harwegiana</i> (O. Berg) Kiaersk.	Amorim 1925	Brazil (São Paulo)	MH880947*	KU898408	MK157106*	MK175023*	MK182492*		MK202498*
<i>Myrcia hatschbachii</i> D.Legrand	Santos 661	Brazil (Paraná)	KU898304		KU898408				KU898518.
<i>Myrcia hebeperata</i> DC.	Lucas 64	Brazil (São Paulo)	AM234111		AM489934				MK202499*
<i>Myrcia hexasticha</i> Kiaersk.	Lucas 194	Brazil (Paraná)	JN091227	KP722438	JN091418				KP722214
<i>Myrcia aff. hirriflora</i> DC.	Lucas 1181	Brazil (Bahia)	KP722409	KP722487	KP722317				JN091354
<i>Myrcia ilheosensis</i> Kiaersk.	Amorim 2037	Brazil (Espírito Santo)	MH880948*		MK157107*	MK175025*	MK182494*		KP722367

Species	Voucher	Collection locality	ETS	ITS	matK	ndhF	psbA-trnH	rpl16	rpl32-trnL	rps16-trnQ	trnL-trnF
<i>Myrcia inaequiloba</i> (DC.) Lemée	Lucas 105	Brazil	JN091279	JN091228	JN091310	KP722428	JN091419			KP722204	JN091355
<i>Myrcia isaiana</i> G.M.Barroso & Peixoto	Lucas 60	Brazil (São Paulo)	JN091280	JN091229	JN091311	KP722423	JN091420			KP722249	JN091356
<i>Myrcia larioiteana</i> Cambess.,	Mello Silva 1705	Brazil (Minas Gerais)	AM489939	AM234115	AM490002	AM489856	AM489856			KU171297	JN091357
<i>Myrcia laxiflora</i> Cambess.	Meirelles 307	Brazil (Espírito Santo)		KP722403		KP722311				KP722257	
<i>Myrcia lenhiensis</i> Kiaersk.	Lucas 263	Brazil (Minas Gerais)	JN091281	JN091230	JN091312	KU898342	JN091421			KU898503	JN091358
<i>Myrcia aff. lucida</i> McVaugh	Araújo 311	Brazil (Amazonas)				KU898380	KU898429				KU898484
<i>Myrcia lughadhae</i> B.S. Amorim	Hurbath 92	Brazil (Bahia)		MH880949*		MK157108*					
<i>Myrcia magnifolia</i> (O. Berg) Kiaersk.	Amorim 2000	Brazil (Rio de Janeiro)		MH880950*		MK157109*		MK175026*			
<i>Myrcia marianae</i> Staggemeier & Lucas	Staggemeier 764	Brazil (Bahia)		KP722381		KP722458	KP722288			KP722235	KP722337
<i>Myrcia maritcaensis</i> Alain	Acevedo-Rodg. 7160	Puerto Rico		KU898330		KU898388	KU898438			KU898545	KU898493
<i>Myrcia maximiliana</i> O. Berg	Santos 750	Brazil (Bahia)		KU898318		KU898376	KU898425			KU898535	KU898480
<i>Myrcia mcvaughii</i> (B. Holst) E. Lucas & C.E. Wilson	Caddah 547	Brazil (Amazonas)		KU898333		KU898391	KU898441			KU898547	KU898496
<i>Myrcia megaphylla</i> M.F.Santos & Sobral	Santos 721	Brazil (Minas Gerais)		KU898317		KU898375	KU898424			KU898534	KU898479
<i>Myrcia micropetala</i> (Mart.) Nied.	Paixão 289	Brazil (Bahia)	JN091282	JN091231		JN091423					
<i>Myrcia microphylla</i> O. Berg,	Santos 617	Brazil (Goiás)		KU898325		KU898384	KU898433			KU898542	KU898488
<i>Myrcia multiflora</i> Sagot	Sasaki 2394	Brazil (Mato Grosso)		KP722399		KP722477	KP722307			KP722254	KP722357
<i>Myrcia mischophylla</i> Kiaersk.	Faria 1225	Brazil (Minas Gerais)	JN091283	MH880951*							JN091359
<i>Myrcia montana</i> DC.	Lucas 261	Brazil (Minas Gerais)		MH880952*				MK175027*		MK202501*	
Species	Voucher	Collection locality	ETS	ITS	matK	ndhF	psbA-trnH	rpl16	rpl32-trnL	rps16-trnQ	trnL-trnF
<i>Myrcia muatgensis</i> Sobral	Santos 823	Brazil (Bahia)		KU898299		KU898356	KU898403			KU898458	KU898514
<i>Myrcia multiflora</i> (Lam.) DC.	Staggemeier 422	Brazil (Mato Grosso)		KP722377	AM490003	KP722456	KP722286			KU898458	KU898514
<i>Myrcia multipunctata</i> Mazine	Santos 836	Brazil (Bahia)		KU898311		KU898368	KU898416			KU898526	KU898471
<i>Myrcia mutabilis</i> (O. Berg) N.Silveira	Mazine 1052	Brazil (Minas Gerais)	JN091284	JN091233	JN091313	KP722435	JN091424			KP722241	KP722344
<i>Myrcia myrtilifolia</i> DC.	Lima 381	Brazil (Minas Gerais)		MH880953*				MK175041*		MK202502*	
<i>Myrcia neodimorpha</i> (O. Berg) E.Lucas & C.E.Wilson	Folli 6649	Brazil (Espírito Santo)		KP722416		KP722494	KP722324			KP722271	KP722374
<i>Myrcia neoglabra</i> E.Lucas & C.E.Wilson	Staggemeier 935	Brazil (Rio de Janeiro)		KP722391		KP722469	KP722299	MK175029*		KP722245	KP722349
<i>Myrcia aff. neonotiana</i> (Aubl.) E.Lucas & C.E.Wilson	Holst 9384	Brazil		KP722377		KP722453	KP722285			KP722229	KP722333
<i>Myrcia neobscura</i> (O. Berg) E.Lucas & C.E.Wilson	Matsumoto 836	Brazil (Minas Gerais)	JN091256	JN091205		KP722452	JN091396			KP722228	JN091330
<i>Myrcia neoregeliana</i> E.Lucas & C.E.Wilson	Matsumoto 814	Brazil (Espírito Santo)	JN091259	JN091208		KP722448	JN091399			KP722225	JN091333
<i>Myrcia neoriedeliana</i> E.Lucas & C.E.Wilson	Lucas 88	Brazil (São Paulo)	AM489930	AM234109	AM489997	KP722432	AM489847			KP722208	KP722330
<i>Myrcia neospruceana</i> E. Lucas & Sobral	Lucas 601	Brazil (Minas Gerais)		KU898324		KU898383	KU898432			KU898541	KU898487
<i>Myrcia neosuraveolens</i> E.Lucas & C.E.Wilson	Lucas 85	Brazil (São Paulo)	AM489929	AM234108		KP722431	AM489846			KP722207	KP722329
<i>Myrcia neonotensis</i> E.Lucas & C.E.Wilson	Matsumoto 798	Brazil	JN091261	JN091210		JN091401		MK175030*		KP722224	JN091336
<i>Myrcia newwiediana</i> (O. Berg) E.Lucas & C.E.Wilson	Staggemeier 793	Brazil (Sergipe)		KP722402		KP722480	KP722310			KP698774	KP722360
<i>Myrcia nitida</i> Cambess.	Santos 720	Brazil (Minas Gerais)		KU898306		KU898363	KU898410			KU898520	KU898465
<i>Myrcia nivea</i> Cambess.	Lima 538	Brazil (Minas Gerais)		MH880954*				MK175031*		MK202503*	
Species	Voucher	Collection locality	ETS	ITS	matK	ndhF	psbA-trnH	rpl16	rpl32-trnL	rps16-trnQ	trnL-trnF
<i>Myrcia oblongata</i> DC.	Santos 667	Brazil (Santa Catarina)		KU898295		KU898352	KU898399			KU898510	KU898454
<i>Myrcia obversa</i> (D.Legrand) E.Lucas & C.E.Wilson	Matsumoto 820	Brazil (Espírito Santo)	JN091257	JN091206		KP722450	JN091397			KP722227	JN091331
<i>Myrcia palustris</i> DC.	Broto 1546	Brazil (Rio Grande do Sul)		MH880955*				MK175032*		MK202504*	
<i>Myrcia paracatuensis</i> Kiaersk.	Mello-Silva 1713	Brazil (Minas Gerais)	AM489942	AM234118		KP722421	AM489859			KP722230	KP722328a
<i>Myrcia pendula</i> Sobral	Lucas 1206	Brazil (Bahia)		MH880956*				MK175033*		MK202505*	
<i>Myrcia pinifolia</i> Cambess.	Santos 613	Brazil (Goiás)		KU898372		KU898421				KU898531	KU898476
<i>Myrcia playglada</i> DC.	Hawthorne 502	Grenade		KU898327		KU898385	KU898435			KP722250	KU898490
<i>Myrcia aff. plusiantha</i> Kiaersk.	Staggemeier 737	Brazil (Espírito Santo)		KP722395		KP722303		MK174999*		KP722250	KP722353
<i>Myrcia polyantha</i> DC.	Staggemeier 797	Brazil (Sergipe)		KP722400		KP722478	KP722308a			KP722255	KP722358
<i>Myrcia pseudomartiana</i> Sobral	Souza 1139	Brazil		KP722404		KP722482	KP722312	MK175034*		KP722258	KP722362

<i>Myrcia pseudospectabilis</i> Sobral	Amorim 2005	Brazil (Bahia)	JN091285	MH880957*	MK157116*	MK175035*	MK182504*	MK202506*	JN091363
<i>Myrcia pubescens</i> DC.	IBGE s.n.	Brazil (Distrito Federal)	JN091285	JN091234	JN091425	MK175036*	MK182505*	MK202507*	JN091363
<i>Myrcia aff. pubescens</i> DC.	Faria s.n. (28.11.2014)	Brazil (Distrito Federal)	MH880931*	MH880931*	MK175000*	MK182474*	MK182474*	MK202509*	JN091367
<i>Myrcia pubipetala</i> Miq.	Lucas 86	Brazil (São Paulo)	AM234114	AM234114	AM489855	MF954259	MF954259	KP722273	JN091364
<i>Myrcia pulchra</i> (O. Berg) Kiaersk.	Lucas 138	Brazil (Paraná)	JN091286	JN091235	JN091426	MF954361	MF954361	KU898501	JN091365
<i>Myrcia pubinrata</i> B.S. Amorim	Amorim 1901	Brazil (Bahia)	MH880958*	MH880958*	MK157117*	MK182506*	MK182506*	MK202508*	trnL-trnF
Species	Voucher	Collection locality	ITS	ITS	psbA-trnH	rpl16	rpl32-trnL	tps16-trnQ	JN091366
<i>Myrcia racemosa</i> (O. Berg) Kiaersk.	Lucas 63	Brazil (São Paulo)	AM489944	AM490005	KP722424	KP722424	KP722424	KP722259	JN091366
<i>Myrcia aff. racemosa</i> (O. Berg) Kiaersk.	Staggemeier 751	Brazil (Bahia)	KP722380	KP722380	KP722287	KP722287	KP722287	KP722234	KP722236
<i>Myrcia reticulata</i> Cambess.	Santos 803	Brazil (Rio de Janeiro)	MH880959*	MH880959*	MK157118*	MK182507*	MK182507*	MK202509*	JN091367
<i>Myrcia reticulata</i> Miq.	Hanley 50,309	Brazil	JN091287	JN091236	JN091427	MK182508*	MK182508*	KP722243	KP722246
<i>Myrcia riococensis</i> G.M.Barroso & Peixoto	Staggemeier 917	Brazil (Espírito Santo)	JN091287	JN091236	KP722296	KP722296	KP722296	KP722243	KP722246
<i>Myrcia robusta</i> Sobral	Lucas 727	Brazil (Espírito Santo)	KU898289	KU898289	KU898393	KU898393	KU898393	KU898448	KU898448
<i>Myrcia norida</i> (O. Berg) Liaersk.	Bridgewater 1076	Brazil (Tocantins)	JN091289	JN091238	JN091429	JN091429	JN091429	MK202510*	JN091368
<i>Myrcia rosangelae</i> NicLugh.	Amorim 1499	Brazil (Sergipe)	MH880960*	MH880960*	MK157119*	MK182509*	MK182509*	MK202510*	JN091370
<i>Myrcia rotundata</i> (Amshoff) McVaugh	Caddah 555	Brazil (Amazonas)	MH880961*	MH880961*	KU898419	KU898419	KU898419	KU898529	KU898474
<i>Myrcia ruschii</i> B.S. Amorim	Amorim 1941	Brazil (Espírito Santo)	MH880962*	MH880962*	MK157120*	MK182510*	MK182510*	KU898529	KU898474
<i>Myrcia rufipes</i> DC.	Lucas 280	Brazil	JN091290	JN091239	JN091430	JN091430	JN091430	KU898508	JN091369
<i>Myrcia rupestris</i> M.F.Santos	Santos 640	Brazil (Minas Gerais)	KU898293	KU898293	KU898397	KU898397	KU898397	KU898452	KU898452
<i>Myrcia rupestris</i> M.F.Santos	Vasconcelos 311	Brazil (Amazonas)	MF954055	MF954055	MF954391	MF954391	MF954391	MF954113	JN091370
<i>Myrcia rupestris</i> M.F.Santos	Lucas 98	Brazil	JN091291	AM234119	AM489860	AM489860	AM489860	KP722203	JN091370
<i>Myrcia saxatilis</i> (Amshoff) McVaugh	Lucas 110	Brazil (Bahia)	JN091291	JN091240	JN091431	JN091431	JN091431	KP722212	JN091371
<i>Myrcia seloi</i> (Spreng.) N.Silveira	Amorim 2013	Brazil (Bahia)	MH880962*	MH880962*	MK157121*	MK182511*	MK182511*	MK202511*	JN091371
Species	Voucher	Collection locality	ITS	ITS	psbA-trnH	rpl16	rpl32-trnL	tps16-trnQ	trnL-trnF
<i>Myrcia aff. servata</i> McVaugh	Santos 777	Brazil (Amazonas)	KU898319	KU898319	KU898426	KU898426	KU898426	KU898536	KU898481
<i>Myrcia sessilissima</i> M.F.Santos	Santos 641	Brazil (Minas Gerais)	KU898316	KU898316	KU898423	KU898423	KU898423	KU898533	KU898478
<i>Myrcia spathulifolia</i> Proença	Faria 4214	Brazil (Bahia)	MF954058	MF954058	MF954490	MF954490	MF954490	MF954115	KU898478
<i>Myrcia spectabilis</i> DC.	Amorim 1989	Brazil (Rio de Janeiro)	MH880963*	MH880963*	MK157122*	MK182512*	MK182512*	MK202512*	JN091372
<i>Myrcia splendens</i> (Sw.) DC.	Lucas 73	Brazil (Minas Gerais)	AM234122	AM234122	AM489863	AM489863	AM489863	KP722274	JN091374
<i>Myrcia springiana</i> O. Berg [BA]	Amorim 2007	Brazil (Bahia)	MH880964*	MH880964*	MK157123*	MK182513*	MK182513*	MK202513*	JN091374
<i>Myrcia springiana</i> O. Berg [PE]	Amorim 1985	Brazil (Pernambuco)	MH880965*	MH880965*	MK157124*	MK182514*	MK182514*	MK202514*	JN091374
<i>Myrcia squamata</i> (Mattos & D. Legrand) Matos	Vieira 800	Brazil (Paraná)	MH880966*	MH880966*	MK157125*	MK182515*	MK182515*	MK202515*	JN091374
<i>Myrcia stricta</i> (O. Berg) Kiaersk.	Santos 608	Brazil (Goiás)	KU898314	KU898314	KU898420	KU898420	KU898420	KU898475	KU898530
<i>Myrcia subavenia</i> (O. Berg) N.Silveira	Santos 585	Brazil (Minas Gerais)	KU898291	KU898291	KU898395	KU898395	KU898395	KU898506	KU898450
<i>Myrcia subcordata</i> DC.	Santos 586	Brazil (Minas Gerais)	KU898302	KU898302	KU898406	KU898406	KU898406	KU898516	KU898461
<i>Myrcia aff. subobliqua</i> (Benth.) Nied.	Staggemeier 839	Brazil (Amazonas)	KP722396	KP722396	KP722304	KP722304	KP722304	KP722251	KP722354
<i>Myrcia subsericea</i> A. Gray	Santos 797	Brazil (Rio de Janeiro)	MH880967*	MH880967*	MK157126*	MK182514*	MK182514*	MK202515*	KP722354
<i>Myrcia subterminalis</i> M.F.Santos	Santos 733	Brazil (Espírito Santo)	KU898307	KU898307	KU898411	KU898411	KU898411	KU898521	KU898466
<i>Myrcia subverticillaris</i> (O. Berg) Kiaersk.	Lucas 251	Brazil (Minas Gerais)	JN091295	JN091244	JN091435	JN091435	JN091435	KP722222	JN091335
<i>Myrcia sucreti</i> (G.M.Barroso & Peixoto) E.Lucas & C.E.Wilson	Matsumoto 824	Brazil (Espírito Santo)	JN091260	JN091209	JN091400	JN091400	JN091400	KP722222	JN091335
Species	Voucher	Collection locality	ITS	ITS	psbA-trnH	rpl16	rpl32-trnL	tps16-trnQ	trnL-trnF
<i>Myrcia suffruticosa</i> O. Berg	Mello-Silva 1690	Brazil (Minas Gerais)	JN091296	JN091245	JN091436	JN091436	JN091436	KU898522	JN091377
<i>Myrcia tenuifolia</i> (O. Berg) Sobral	Santos 747	Brazil (Espírito Santo)	KU898308	KU898308	KU898412	KU898412	KU898412	KU898522	KU898467
<i>Myrcia tenuivenosa</i> Kiaersk.	Lucas 87	Brazil (São Paulo)	JN091297	JN091246	JN091437	JN091437	JN091437	KU898500	JN091378
<i>Myrcia tetraphylla</i> Sobral	Staggemeier 926	Brazil (Bahia)	KP722389	KP722389	KP722467	KP722467	KP722467	KP698773	KP722347
<i>Myrcia thyrsoidea</i> O. Berg	Amorim 2019	Brazil (Bahia)	MH880968*	MH880968*	MK157127*	MK182515*	MK182515*	MK202516*	MK202516*

<i>Myrcia tijuacensis</i> Kiaersk.	Amorim 2055	Brazil (Santa Catarina)	AM489915	MH880969*	JK091318	MK157128*	MK175050*	MK182516*	MK202517*	JN091379
<i>Myrcia tomentosa</i> (Aubl.) DC.	Soares-Silva 752	Brazil (Distrito Federal)	AM489940	AM234116	JK091318	AM489857				JN091380
<i>Myrcia torta</i> DC.	Soares 751	Brazil (Distrito Federal)	JK091298	JK091247	JK091318	JK091438				JN091381
<i>Myrcia aff. truncata</i> Sobral	Lucas 1189	Brazil (Bahia)	KP722412	KP722320	KP722490	KP722490				KP722370
<i>Myrcia umbraicicola</i> (Kunth) E.Lucas & C.E.Wilson	Souza s.n.	Brazil (Amazonas)	KP722392	KP722300	KP722470	KP722470	MF954350	MF954230	MF954246	KP722350
<i>Myrcia aff. unana</i> Sobral	Amorim 2024	Brazil (Bahia)	MH880932*	MH880932*	MH880932*	MH880932*	MK175001*	MK182475*	MK202484*	
<i>Myrcia variabilis</i> DC.	Lucas 277	Brazil	JK091299	JK091248	JK091319	JK091439				JN091382
<i>Myrcia venulosa</i> DC.	Crux 195	Brazil (Paraná)	AM489949	AM234125	AM489866	AM489866	MK175051*	MK182517*	KU898537	JN091383
<i>Myrcia vesita</i> DC.	Lucas 93	Brazil (São Paulo)	JK091300	JK091249	JK091440	JK091440				JN091384
<i>Myrcia vitrotiana</i> Kiaersk.	Amorim 2008	Brazil (Bahia)	JK091301	MH880970*	KU898382	KU898382	MK175052*	MK182518*	MK202518*	JN091385
<i>Myrcia</i> sp. [Harms 20]	Harms 20	Brazil (Amazonas)	KU898323	KU898323	KU898431	KU898431	MF954362	MF954260	KU898540	KU898486
<i>Myrcia</i> sp1 [T]	Vasconcelos 307	Brazil (Amazonas)	MF954056	MF954056	MF954488	MF954488	MF954362	MF954260	MF954114	MF954174
Species	Voucher	Collection locality	ITS	ITS	<i>ndhF</i>	<i>ndhF</i>	<i>rpl16</i>	<i>rpl32-trnL</i>	<i>rps16-trnQ</i>	<i>trnL-trnF</i>
<i>Myrcia</i> sp2	Staggemeier, V.G. 792	Brazil (Sergipe)	KP722382	KP722382	KP722459	KP722459	KP722309		KP722236	KP722338
<i>Myrcia</i> sp2 [T]	Faria 4193	Brazil (Bahia)	MF954057	MF954057	MF954489	MF954489	MF954364	MF954262		
<i>Myrcia</i> sp3	Lucas 1169	Brazil (Bahia)	KP722410	KP722318	KP722471	KP722301			KP722265	KP722368
<i>Myrcia</i> sp4	Staggemeier 927	Brazil (Bahia)	KP722390	KP722298	KP722468	KP722298			KP722244	KP722348
<i>Myrcia</i> sp5	Lucas 1192	Brazil (Bahia)	KP722414	KP722322	KP722492	KP722322			KP722269	KP722372
<i>Myrcia</i> sp6	Souza 1131	Brazil	KP722405	KP722313	KP722483	KP722313			KP722260	KP722363
<i>Myrcia</i> sp7	Lucas 1190	Brazil (Bahia)	KP722413	KP722321	KP722491	KP722321			KP722268	KP722371
<i>Myrcia</i> sp8	Staggemeier 901	Brazil (Espírito Santo)	KP722401	KP722309	KP722479	KP722309			KP722256	KP722359
<i>Myrcia</i> sp11	Staggemeier 845	Brazil (Amazonas)	KP722398	KP722306	KP722476	KP722306			KP722253	KP722356
<i>Myrcia</i> sp12	Staggemeier 762	Brazil (Bahia)	KP722393	KP722301	KP722471	KP722301			KP722247	KP722351
<i>Myrcia</i> sp13	Staggemeier 896	Brazil (Espírito Santo)	KP722407	KP722315	KP722485	KP722315			KP722262	KP722365a
<i>Myrciaria cuspidata</i> O. Berg	ICN 167,445	Brazil	JQ033316	JQ033345	JQ033345	JQ033345				
<i>Myrciaria floribunda</i> (H.West ex Willd.) O. Berg	Mazine, F. 796	Brazil	AM234094	AM489870	AM489870	AM489870	MF954369	MF954267	KP722282	
<i>Myrciaria glazioviana</i> (Kiaersk.) G.M. Barroso ex Sobral	Vasconcelos 413	Brazil (Bahia)	MF954061	MF954397	MF954493	MF954397	MF954368	MF954266	MF954117	MF954177
<i>Myrciaria vexator</i> McVaugh	Vasconcelos 709	Singapore BG (cultivated)	MF954063	MF954399	MF954495	MF954399	MF954414	MF954268	MF954119	MF954179
<i>Myrtus communis</i> L.	Lucas 211	RBG Kew (cultivated)	AM234149	AM490009	KP722420	AM489872	JN660939	MF954420	KP722221	KP722327
<i>Neomitranthes cordifolia</i> (D.Legrand) D.Legrand	Foster 1011	Brazil	AM489413	AM489410	AM489413	AM489569	MF954418	MF954421	JN091386	MF954123
<i>Plinia cordifolia</i> (D.Legrand) Sobral	Mazine 957a	Brazil (Minas Gerais)	AM489411	AM489411	AM489411	AM489570	This study		KP722219	
Species	Voucher	Collection locality	ITS	ITS	<i>ndhF</i>	<i>ndhF</i>	<i>rpl16</i>	<i>rpl32-trnL</i>	<i>rps16-trnQ</i>	<i>trnL-trnF</i>
<i>Plinia nana</i> Sobral	Mazine 662	Brazil (Minas Gerais)	MF954068	MF954068	MF954504	MF954504	MF954375	MF954237	KP722276	MF954187
<i>Plinia pauciflora</i> M.L.Kawas. & B.Holst	Mazine 957b	Brazil (Minas Gerais)	AM489414	AM489411	AM489414	AM489570	MF954376	MF954238	JN091388	JN091388
<i>Plinia</i> sp1	Holst 9482	French Guiana	MF954069	MF954069	MF954505	MF954405	MF954376	MF954238	MF954188	MF954188
<i>Siphoneugeta densiflora</i> O. Berg	Mazine 1050	Brazil (Minas Gerais)	AM489572	AM489412	KP722444	AM489571	MF954383	MF954245	KP722220	JN091389
<i>Siphoneugeta guilfoyleana</i> C.Proença	Lucas 70	Brazil (São Paulo)	AM489966	AM234085	AM490638	AM490638	MF954383	MF954245		JN091390
<i>Syzygium jambos</i> (L.) Alston in H. Trimen	Lucas 214	RBG Kew (cultivated)	AM234135	AM234135	AM490016	AM489882				

Appendix B. Supplementary material

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

References

- Acevedo-Rodriguez, P., Strong, M.T., 2017. Flora of the West Indies. Available from: <http://botany.si.edu/Antilles/Westindies/> (accessed 10.07.17).
- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Tran. Automat. Contr.* 19, 716–723.
- Amorim, B.S., 2017. Filogenia e taxonomia do clado Gomidesia (*Myrcia* s.l., Myrtaceae) na Floresta Atlântica do Brasil. Ph.D. dissertation. Universidade Federal de Pernambuco, 190pp.
- Amorim, B.S., Alves, M., 2015. Two new species of the *Gomidesia* clade of *Myrcia* s.l. (Myrteae, Myrtaceae) from the Atlantic Forest of southern Bahia Brazil. *Brittonia* 67, 311–318.
- Amorim, B.S., Alves, M., 2016. Taxonomic novelties in *Gomidesia* clade (*Myrcia* s.l., Myrtaceae) from the Atlantic Forest of Brazil. *Phytotaxa* 272 (4), 287–293.
- Amorim, B.S., Lucas, E., Alves, M., 2014. *Myrcia lughadhii* sp. nov. (*Myrcia* s.l., Myrtaceae), a new endemic species from the Brazilian highlands. *Kew Bull.* 69, 9535.
- Antonelli, A., Verola, C.F., Parisod, C., Gustafsson, A.L.S., 2010. Climate cooling promoted the expansion and radiation of a threatened group of South American orchids (Epidendroideae: Laeliinae). *Biol. J. Linn. Soc.* 100, 597–607.
- Antonelli, A., Hettling, H., Condamine, F.L., Vos, K., Nilsson, R.H., Sanderson, M.J., Sauquet, H., Scharn, R., Silvestro, D., Töpel, M., Bacon, C.D., Oxelman, B., Vos, R.A., 2017. Towards a Self-Updating Platform for Estimating Rates of Speciation and Migration, Ages, and Relationships of Taxa (SUPERSMART). *Syst. Biol.* 66, 152–166. <https://doi.org/10.1093/sysbio/syw066>.
- Antonelli, A., Zizka, A., Carvalho, F.A., Scharn, R., Bacon, C.D., Silvestro, D., Condamine, F., 2018. Amazonia is the primary source of Neotropical biodiversity. *Proc. Nat. Acad. Sci. U.S.A.* 115, 6034–6039.
- Bacon, C., Mora, A., Warren, W., Jaramillo, C., 2013. Testing geological models of evolution of the Isthmus of Panama in a phylogenetic framework. *Bot. J. Linn. Soc.* 171, 287–300.
- Bacon, C.D., Silvestro, D., Jaramillo, C., Smith, B.T., Chakrabarty, P., Antonelli, A., 2015. Biological evidence supports an early and complex emergence of the Isthmus of Panama. *Proc. Nat. Acad. Sci. U.S.A.* 112, 6110–6115.
- Batalha-Filho, H., Fjelds, J., Fabre, P.-H., Miyaki, C.Y., 2013. Connections between the Atlantic and the Amazonian forest avifaunas represent distinct historical events. *J. Ornithol.* 154, 41–50.
- Benson, D.A., Cavanaugh, M., Clark, K., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J., Sayers, E.W., 2013. GenBank. *Nucleic Acids Res.* 41, D36–D42. <https://doi.org/10.1093/nar/gks1195>.
- Berg, O., 1855–1856. Revisio Myrteacearum Americae. *Linnaea* 27, 1–472.
- Berg, O., 1857. Myrtaceae. In: Martius, C.F.P. von. *Fl. bras.* 14, pp. 1–528.
- BFG [the Brazil Flora Group], 2015. Growing knowledge: an overview of seed Plant diversity in Brazil. *Rodriguésia* 66, 1085–1113. <https://doi.org/10.1590/2175-7860201566411>.
- Bünger, M.O., Mazine, F.F., Forest, F., Bueno, M.L., Stehmann, J.R., Lucas, E.J., 2016. The evolutionary history of *Eugenia* sect. *Phyllocalyx* (Myrtaceae) corroborates historically stable areas in the southern Atlantic Forests. *Ann. Bot.* 118, 1209–1223.
- Carnaval, A.C., Moriz, C., 2008. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic Forest. *J. Biogeogr.* 35 (7), 1187–1201.
- Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P., Linder, P., 2009. Phylogenetic biome conservatism on a global scale. *Nature* 458, 754–756.
- Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nat. Methods* 9, 772.
- Donoghue, M.J., 2008. A phylogenetic perspective on the distribution of plant diversity. *Proc. Nat. Acad. Sci. U.S.A.* 105, 11549–11555.
- Doyle, J.J., Doyle, J.L., 1987. A rapid isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull.* 19, 11–15.
- Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* 32, 1792–1797.
- Erixon, P., Svennblad, B., Britton, T., Oxelman, B., 2003. Reliability of Bayesian Posterior Probabilities and Bootstrap Frequencies in Phylogenetics. *Syst. Biol.* 52, 665–673.
- Fine, P.V.A., Zapata, F., Daly, D.C., 2014. Investigating processes of Neotropical rainforest tree diversification by examining the evolution and historical biogeography of the Protieae (Burseraeae). *Evolution* 68, 1988–2004.
- Forni-Martins, E.R., Martins, F.R., 2000. Chromosome studies on Brazilian *cerrado* plants. *Gen. Mol. Biol.* 23, 947–955.
- Franck, A.R., Cochrane, B.J., Garey, J.R., 2013. Phylogeny, biogeography, and infra-generic classification of *Harrisia* (Cactaceae). *Syst. Bot.* 38, 210–223. <https://doi.org/10.1600/036364413X662105>.
- Françoso, R.D., Haidar, R.F., Machado, R.B., 2016. Tree species of South America central savanna: endemism, marginal areas and the relationship with other biomes. *Acta Bot. Bras.* 30, 78–86. <https://doi.org/10.1590/0102-33062015abb0244>.
- Galindo-Leal, C., Câmara, I.G., 2003. Atlantic Forest hotspot status: an overview. In: Galindo-Leal, C., Câmara, I.G. (Eds.), *The Atlantic Forest of South America: Biodiversity Status, Threats and Outlook*. CABS and Island Press, Washington, pp. 3–11.
- Giulietti, A.M., Pirani, J.R., 1988. Patterns of geographic distribution of some plant species from the Espinhaço Range, Minas Gerais and Bahia. In: Vanzolini, P.F., Heyer, W.R. (Eds.), *Proceedings of a Workshop on Neotropical Distribution Patterns Held 12–16 January 1987*. Academia Brasileira de Ciências, Rio de Janeiro.
- Hansen, A.K., Gilbert, L.E., Simpson, B.B., Downie, S.R., Cervi, A.C., Jansen, R.K., 2006. Phylogenetic relationships and chromosome number evolution in *Passiflora*. *Syst. Bot.* 31, 138–150.
- Harvey, P.H., Pagel, M.D., 1991. *The Comparative Method in Evolutionary BIOLOGY*. Oxford University Press, Oxford.
- Hillis, D.M., Bull, J.J., 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst. Biol.* 42, 182–192.
- Kawasaki, M.L., Holst, B., 2004. Myrtaceae. In: Smith, N., Mori, S.A., Henderson, A., Stevenson, D.W., Heald, S. (Eds.), *Flowering Plants of the Neotropics*. Princeton University Press, New Jersey, pp. 264–266.
- Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Mentjies, P., Drummond, A., 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28, 1647–1649.
- Kiaerskou, H.F.C., 1893. Enumeratio myrtacearum brasiliensium. In: Warming, Symbolarum ad floram Brasiliae Centralis cognoscendam, vol. 39, pp. 1–199.
- Landrum, L.R., 1984. Taxonomic implications of the discovery of calyptrate species of *Myrceugenia* (Myrtaceae). *Brittonia* 35, 161–166.
- Landrum, L.R., 1986. *Campomanesia, Pimenta, Blepharocalyx, Legrandia, Acca, Myrrhinium, and Luma* (Myrtaceae). *Fl. Neotrop. Monogr.* 45, 1–179.
- Legrand, C.D., 1958. Las especies tropicales del género *Gomidesia* (Myrtaceae). *Com. Bot. Mus. Hist. Nat. Mont.* 3, 1–30.
- Lima, D.F., 2017. Estudos Filogenéticos e Taxonômicos em *Myrcia* DC. sensu lato (Myrtaceae), com ênfase no clado Guianensis. Ph.D. dissertation. Universidade Estadual de Campinas, 334 pp.
- Lucas, E.J., Harris, S.A., Mazine, F.F., Belsham, S.R., NicLughadha, E.M., Telford, A., Gasson, P.E., Chase, M.W., 2007. Suprageneric phylogenetics of Myrteae, the generically richest tribe in Myrtaceae (Myrtales). *Taxon* 56, 1105–1128.
- Lucas, E., Matsumoto, K., Harris, S.A., Nic Lughadha, E.M., Benardini, B., Chase, M.W., 2011. Phylogenetics, morphology, and evolution of the large genus *Myrcia* s.l. (Myrtaceae). *Int. J. Pl. Sci.* 172, 915–934.
- Lucas, E., Amorim, B.S., Lima, D.F., Lima, L., Lima-Lourenço, A.R., Nic Lughadha, E.M., Proença, C., Rosa, P.O., Rosário, A., Santos, M.F., Souza, M.C., Staggemeier, V.G., Vasconcelos, T., Sobral, M., 2018. A new infra-generic classification of the species rich Neotropical genus *Myrcia* s.l. *Kew Bull.* 73, 9.
- Maciell, J.R., Sánchez-Tapia, Andrea, Siqueira, M.F., Alves, M., 2017. Paleodistribution of epiphytic bromeliads points to past connections between the Atlantic and Amazon forests. *Bot. J. Linn. Soc.* 183, 348–359.
- Mazine, F.F., Souza, V.C., Sobral, M., Forest, F.F., Lucas, E., 2014. A preliminary phylogenetic analysis of *Eugenia* (Myrtaceae: Myrteae), with a focus on Neotropical species. *Kew Bull.* 69, 1–14.
- McVaugh, R., 1968. The genera of American Myrtaceae – an interim report. *Taxon* 17, 354–418.
- McVaugh, R., 1969. Myrtaceae. In: Maguire, B., et al., *Botany of the Guayana Highland – Part VIII*. *Mem. New York Bot. Gard.* 18, 55–286.
- Michelangeli, F.A., Guimarães, P.J.F., Penneys, D.S., Almeda, F., Kriebel, R., 2013. Phylogenetic relationships and distribution of New World Melastomeae (Melastomataceae). *Bot. J. Linn. Soc.* 171, 38–60.
- Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*. Available at: <http://www.phylo.org/index.php/>.
- Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J.C., Valencia, V., Ayala, C., Pérez-Angel, L.C., Rodríguez-Parra, L.A., Ramirez, V., Niño, H., 2015. Middle Miocene closure of the Central American Seaway. *Science* 348 (6231), 226–229.
- Morrone, J.J., 2006. Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistics analyses of the entomofauna. *Ann. Rev. Entomol.* 51, 467–494.
- Morrone, J.J., 2014. Cladistic biogeography of the Neotropical region: identifying the main events in the diversification of the terrestrial biota. *Cladistics* 30, 202–214.
- Murillo, A.J., Ruiz, P.E., Landrum, L.R., Stuessy, T.F., Barfuss, M.H.J., 2012. Phylogenetic relationships in *Myrceugenia* (Myrtaceae) based on plastid and nuclear DNA sequences. *Mol. Phylogenet. Evol.* 62, 764–776.
- Murillo, A.J., Stuessy, T.F., Ruiz, E., 2016. Explaining disjunct distributions in the flora of southern South America: evolutionary history and biogeography of *Myrceugenia* (Myrtaceae). *J. Biogeogr.* 43, 979–990.
- Murillo, A.J., Stuessy, T.F., Ruiz, E., 2013. Phylogenetic relationships among *Myrceugenia*, *Blepharocalyx*, and *Luma* (Myrtaceae) based on paired-sites models and the secondary structures of ITS and ETS sequences. *Plant Syst. Evol.* 299, 713–729.
- Myers, N., 2003. Biodiversity hotspots revisited. *Bioscience* 53, 916–917.
- Myrcia in Flora do Brasil 2020, in preparation. Jardim Botânico do Rio de Janeiro. Disponível em: < <http://floradobrasil.jbrj.gov.br/rflora/floradobrasil/FB10660> > . (accessed 07.07.17).
- Nic Lughadha, E.M., 1997. Systematic studies in Gomidesia. Ph.D. dissertation. University of St. Andrews, pp. 254.
- Nieto-Blázquez, M.E., Antonelli, A., Roncal, J., 2017. Historical biogeography of endemic seed plant genera in the Caribbean: Did GAARlandia play a role? *Ecol. Evol.* 7,

- 10158–10174.
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290.
- Pirie, M.D., 2015. Phylogenies from concatenated data: Is the end nigh? *Taxon* 64, 421–423. <https://doi.org/10.12705/643.1>.
- Prance, G.T., 1982. Forest refuges: Evidence from Woody angiosperms. In: Prance, G.T. (Ed.), *Biological Diversification in the Tropics*. Columbia University Press, New York, pp. 137–157.
- R Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available: <http://www.R-project.org/>.
- Rambaut A., 2014. FigTree v1.4.2. Available from: <http://tree.bio.ed.ac.uk/software/figtree/>.
- Rambaut A., Suchard, M.A., Xie, W., Drummond, A.J., 2014. TRACER v1.6, Available from <http://tree.bio.ed.ac.uk/software/tracer/>.
- Roncal, J., Zona, S., Lewis, C.E., 2008. Molecular Phylogenetic Studies of Caribbean Palms (Arecaceae) and Their Relationships to Biogeography and Conservation. *Bot. Rev.* 74, 78–102.
- Ronquist, F., Teslenko, M., van der Mark, P., 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61, 539–542.
- Santiago-Valentin, E., Olmstead, R.G., 2004. Historical biogeography of Caribbean plants: introduction to current knowledge and possibilities from a phylogenetic perspective. *Taxon* 53, 299–319.
- Santos, M.F., Sano, P.T., Forest, F., Lucas, E., 2016. Phylogeny, morphology and circumscription of *Myrcia* sect. *Sympodiomyrcia* (*Myrcia* s.l., Myrtaceae). *Taxon* 65, 759–774.
- Santos, M.F., Lucas, E., Sano, P.T., Buerki, S., Staggemeier, V.G., Forest, F., 2017. Biogeographical patterns of *Myrcia* s.l. (Myrtaceae) and their correlation with geological and climatic history in the Neotropics. *Mol. Phylogenet. Evol.* 108, 34–48.
- Simon, M.F., Pennington, R.T., 2012. The evolution of adaptations of woody plants in the savannas of the Brazilian Cerrado. *Int. J. Plant Sci.* 173, 711–723.
- Simon, M.F., Grether, R., Queiroz, L.P., Skema, C., Pennington, R.T., Hughes, C.E., 2009. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proc. Nat. Acad. Sci. U.S.A.* 106, 20359–20364.
- Sobral, M., 2010. Ten New Myrtaceae From Eastern and Northeastern Brazil. *J. Bot. Res. Inst. Texas* 4, 133–158.
- Staggemeier, V.G., Diniz-Filho, J.A.F., Forest, F., Lucas, E., 2015. Phylogenetic analysis in *Myrcia* section *Aulomyrcia* and inferences on plant diversity in the Atlantic rainforest. *Ann. Bot.* 115, 747–761.
- Stamatakis, A., 2006. RAxML-VI-HPC: Maximum Likelihood-based Phylogenetic Analyses with Thousands of Taxa and Mixed Models. *Bioinformatics* 22, 2688–2690.
- Stamatakis, A., 2014. RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. *Bioinformatics*. <https://doi.org/10.1093/bioinformatics/btu033>.
- Sytsma, K.J., Litt, A., Zjhra, M.L., Pires, J.C., Nepokroeff, M., Conti, E., Walker, J., Wilson, P.G., 2004. Clades, clocks, and continents: historical and biogeographical analysis of Myrtaceae, Vochysiaceae, and relatives in the Southern Hemisphere. *Int. J. Plant Sci.* 165, S85–S105.
- Thornhill, A.H., Ho, S.Y.W., K ulheim, C., Crisp, M.D., 2015. Interpreting the modern distribution of Myrtaceae using a dated molecular phylogeny. *Mol. Phylogenet. Evol.* 93, 29–43.
- Turchetto-Zolet, A.C., Salgueiro, F., Turchetto, C., Cruz, F., Veto, N.M., Barros, M.J.F., Segatto, A.L.A., Freitas, L.B., Margis, R., 2016. Phylogeography and ecological niche modelling in *Eugenia uniflora* (Myrtaceae) suggest distinct vegetational responses to climate change between the southern and the northern Atlantic Forest. *Bot. J. Linn. Soc.* 182, 670–688.
- Vasconcelos, T.N.C., Prenner, G., B unger, M.O., De-Carvalho, P.S., Wingler, A., Lucas, E.J., 2015. Systematic and evolutionary implications of stamen position in Myrteae (Myrtaceae). *Bot. J. Linn. Soc.* 179, 388–402.
- Vasconcelos, T.N.C., Amorim, B.S., Kooij, P.W., Soewarto, J., Campbell, K., Aguilar, R., Peguero, B., Lima, D.F., Faria, J.E.Q., Giaretta, A., De-Carvalho, P.S., Costa, I.R., Mazine, F.F., Santos, M.F., Wingler, A., Prenner, G., Lucas, E., 2017a. Myrteae phylogeny, biogeography and diversification patterns: increased understanding of the most species rich tribe of Myrtaceae. *Mol. Phylogenet. Evol.* 109, 113–137.
- Vasconcelos, T.N.C., Prenner, G., Santos, M.F., Wingler, A., Lucas, E.J., 2017b. Links between parallel evolution and systematic complexity in angiosperms – A case study of floral development in *Myrcia* s.l. (Myrtaceae). *Perspect. Plant Ecol. Syst.* 24, 11–24.
- Yu, Y., Harris, A.J., Blair, C., He, X.J., 2015. RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. *Mol. Phylogenet. Evol.* 87, 46–49.
- WCSP [World Checklist of Selected Plant Families], 2017. Facilitated by the Royal Botanic Gardens, Kew. Available from: <http://apps.kew.org/wcsp/> (accessed 10.07.17).
- Wilson, C.E., Forest, F., Devey, D.S., Lucas, E.J., 2016. Phylogenetic Relationships in *Calyptanthes* (Myrtaceae) with Particular Emphasis on its Monophyly Relative to *Myrcia* s.l. *Syst. Bot.* 41, 378–386.
- Wilson, P.G., O'Brien, M.M., Heslewood, M.M., Quinn, C.J., 2005. Relationships within Myrtaceae sensu lato based on a *matK* phylogeny. *Plant Syst. Evol.* 251, 3–19.
- Wilson, P.G., 2011. Myrtaceae. In: Kubitzki, K. (Ed.), *The families and genera of vascular plants*. Vol. X. Flowering plants Eudicots: Sapindales, Cucurbitales, Myrtaceae. Springer-Verlag, Heidelberg, pp. 212–271.
- Zizka, A., Steege, H.T., Pessoa, M.C.R., Antonelli, A., 2017. Finding needles in the haystack: Where to look for rare species in the American tropics. *Ecography* 40 (1), 001–009.