Phylogeny and biogeography of the hyper-diverse genus *Eugenia* (Myrtaceae: Myrteae), with emphasis on *E.* sect. *Umbellatae,* the most unmanageable clade

Fiorella Fernanda Mazine,[1] **Jair Eustáquio Quintino Faria,**[2] **Augusto Giaretta,**[3] **Thais Vasconcelos,**[4] **Félix Forest**[5] **& Eve Lucas**[4]

1 *Universidade Federal de São Carlos, campus Sorocaba, Departamento de Ciências Ambientais, Rod. João Leme dos Santos (SP 264), km 110, 18052-780, Sorocaba – SP, Brazil*
2 *Universidade de Brasília, Instituto de Ciências Biológicas, Departamento de Botânica, 70910-900, Brasília – DF, Brazil*
3 *Universidade de São Paulo, Instituto de Biociências, Departamento de Botânica, Lab. Sistemática Vegetal, R. do Matão 277, 05508-090, São Paulo – SP, Brazil*
4 *Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, U.K.*
5 *Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, U.K.*
Author for correspondence: *Fiorella Fernanda Mazine, fiorella@ufscar.br*

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Abstract   *Eugenia*, comprising ca. 1100 species, is the largest genus of Neotropical Myrtaceae. *Eugenia* sect. *Umbellatae* (formerly referred to as "clade 9") is the most speciose lineage of *Eugenia*. This study aims to better delimit *E.* sect. *Umbellatae*, to identify and understand relationships between manageable subgroups of this large clade for future discrete systematic studies and to explain biogeographical patterns in the genus. In total, 103 samples were used in this study. These include representatives of the nine clades of the "*Eugenia* group" with a particular focus on *Eugenia* clade 9, representing the morphological and geographical diversity found in the genus. Phylogenetic reconstructions were performed using maximum likelihood (ML) and Bayesian inference (BI) for the combined dataset, using the markers ITS, *rpl16*, *psbA-trnH*, *rpl32-trnL*, *trnQ-rps16*. The resultant tree was fossil calibrated and used for historical biogeographical analysis using DEC implemented in RASP. The mid Oligocene is the most likely period in which the crown node of *Eugenia* s.l. diversified. The earliest *Eugenia* appear to be associated with dry biomes and to have arisen from non-tropical southern South America, as did ancestors of the earliest American Myrteae. *Eugenia* subg. *Pseudeugenia* also most likely diversified in dry biomes, while *E.* subg. *Hexachlamys* and *E.* subg. *Eugenia* are likely to have diverged in the Atlantic Forests biome. *Eugenia* sect. *Umbellatae* is morphologically very variable; some clades can be circumscribed based on morphology while some remain morphologically undiagnosable. The study presented here provides discussion of the earliest origins of *Eugenia* and its response to climate-driven changes in the Neotropics as humid, forest biomes became more widespread in the Miocene. In addition, important practical conclusions are drawn regarding relationships within *Eugenia*. Three clades are newly classified as subgenera: *E.* subg. *Pseudeugenia* (including species of *E.* sect. *Pseudeugenia*); *E.* subg. *Hexachlamys* (including *E.* sect. *Hexachlamys*) and *E.* subg. *Eugenia* (including *E.* sect. *Umbellatae*, *E.* sect. *Jossinia*, *E.* sect. *Phyllocalyx*, *E.* sect. *Pilothecium*, *E.* sect. *Racemosae*, *E.* sect. *Schizocalomyrtus*, *E.* sect. *Speciosae* and *Eugenia* sect. *Excelsae*). Two previously unidentified clades are published as *E.* sect. *Excelsae* and recognized as *E.* sect. *Jossinia*, the latter consisting entirely of Old World species.

Keywords   Atlantic Forest; *Jossinia*; Neotropics; *Racemosae*; *Schizocalomyrtus*; systematics

Supplementary Material   The Electronic Supplement (Tables S1, S2; Figs. S1–S7) and DNA sequence alignments are available from https://doi.org/10.12705/674.5.S1 and https://doi.org/10.12705/674.5.S2, respectively.

■ INTRODUCTION

Comprising ca. 1100 species (WCSP, 2017), *Eugenia* L. is the largest genus of Neotropical Myrtaceae. It is also the most species-rich angiosperm genus in Brazil (BFG, 2015), the second-most species-rich genus of trees in the world (Beech & al., 2017) and the most species-rich tree genus in the ombrophilous forest that surrounds the Atlantic coast of Brazil, locally referred to as the "Mata Atlântica" (Oliveira-Filho & Fontes, 2000). The natural distribution of *Eugenia* ranges from southern Mexico, Cuba and the Antilles to Uruguay and Argentina,

with a small number of species (ca. 20%) in Africa, Southeast Asia and the Pacific.

Eugenia and *Myrcianthes* O.Berg comprise a single clade, named the "*Eugenia* group" (Lucas & al., 2007; Vasconcelos & al., 2017). Mazine & al. (2014) investigated the classical infra-generic groups of *Eugenia* (Berg, 1857, 1858) and provided suites of morphological characters with which to distinguish them. The resulting topology (Mazine & al., 2014) confirmed that a monophyletic *Eugenia* can only be preserved by including the traditional Neotropical genera *Calycorectes* O.Berg, *Hexachlamys* O.Berg, *Phyllocalyx* O.Berg and *Stenocalyx*

O.Berg. Within *Eugenia* s.l. and *Myrcianthes*, nine clades were identified as morphologically diagnosable groups. *Eugenia* morphology and current phylogenetic and taxonomic understanding of the "*Eugenia* group" considering recent nomenclatural updates (Bünger & al., 2016a; Mazine & al., 2016; Giaretta & al., unpub. data) are summarised below. Clade numbers refer to the work of Mazine & al. (2014) where more details are provided.

Myrcianthes (clade 1) is sister to the rest of *Eugenia* (Lucas & al., 2007; Mazine & al., 2014). *Eugenia* sect. *Pseudeugenia* Mazine & Faria (clade 2) includes species with filiform, deciduous bracteoles and large, often edible yellow fruits. Faria & al. (unpub. data) suggest this clade comprises ca. 25 species that occur from northern South America to northern Argentina. It includes species such as *E. klotzschiana* O.Berg and *E. dysenterica* DC. *Eugenia* sect. *Hexachlamys* (O.Berg) Mazine (clade 3) is a group of ca. ten southern South American species formerly recognised as *Hexachlamys* but synonymised in *Eugenia* by later authors (Mattos, 1995; Landrum & Kawasaki, 1997; Sobral, 2003; Cruz & al., 2013; Mazine & al., 2016). *Eugenia* sect. *Pilothecium* (Kiaersk.) D.Legrand (clade 4) is characterised by a set of common characters, including flowers usually in dichasia, presence of hairs inside the ovary locules, embryo with free cotyledons and edible, large and yellow fruits; most species of this section were recognised by Berg (1856, 1857) in *E.* sect. *Dichotomae* O.Berg. *Eugenia* sect. *Pilothecium* comprises ca. 20 species and occurs from the Guianas, Colombia and Ecuador to Argentina. *Eugenia* clade 5 includes species that were formerly accepted in the genus *Stenocalyx*. These species share vegetative axes that continue to develop leaves beyond the flowering region ("auxotelic" according to Briggs & Johnson, 1979; "late proliferation" according to Prenner & al., 2009), generally with oblong, densely clustered cataphylls (bracts) at the base (Sobral, 2003). This clade contains ca. 30 species, most of them restricted to Brazil, and is now recognised as *E.* sect. *Eugenia* as it contains the type of the genus, *E. uniflora* L.

Molecular phylogenetic studies of the genus described as *Phyllocalyx* (Bünger & al., 2016b) show that it is paraphyletic, with the well-supported clade containing most species previously placed in *E.* sect. *Phyllocalyx* and its type (*E. involucrata* DC.) now recognised as *E.* sect. *Phyllocalyx* Nied. (clade 6). The species in this group share showy flowers with equally showy, frequently foliaceous calyx lobes (Niedenzu, 1893). Bünger & al. (2016b) assigned 26 species to this clade, distributed from northeast Brazil to Argentina. Six species previously treated as members of *E.* sect. *Phyllocalyx* are known to have an independent origin from the latter section and have been assigned to a new section, *E.* sect. *Speciosae* Bünger & Mazine (Bünger & al., 2016a); these are *E. bunchosiifolia* Nied., *E. hermesiana* Mattos, *E. longipetiolata* Mattos, *E. macedoi* Mattos & D.Legrand, *E. speciosa* Cambess. and *E. wentii* Amshoff. Clade 7 comprises species previously ascribed to genus *Calycorectes*, usually distinguished by the presence of calyx lobes partially or completely fused along their edges, tearing in three to five regular or irregular lobes at anthesis (Giaretta & al., unpub. data). Unpublished molecular data and resulting taxonomic adjustment (Giaretta & al., unpub. data) provides an existing name for clade 7, *E.* sect. *Schizocalomyrtus* (Kausel) Mattos and relegates *E.* sect. *Calycorectes* (O.Berg) Mazine to synonymy of *E.* sect. *Umbellatae* O.Berg where the type of *Calycorectes* (*E. neograndifolia* Mattos) emerges. *Eugenia* sect. *Schizocalomyrtus* includes ca. 15 species, mainly distributed in the Brazilian Atlantic Forest but also in Argentina and Paraguay. *Eugenia* sect. *Racemosae* O.Berg (clade 8) comprises all species displaying racemes with conspicuous rachis bearing decussate pairs of pedicellate flowers (Mazine & al., 2014). This clade comprises ca. 60 species from throughout the Neotropics.

The nine clades described above (clades 1 to 8 sensu Mazine & al., 2014; and *E.* sect. *Speciosae* sensu Bünger & al., 2016a) comprise ca. 200 species. All remaining species of *Eugenia* (ca. 900) are classified as *E.* sect. *Umbellatae* by Mazine & al. (2014; clade 9), the focus of the present study. *Eugenia* sect. *Umbellatae* is the most speciose section in genus *Eugenia*, including species with solitary flowers, flowers borne in glomerules, fascicles or arranged in short racemes and fascicles on the same branch or in racemes with pedicels much longer than the floral internodes. All non-American species of *Eugenia* sampled by Mazine & al. (2014) are found in this large clade, suggesting that every dispersal outside South and Central Americas in *Eugenia* was from this group. Old World *Eugenia* total approximately 120 species in Africa and neighbouring islands and ca. 70 species in Southeast Asia and the Pacific. A molecular phylogenetic analysis of *Eugenia* with an emphasis on southern African taxa by Van der Merwe & al. (2005) points towards the existence of two natural groups of Paleotropical species, referred to as groups X and Y. That study hypothesised that *Eugenia* had two origins in southern Africa, that species included in group X were more closely related to Neotropical *Eugenia* species, and that group X was the most widespread and speciose clade in Africa. While this complex configuration was partially confirmed by Mazine & al. (2014), Wilson & Heslewood (2016) and Vasconcelos & al. (2017), all three studies show all Old World species of *Eugenia* as a monophyletic group. In a recent study, Vasconcelos & al. (2018) provide an overview of flower development in *Eugenia*, including discussion of variation in perianth growth rate, style gigantism in *E.* sect. *Umbellatae*, hypanthium elongation and androecium development. Several of these characters corroborate the taxonomic arrangement presented here, demonstrating the continuous cycle of reciprocal illumination (Hennig, 1966) between molecular and morphological systematics.

This study aims to better delimit *E.* sect. *Umbellatae* (sensu Mazine & al., 2016), to understand the relationships between clade 9 (sensu Mazine & al., 2014) with the remaining *Eugenia* clades and to identify and understand relationships between manageable subgroups of this large clade for future discrete systematic studies. A more extensive sampling of *Eugenia* species from Africa and Asia has been included here with the aim of better understanding the biogeographic events that produced the current pantropical distribution patterns observed within *Eugenia*.

■ MATERIALS AND METHODS

Taxonomic sampling. — In total, 103 samples were used in this study (Appendix 1). This includes representative samples of the nine clades of the "*Eugenia* group" (sensu Mazine & al., 2014) and the maximum available species of *Eugenia* clade 9 selected to represent the morphological and geographical diversity found in the genus. Five outgroup taxa were selected from other genera of tribe Myrteae. For this study 430 sequences were newly produced.

DNA extraction, sequencing and alignment. — Extraction of total genomic DNA and amplification and purification of target DNA regions were performed according to the protocols outlined in Bünger & al. (2016b). DNA markers selected are the most variable markers reported by recent studies of other Myrtaceae genera (Murillo-A. & al., 2012) as well as *Eugenia* (Faria-Jr., 2014).

The following five DNA markers were used: the nuclear internal transcribed spacers (ITS), the plastid intron *rpl16*, the plastid intergenic spacers *psbA-trnH*, *rpl32-trnL* and *trnQ-rps16*. The ITS region was amplified using primers AB101 and AB102 (Sun & al., 1994) and the following PCR conditions: 5 min at 94°C followed by 28 cycles of 1 min at 94°C, 1 min at 48°C, 1 min at 72°C with a final extension of 7 min at 72°C. The plastid *psbA-trnH* was amplified using the corresponding primers of Hamilton (1999) and the following PCR conditions: 5 min at 94°C followed by 28 cycles of 1 min at 94°C, 1 min at 48°C, 1 min at 72°C, and a final extension of 7 min at 72°C. The plastid intergenic spacer *trnQ-rpS16* was amplified using the primers trnQ(UUG) and rpS16x1 of Shaw & al. (2007) and the internal primers MytrnQR and MyrpS16F of Murillo-A. & al. (2012) and the following PCR conditions: 5 min at 80°C followed by 35 cycles of 1 min at 95°C, 1 min at 50°C, 5 min at 65°C, and a final extension of 4 min at 65°C. The plastid intergenic spacer *rpl32-trnL* was amplified using the primers trnL(UAG) and rpL32F of Shaw & al. (2007) and trnL292F and trnL636 (Faria-Jr., 2014) of this study and the same PCR conditions as for *trnQ-rps16*. The intron *rpl16* was amplified using the primers rpl16-F71 and rpl16-R1516 of Jordan & al. (1996) and again the same PCR conditions as *trnQ-rps16*. Sequencing protocols followed Bünger & al. (2016b). Sequences were assembled using MUSCLE v.3.8.31 (Edgar, 2004), edited and aligned in GENEIOUS v.9 (Kearse & al., 2012) making manual adjustments where necessary. Doubtful and phylogenetically informative base changes were compared to the consensus and individually checked. The four plastid regions were combined into a single partition in further analyses. Regions with variable presence or absence of bases for which the homology was equivocal (e.g., the ends of polybase regions) were removed from the analysis.

Phylogenetic analyses. — Phylogenetic reconstructions were performed using maximum likelihood (ML) and Bayesian inference (BI) for the combined dataset. Topological incongruence was assessed by comparing individual ML and BI analyses for each data partition as well as ITS vs. the four combined plastid regions. Congruence among datasets was evaluated by visual inspection of resulting cladograms, with incongruence

recognised as relative inconsistencies of greater than 75% bootstrap support from ML or 0.75 posterior probability (PP) from BI. No such incongruence was detected, and the partitions were combined with the same partitions implemented in all further analyses, all run using the CIPRES portal (Miller & al., 2010).

ML was implemented using RAxML v.7.6.3 (Stamatakis, 2006) using the fast algorithm with 1000 bootstrap replicates and the remaining criteria set to default. BI was implemented using MrBayes v.3.1.1 (Huelsenbeck & Ronquist, 2001; Ronquist & al., 2005). Models of nucleotide substitution for the BI analyses were calculated for each sequence partition, using MrModeltest2 v.2.2 (Nylander, 2004), run in PAUP* v.4.0b2 (Swofford, 2002). The models recommended under the Akaike information criterion were SYM+I+Γ for ITS and GTR+I+Γ for the plastid partition. Datasets were analysed in combination with these model parameters fitted independently to each data partition. *Myrtus communis* L. was designated as outgroup taxon in all analyses in accordance to previous studies of tribe Myrteae (e.g., Lucas & al., 2007; Vasconcelos & al., 2017). Two independent Bayesian runs were conducted simultaneously with 5 million generations and using four Markov chain Monte Carlo (MCMC) and the sampling frequency was 1000. Results of the Bayesian analyses were examined in Tracer v.1.4.1 (Rambaut & Drummond, 2007) to ensure that the analyses reached convergence and that the effective sample size of each parameter was sufficient (>200). A maximum clade credibility tree with posterior probabilities combining both analyses was generated with the "sumt" option in MrBayes, using a burn-in of 10% (500 trees). Figtree v.1.4.0 (Rambaut, 2006) was used to visualise the maximum clade credibility tree and posterior probabilities.

Dating and biogeographical analysis. — Divergence times were estimated using the Bayesian approach implemented in BEAST v.1.8.3 (Drummond & al., 2012) based on the combined datasets, an uncorrelated relaxed molecular clock and a Yule speciation model assuming a lognormal distribution of rates. Four runs of 50 million generations were performed, sampling one tree every 1000th generations. Posterior distributions of parameters were checked for convergence using Tracer v.1.4.1 (Rambaut & Drummond, 2007). MCMC sampling was stopped when the effective sample size (ESS) of each parameter exceeded 200. A burn-in period of 5 million generations was applied for each run and TreeAnnotator v.1.8 (Drummond & al., 2012) was used to build a maximum clade credibility tree from the remaining trees, presenting median branch lengths and 95% highest posterior density intervals on nodes. Two analyses were run, the first used normal prior means of 29.29 and 35.36 Ma that correspond to the ages given in Vasconcelos & al. (2017) for the crown nodes of the *Eugenia* supergroup (*Eugenia* and *Myrcianthes*) and the Neotropical lineage, each with a standard deviation of 1.4 that gives a 95% confidence interval similar to the HPD 95% interval of the BEAST analysis of Vasconcelos & al. (2017) approach B. A second analysis is presented allowing comparison with other recent dated analyses of Neotropical Myrtaceae (e.g., Staggemeier & al., 2015; Santos & al., 2016) that use the macrofossil fruit of *Paleomyrtinaea princetonensis* Pigg & al. from the Paleocene to early Eocene of British Colombia (Crane & al., 1990; Pigg & al., 1993; Manchester,

1999) for calibration. In this case the crown group of Myrteae was constrained, following the recommendations of Forest (2009), and a lognormal distribution applied with a median of 55.8 Ma (the lower bound of the Eocene), lower quartile (2.5%) of 54.94 Ma and upper quartile of (97.5%) 61.9 Ma, achieved using an offset value of 54.8 Ma.

Ancestral area analysis. — A matrix was compiled indicating the presence or absence of each sampled species in one of six geographic areas. Areas used are modified from those defined by Santos & al. (2017) and are designed to strike a balance between a small enough number of areas to reduce multiple combinations of possible ancestral areas while detecting variation in *Eugenia* distribution patterns. The following biogeographic areas were used: regions in parentheses are combined from Santos & al. (2017): A: Caribbean, B: Amazon, C: Dry Biomes (Cerrado+Campo Rupestre+Caatinga), D: Atlantic Forest (Montane+Lowland Atlantic Forest), E: North-western and Central America (Mesoamerica+Northern-Western South America), F: Extra-Neotropical. Dispersal extinction cladogenesis (DEC; Ree & Smith, 2008) was implemented using the package RASP v.3.0 (Yu & al., 2014), constraining range to two biogeographic units and dispersal probability between adjacent units set to 1.0, non-adjacent proximal (<2000 km distant) units with floristic links set to 0.5, non-adjacent proximal units without floristic links set to 0.1 and non-adjacent units (>2000 km distant) set to set to 0.01 (Electr. Suppl.: Table S1).

■ RESULTS

Phylogenetic analysis. — The resulting phylogenetic hypothesis is used to update the classification of *Eugenia* in the most logical and user-friendly way, in light of observable morphological characters presented by the taxa. New subgenera and sections are described at the end of the work. Clades are discussed in order of the age of their nodes; arrangements that results in no taxonomic change are not discussed in detail.

No strongly supported incongruence was observed among the independent analyses of the ITS vs. independent and combined plastid partitions (Electr. Suppl.: Figs. S1–S6), thus partitions were combined in subsequent analyses. Figure 1 shows the maximum clade credibility tree resulting from the ML analysis of the combined data with bootstrap support from the ML analysis shown and branches receiving 0.95 or greater PP from Bayesian analysis marked in bold. Soft incongruence between analyses is marked. Support values for nodes given here are from these analyses unless specified otherwise.

Three clades are here identified and newly classified as subgenera. *Eugenia* subg. *Pseudeugenia* (MLBS 45%; PP 0.97) includes species of *E.* sect. *Pseudeugenia*; *E.* subg. *Hexachlamys* (O.Berg) Mattos (MLBS 100%; PP 1) includes *E.* sect. *Hexachlamys*. *Eugenia* subg. *Eugenia* (MLBS 97%; PP 0.98) includes *E.* sect. *Umbellatae* (MLBS 40%; PP 1), *E.* sect. *Pilothecium* (MLBS 100%; PP 1), *E.* sect. *Phyllocalyx* (represented only by *E. expansa* Spring ex Mart.), *E.* sect. *Racemosae* (MLBS 99%; PP 1), *E.* sect. *Schizocalomyrtus* (MLBS 100%; PP 1), *E.* sect. *Speciosae* (represented only by

E. wentii), a previously unidentified clade published here as *E.* sect. *Excelsae* sect. nov. (MLBS 100%; PP 1) and a clade consisting entirely of Old World species that corresponds to *E.* sect. *Jossinia* (DC.) Nied. (MLBS 100%; PP 1). Of these clades, *E.* sect. *Racemosae*, *E.* sect. *Jossinia*, *E.* sect. *Speciosae* and *E.* sect. *Umbellatae* share a direct common ancestor (the crown node of clade PB in Fig. 1: MLBS 57%; PP 1) and, with few exceptions, share the presence of persistent bracteoles at anthesis. Clade PB and *E.* sect. *Excelsae*, *E.* sect. *Phyllocalyx* and *E.* sect. *Schizocalomyrtus* (MLBS 51%; PP 1) are in turn sister to the pair *E.* sect. *Pilothecium* and *E.* sect. *Eugenia*. Clade PB is subdivided into two clades, each containing two sections. *Eugenia* sect. *Racemosae* (sensu Mazine & al., 2016) is sister to *E.* sect. *Jossinia* (PP 0.56). *Eugenia* sect. *Speciosae* is represented by *E. wentii* (previously *Phyllocalyx*) and emerges sister to *E.* sect. *Umbellatae* (MLBS 67%; PP 0.79) that includes *E. umbellata* DC., the type of *E.* sect. *Umbellatae* (sensu Berg, 1856), included in this analysis under the accepted name *E. bimarginata* DC. *Eugenia* sect. *Umbellatae* is morphologically very variable; some clades can be circumscribed based on morphology while some remain morphologically undiagnosable. Within this section, seven clades are judged to have either geographical or morphological significance and are discussed in detail. The relationship between *E.* sect. *Jossinia* and *E.* sect. *Racemosae* is not returned in the ML analysis where *E.* sect. *Jossinia* emerges sister (MLBS 57%) to a clade comprising *E.* sect. *Umbellatae* and *E.* sect. *Racemosae* (MLBS 31%). *Eugenia* sect. *Eugenia* is not returned as a clade in this analysis with its two representative species *E. brasiliensis* Lam. and *E. uniflora* L. emerging paraphyletic, as subsequent sisters to *E.* sect. *Pilothecium*; support is very low at the nodes concerned, likely an artefact of the sample used here.

Dating and ancestral area analysis. — Figure 2 presents the dated phylogenetic reconstruction resulting from BEAST analysis calibrated with prior means, with ancestral area probabilities (AAP) presented as pie charts at numbered nodes resulting from RASP analysis. Unless specified, all results and discussion are based on Fig. 2. Results from the analysis calibrated by the macrofossil *Paleomyrtinaea princetonensis* can be found in Fig. S7 (Electr. Suppl.). The mean age for *Eugenia* s.l. (sensu Mazine & al., 2014) is 30.3 million years (myr) with 95% confidence limits of 27.9 to 32.8 myr (Oligocene). The three *Eugenia* subgenera are estimated to have originated from the late Oligocene to mid-Miocene, with the following date estimates and 95% confidence limits: *E.* subg. *Pseudeugenia*: 24.5 myr (20.3–28.4 myr), *E.* subg. *Hexachlamys*: 12.4 myr (7.2–18.4 myr), and *E.* subg. *Eugenia*: 23.7 myr (20.2–27 myr). The most likely ancestral area of *Eugenia* s.l. is the Atlantic Forest (node 198, AAP 1); this is the case also for *E.* subg. *Pseudeugenia* and *E.* subg. *Hexachlamys* (respectively, node 197, AAP 0.81; node 191, AAP 0.76). *Eugenia* subg. *Eugenia* is also highly likely to have diverged in the Atlantic Forest biome (node 189, AAP 1.0). Table 1 provides a summary of dates and ancestral area probabilities for the named and lettered clades within *E.* subg. *Eugenia*. The majority of nodes within *Eugenia* appear to have diverged within the Atlantic Forest biome with some key dispersal/vicariance events in the late Oligocene and

Fig. 1. Phylogenetic tree of *Eugenia* resulting from a maximum likelihood (ML) analysis based on nuclear ITS and four plastid regions. Thickened branches have a posterior probability (PP) of 0.95 or greater recovered in the Bayesian inference (BI). Numbers above/below branches represent bootstrap percentages based on the ML analysis. Asterisks (*) indicates nodes with PP ≥ 0.95, but not recovered in the ML analysis; dashed lines indicate branches with PP < 0.95 not recovered by ML analysis. Shaded boxes indicate the three *Eugenia* subgenera. Clade PB ("Persistent bracteoles") is indicated.
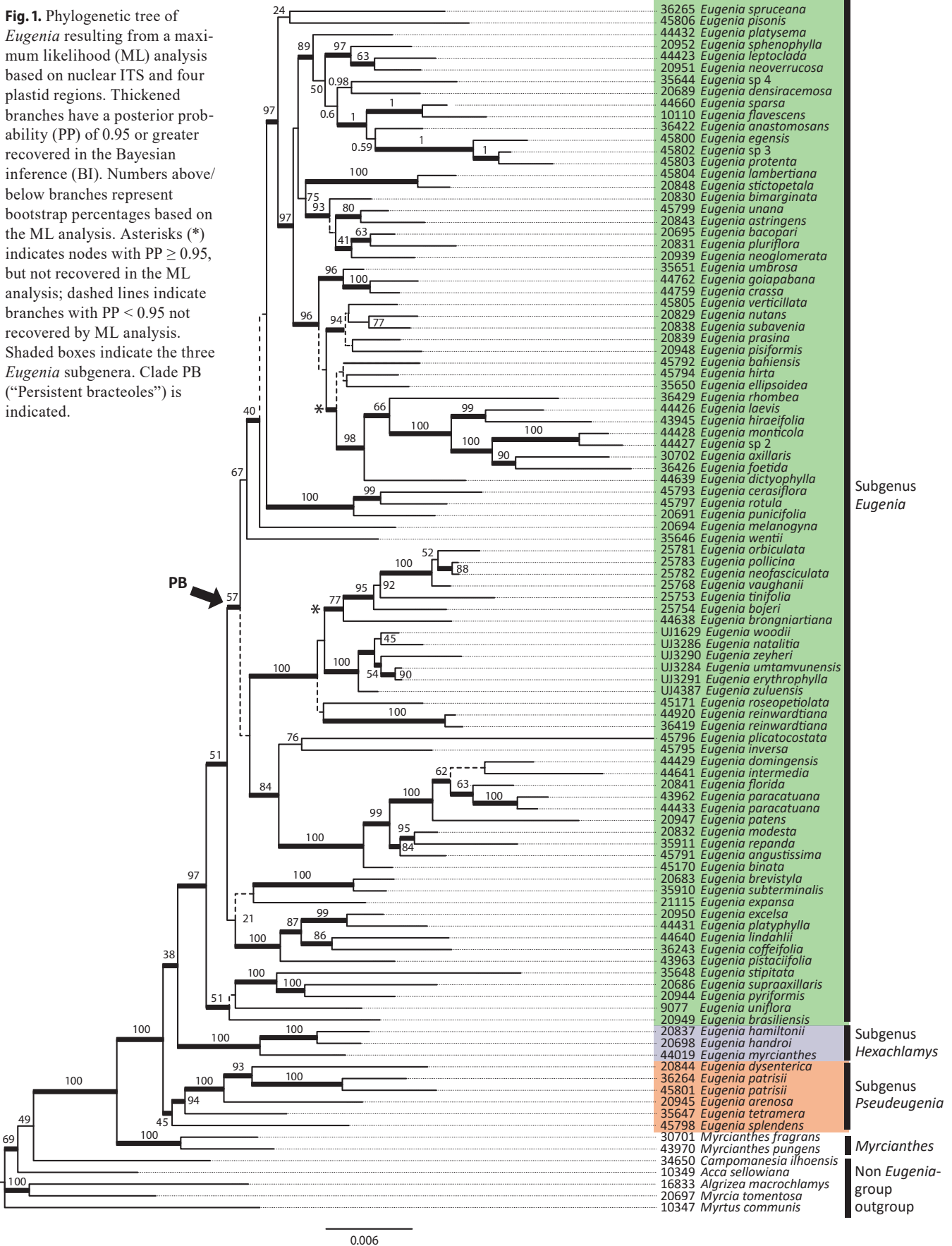
Fig. 2. Phylogenetic tree of *Eugenia* resulting from a Bayesian inference using BEAST and based on nuclear ITS and four plastid regions and calibrated using prior means obtained from Vasconcelos & al. (2017). Nodes numbered for identification; pie charts reflect the probabilities assigned to each area or group of areas and are coded as per the legend. Clade PB is indicated; scale below the tree is in million of years. A, Caribbean; B, Amazon; C, Dry Biomes (Cerrado+Campo Rupestre+Caatinga); D, Atlantic Forest (Montane+Lowland Atlantic Forest); E, North-western and Central America (Mesoamerica+Northern-Western South America); F, Extra-Neotropical. Clades from Mazine & al. (2014) are indicated by black bars and indicated by the numbers 2–8 with the names of the sections; clades not shown by Mazine & al. (2014) are not numbered.
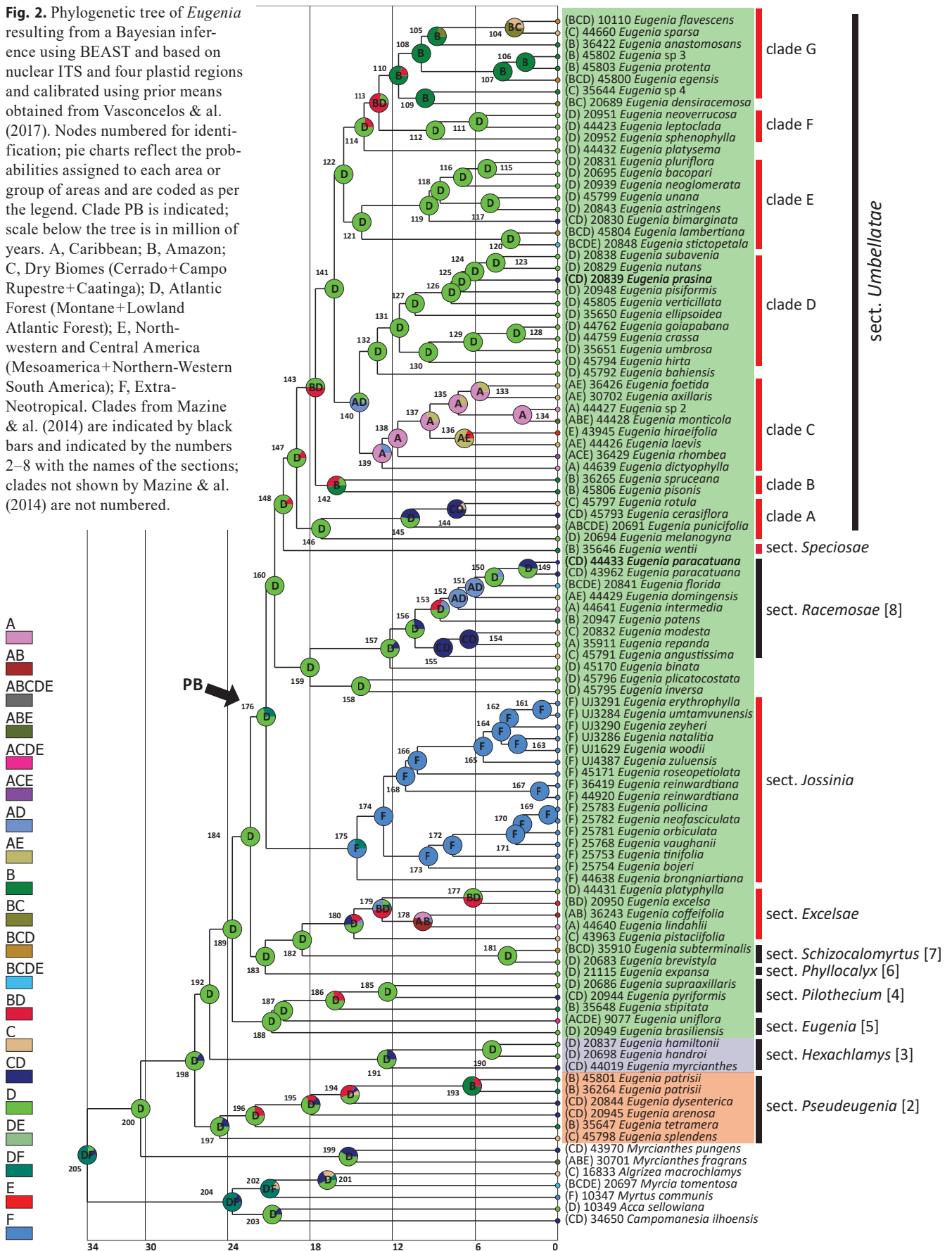
Table 1. Dates and most probable ancestral areas for the named and lettered clades within *Eugenia* subgenus *Eugenia*.

	Node	Ancestral Area	PP	Mean Date (myr)	95% CI (myr)
Eugenia	198	Atlantic Forest	1	30.3 (40.9)	27.9–32.8
E. subg. *Pseudeugenia*	197	Atlantic Forest	0.97	24.5 (37.6)	20.3–28.4
E. subg. *Hexachlamys*	191	Atlantic Forest	1	12.4 (21.2)	7.2–18.4
E. subg. *Eugenia*	189	Atlantic Forest	1	23.7 (37.5)	20.2–27
clade PB	176	Atlantic Forest	0.99	22.4 (34.4)	18.9–25.6
E. sect. *Eugenia*		not recovered			
E. sect. *Pilothecium*	186	Atlantic Forest	1	16.2 (31.8)	11.3–20.7
E. sect. *Phyllocalyx**	na	Atlantic Forest		20.6	27.5–14
E. sect. *Excelsae*	180	Atlantic Forest	1	14.8 (30.3)	10.9–18.9
E. sect. *Schizocalomyrtus*	181	Atlantic Forest	1	3.7 (7.0)	1.4–6.9
E. sect. *Racemosae*	156	Atlantic Forest	0.74	10.4 (21.4)	7.8–13.4
E. sect. *Jossinia*	175	Not Tropical America	1	14.6 (24.7)	10–18.3
E. sect. *Speciosae**	na	Atlantic Forest		16.9	23–10
E. sect. *Umbellatae*	147	Atlantic Forest	0.85	19 (33)	16.6–23.2
Umbellatae clade A	146	Atlantic Forest	0.68	17.2 (18.8)	13.4–20.9
Umbellatae clade B	142	Amazon	0.74	16.1 (26.8)	12.3–19.9
Umbellatae clade C	139	Caribbean	1	12.8 (22.2)	10–15.7
Umbellatae clade D	131	Atlantic Forest	0.99	11.51 (20.8)	8.3–14.9
Umbellatae clade E	121	Atlantic Forest	0.74	14.3 (24.8)	10.7–17.91
Umbellatae clade F	112	Atlantic Forest	1	8.9 (16.5)	5.2–12.7
Umbellatae clade G	110	Amazon	0.92	11.6 (20.9)	8.8–14.6

Nodes numbers correspond to Fig. 2, ancestral areas from DEC analysis, PP, mean dates and 95% confidence intervals from BEAST analysis (Electr. Suppl.: Fig. S7). Dates in brackets are from the macrofossil calibrated analysis; * signifies single species representation, in these cases ancestral areas and dates from Bünger & al. (2016b).

Miocene leading to diversification events in other areas such as the Amazon forest (e.g. node 110, AAP 0.92; mean divergence age: 11.6 mya), the Caribbean (node 139, AAP 0.74; mean divergence age: 12.8 mya) and to the Asia/Pacific region (node 175, AAP 0.7; mean divergence age: 14.6 mya). All posterior probabilities from the BEAST analysis and ancestral areas probabilities for each node are listed in Table S2 (Electr. Suppl).

■ DISCUSSION

Phylogenetic relationships in *Eugenia*. — The study presented here provides important additions to the understanding of relationships and historical biogeography within *Eugenia*, the largest genus within Neotropical Myrtaceae. Topological results can be summarised as follows: *Eugenia* clades 1, 2, 3, 4 and 6 sensu Mazine & al. (2014) are returned as monophyletic with no significant change to recognised systematic relationships. Clade 5 sensu Mazine & al. (2014) returns paraphyletic, but the low support of these relationships means no systematic adjustments can be done at this point. However, neither *Eugenia* clade 9 (sensu Mazine & al., 2014) nor *E.* sect. *Umbellatae* (sensu Berg, 1856) are monophyletic. The systematic discussion

that follows is focused on species of *E.* subg. *Eugenia* that match the circumscription of *E.* sect. *Umbellatae* sensu Mazine & al. (2016) or that are newly implicated within it. The morphological circumscription used by Mazine & al. (2016) is revised below as species that fall within it are here found in molecular analyses to emerge in other clades, notably in *E.* sect. *Excelsae* and *E.* sect. *Jossinia*.

Historical biogeography of *Eugenia*. — Divergence dates correspond well to those returned by Vasconcelos & al. (2017). Those obtained using macrofossils are predictably older, with most divergences occurring from the late Eocene to late Miocene. However, reconstructed biogeographical patterns do not change significantly regardless of when within this range they are thought to have happened. Results suggest the mid-Oligocene to have been the most likely period in which the crown node of *Eugenia* s.l. began to diversify. The earliest *Eugenia* appear to have occurred in a mixture of Atlantic Forest and drier biomes, evidenced by the possibility of CD (dry biomes or Atlantic Forest) as ancestral area at nodes 197 and 198. These ancestors may have arisen from non-tropical southern South America, as did ancestors of the earliest American Myrteae (Vasconcelos & al., 2017). A more or less complete transition to wet forests occurred for ancestors of *E.* subg. *Eugenia* during

the same period, also during the transition from Oligocene to Miocene. The 11 sections of *Eugenia* were all established by the middle of the Miocene (node 147). The biogeographic reconstruction at the crown node of *Eugenia* (node 198) indicates that the genus started to diverge in both the dry biomes and the Atlantic Forests biomes. The species of *E.* sect. *Pseudeugenia*, the earliest-diverging section, sister to the remainder of the genus, today occurs in a mixture of dry and moist habitats (the leaves of *E. dysenterica*, for example, are abruptly deciduous just before flowering, associated with cold, dry habitats). These characters associated with drier habitats are shared with *Myrcianthes*. From node 192 onwards, the various clades of *Eugenia* diversified prolifically in the Atlantic Forest biome, with the most likely origin of ancestors of all subsequent backbone nodes found in that region.

The Atlantic Forest is an ecosystem believed to have existed since the Cretaceous when South America was still connected to the African continent, and would thus be older than the Amazon forest (Joly & al., 2014). However, until the late Miocene these biomes were intermittently connected (Hoorn & al., 2010) with mega-thermal elements sometimes extending as far south as Patagonia (Palazzesi & Barreda, 2007). As a result of its previous Gondwanan connection, the Atlantic Forest contains floristic elements from that supercontinent; Myrtaceae is an example of this (Thornhill & al., 2015; Vasconcelos & al., 2017). Myrtaceae is postulated to have migrated from what is now Australia to South America via the then-warmer Antarctica where plant species existed in significant numbers until the late Oligocene–early Miocene when the region underwent glaciation (Francis & al., 2008). It is possible that Myrtaceae occurred simultaneously on all three of these continents as part of a super Gondwana. Occasional Amazonian species scattered within the principally Atlantic Forest clades suggest later sporadic dispersal events or relics of Atlantic Forest–Amazon connections and a greater distribution of *Eugenia* across northern South America than is currently observed (Ortiz-Jaureguizar & Cladera, 2006).

Phylosystematics and biogeography of key *Eugenia* clades

***Eugenia* sect. *Excelsae* and *E.* sect. *Schizocalomyrtus*. —** *Eugenia excelsa* O.Berg has free calyx lobes but emerged previously (Mazine & al., 2014) as sister to a clade of species with fused or partially fused calyx-lobes that tear at anthesis and were previously accepted in *Calycorectes*. *Eugenia excelsa* is here comprised within the newly published *E.* sect. *Excelsae* clade with newly added samples of *E. platyphylla* O.Berg, *E. coffeifolia* DC., *E. lindahlii* Urb. & Ekman and *E. pistaciifolia* DC. These five species fit the diagnosis of *E.* sect. *Umbellatae* (Mazine & al., 2016) with the exception that bracteoles usually fall before fruits are formed and style length is not double the length of the stamens. Deciduous bracteoles are shared by clades 1–7 (except *Phyllocalyx*) as well as *Myrcianthes* (sister to *Eugenia*) and their presence appears to be the plesiomorphic state in the *Eugenia* group. Bracteoles in these species are usually linear and filiform and often equal the flower bud in length. In *Myrcianthes*, fallen bracteoles

sometimes leave prominent auricle-like scars (Grifo, 1992). Vasconcelos & al. (2018) demonstrate that the style of *E.* sect. *Umbellatae* species is twice the length of the stamens while in all other sections, the style is approximately the same length as the stamens. *Eugenia platyphylla* and *E. excelsa* are from the Brazilian Atlantic Forest and *E. pistaciifolia* is from Caatinga, also occurring in areas of Cerrado especially in high altitudes in Espinhaço Range. They share axillary fasciculate inflorescences, flowers with long pedicels and reflexed sepals on the opened flower but erect on the fruit. *Eugenia coffeifolia* has glomerulate inflorescences and sessile flowers with regular sepals. Although *E. coffeifolia* was included in *E.* sect. *Glomeratae* by Berg (1858), fascicles and glomerules differ only by differential elongation of the pedicels that can be related to the flower rather than the inflorescence. Bracteoles of *E. coffeifolia* are unusually persistent in the fruit where the ovary is also bilocular (typical in *Eugenia*), but curiously with 2 (rather than many) ovules per locule. Reduced ovule number (1–4) per locule is rare in *Eugenia*, but is found also in *E. arenosa* and *E. dysenterica* (*E.* sect. *Pseudeugenia* – clade 2 sensu Mazine & al., 2014) and is more common in species in less-derived *Eugenia* clades (i.e., *E.* sect. *Pseudeugenia*, *E.* sect. *Pilothecium* and *E.* sect. *Hexachlamys*). *Eugenia coffeifolia* is also exceptional in its densely pubescent hypanthium in contrast to the glabrous ones found in closely related species (Holst & al., 2003). *Eugenia pistaciifolia* is found in dry habitats in the Brazilian states of Bahia and Minas Gerais and was placed by Berg (1857) in *Stenocalyx*, now recognised as a synonym of *Eugenia*. *Eugenia lindahlii* is endemic to Haiti and the Dominican Republic and has not previously been associated with any group. Both *E. pistaciifolia* and *E. lindahlii* have narrowly lanceolate leaves with characteristic parallel lateral venation (Liogier, 1989: 59) faintly evident and prominent on both leaf surfaces. The species comprising *E.* sect. *Excelsae*, *E.* sect. *Schizocalomyrtus* (represented by *E. brevistyla* and *E. subterminalis*) and *E.* sect. *Phyllocalyx* (represented only by *E. expansa*) form a clade with low support and internal resolution, in which bracteoles at the base of the flower are also often deciduous at or before anthesis (McVaugh, 1968). All three of these clades are estimated to have Atlantic Forest origins with subsequent dispersal events to the Amazon and Caribbean. A monographic account of *E.* sect. *Schizocalomyrtus* (Giaretta & al., unpub. data) will provide detailed description of the species found in this group.

Clade PB (persistent bracteoles). — As described above, clade PB is sister to the clade comprising *E.* sect. *Excelsae*, *E.* sect. *Schizocalomyrtus* and *E.* sect. *Phyllocalyx* and is defined by species with predominantly persistent bracteoles. Bracteoles usually persist until the fruiting stage and are rounded or triangular rather than linear as found in the other clades. Clade PB is most likely to have an Atlantic Forest origin with multiple subsequent events of diversification to a wide variety of Neotropical and extra-Neotropical areas.

***Eugenia* sect. *Racemosae*. —** Mazine & al. (2014) diagnose *E.* sect. *Racemosae* by having flowers exclusively arranged in simple racemes, terminating in a vegetative bud (the botrys or polytelic inflorescence of Weberling, 1988, botryum

of Endress, 2010, or racemiform conflorescence of Briggs & Johnson, 1979), although vegetative buds can be concealed between the ultimate pair of flowers. A further but less common possible arrangement is a compound raceme (i.e., a panicle of racemes; "diplobotrys", "diplobotryum" of Weberling, 1988; Endress, 2010; or racemiform superconflorescence of Briggs & Johnson, 1979). *Eugenia* sect. *Racemosae* species have a length-of-pedicel to internode ratio of 2:1 or less – the rachis of these racemes is conspicuous, bearing decussate pairs of pedicellate flowers. Some authors (e.g., Landrum, 1981; Landrum & Kawasaki, 2000; Cornejo, 2005) use the term "bracteate shoot" to describe the arrangement that Mazine & al. (2014) considered a raceme. *Eugenia paracatuana* O.Berg has inflorescences in botryoids (unique to this clade) and solitary flowers. Inflorescence developmental studies are required to understand whether the inflorescence of *E. paracatuana* is determinate or indeterminate. *Eugenia binata* Mazine & Sobral emerges sister to *E.* sect. *Racemosae* but is not included within it as it has flowers uniquely in pairs. It is possible that when other species with this paired arrangement are sampled and included in this phylogenetic framework, such as *E. lomeroensis* Villarroel & Gomes-Bezerra, they may share a common ancestor. *Eugenia angustissima* O.Berg was included in *E.* sect. *Biflorae* by Berg (1859) but appears in the present analysis with *E. repanda* O.Berg and *E. modesta* DC., two species with shorter racemes (previously from *E.* sect. *Racemulosae* sensu Berg), which is consistent as the sample of *E. angustissima* used here has short racemes. Faria-Jr. (2010) records that the inflorescence of *E. angustissima* is variable, from solitary flowers, flowers in pairs or racemes of 2–16 flowers. *Eugenia plicatocostata* O.Berg and *E. inversa* Sobral emerge together as sister to *E.* sect. *Racemosae*+*E. binata*. *Eugenia plicatocostata* is a tree species from the Atlantic Forest in Espírito Santo and Bahia, originally placed by Berg (1859) in *E.* sect. *Biflorae*. *Eugenia inversa* is a small tree (Sobral, 2005) endemic to vegetation on sandy coastal plains ("restinga") in the state of Espírito Santo. These species both have fasciculate inflorescences with very short pedicels (to 10 mm) and because of this, along with *E. binata*, are not placed in a section here. *Eugenia* sect. *Racemosae* is the clade with least constraints in terms of its ecological niche; its species occur throughout the Neotropics, from ca. 20°N latitude to nearly 31°S latitude, occurring in practically all biomes in all countries of South America (except for Chile and Uruguay) and throughout Central America and the Caribbean islands. Species of *E.* sect. *Racemosae* achieved this relatively wide distribution via dispersal events within continental South America and to the Caribbean during the Miocene. *Eugenia* sect. *Racemosae* also may have undergone unusual migration from dry habitats to the Caribbean and back to Atlantic rainforest, showing the most complex biogeographical history of all *Eugenia* clades considered here.

Eugenia sect. Jossinia. — *Eugenia* sect. *Jossinia* (Fig. 3A) includes all extra-Neotropical species sampled in this study. The WCSP (2017) lists ca. 80 species of *Eugenia* in continental Africa, ca. 70 species from Madagascar, ca. 20 species from Mauritius and ca. 30 from New Caledonia, for a total of ca. 200 Old World species within the genus. WCSP (2017) lists *E. natalitia* Sond. and *E. zeyheri* (Harv.) Harv. as subspecies of *E. capensis* (Eckl. & Zeyh.) Harv. – *E. capensis* subsp. *natalitia* (Sond.) F.White and *E. capensis* subsp. *zeyheri* (Harv.) F.White. Results presented here do not support these entities as a single species as they are not sisters, thus we follow the nomenclature of Van der Merwe & al. (2005). The molecular analysis of Van der Merwe & al. (2005) reports two distinct *Eugenia* species groups (X and Y) in southern Africa that group with *Eugenia* of the New and Old Worlds, respectively. The relationship of Brazilian species with the rest of the African taxa sampled in the analysis of Van der Merwe & al. (2005) is unresolved. The analysis presented here does not recover groups X and Y. Species from South Africa form a well-supported clade that includes species from different clades of the analysis of Van der Merwe & al. (2005) – *E. natalitia* and *E. umtamvunensis* A.E.van Wyk represent clade X and *E. erythrophylla* Strey, *E. woodii* Dummer, *E. zeyheri* and *E. zuluensis* Dummer represent clade Y (sensu Van der Merwe & al., 2005). The same analysis of Van der Merwe & al. (2005) found that species from Mauritius form a well-supported clade (clade MAU). A monophyletic subgroup of Mascarene species was recovered by those authors, including the type of *Jossinia*, *J. tinifolia* (Lam.) DC., plus the only species of *Monimiastrum* J.Guého & A.J.Scott sampled in that analysis, *M. globosum* J.Guého & A.J.Scott. Snow (2008) reduced *Monimiastrum* to synonymy of *Eugenia*. Long-distance dispersal of *E.* sect. *Jossinia* is here estimated to have taken place in the mid-Miocene (later than reported by Vasconcelos & al., 2017), from species with Atlantic Forest origin (Table 1), in contrast to a Caribbean origin as suggested by Vasconcelos & al. (2017).

At the crown node of *E.* sect. *Jossinia* in the analysis presented here, New Caledonian *E. brongniartiana* Guillaumin diverges from the rest of the section ca. 15 Ma. This suggests the section moved from the Neotropics to the Pacific and from there migrated, perhaps by island hopping to South East Asia (*E. reinwardtiana* (Blume) DC.) followed by Madagascar (*E. roseopetiolata* N.Snow & Cable) and then Africa (*E. erythrophylla*, *E. umtamvunensis*, *E. zeyheri*, *E. natalitia*, *E. woodii*, *E. zuluensis*), and apparently separately, just once to the Mascarenes (*E. pollicina* J.Guého & A.J.Scott, *E. neofasciculata* Bennet, *E. orbiculata* Lam., *E. vaughanii* J.Guého & A.J.Scott, *E. tinifolia* Lam., *E. bojeri* Baker). Vectors for these Old World migrations and dispersal events are likely to have been birds that were also speciating rapidly during the Miocene (Hoorn & al., 2010), that are known to ingest and disperse Myrtaceae fruits and seeds in large quantities (Staggemeier & al., 2017) and that are able to migrate across distances comparable to those separating these *Eugenia* habitats. These events took place throughout the late Miocene and Pliocene with the most recent speciation events in *Eugenia* occurring in this clade, in the Pleistocene (e.g., node 169, mean divergence age: 0.7 myr). Van der Merwe & al. (2005) suggested that the close affinity between the species of *Eugenia* from Mauritius reflects a common origin of these taxa on an isolated volcanic island in the Indian Ocean east of Madagascar and this is supported here. Analysis of a larger sample of *E.* sect. *Jossinia*, including

representatives from throughout its range, is required before definitive patterns providing biogeographical, evolutionary and systematic answers can be discerned and a taxonomic framework can be imposed within the section.

Van der Merwe & al. (2005) note that cryptic dioecy (morphologically androdioecious but functionally dioecious) prevails in all African members of the genus (Van Wyk & Lowrey, 1988). Individuals either have male flowers with greatly reduced pistils or structurally hermaphroditic (functionally female) flowers whose anthers do not produce viable pollen (Van der Merwe & al., 2005). This form of sexual dimorphism has not yet been reported in *Eugenia* elsewhere in the world (Nic Lughadha, 1994; Nic Lughadha & Proença, 1996; Van der Merwe & al., 2005). As both groups of African *Eugenia* sampled by Van der Merwe & al. (2005) display morphological androdioecy, those authors believed cryptic dioecy (structural androdioecy) may be due to convergence. In the present phylogeny, cryptic dioecy appears to have emerged only once and to be plesiomorphic for clade SAFR. Wilson & Heslewood (2016) showed that *Meteoromyrtus* Gamble, a genus from India previously considered to be monotypic, is embedded within *Eugenia*, sister to *E. reinwardtiana* and recognise it as a synonym of *Eugenia*. Old World *Eugenia* species mostly have persistent bracteoles although there are some species in which they are deciduous (Strey, 1972; Scott, 1980; Van Wyk, 1982; Snow & al., 2012). The number of ovules in Old World species varies but generally there are more than 5 ovules per locule (usually 8–20, Scott, 1980; Snow & Wilson, 2010; Snow & al., 2012). Wilson (2009) records several to many ovules in a conspectus of the genus in the Philippines. *Eugenia erythrophylla* and *E. umtamvunensis* have 1 or 2 ovules per locule (Strey, 1972; Van Wyk, 1982).

***Eugenia* sect. *Speciosae*. —** *Eugenia wentii* was previously placed in *E.* sect. *Phyllocalyx* by Berg. This analysis corroborates the detailed results of Bünger & al. (2016a, b) who report a well-supported clade (with six species, including *E. wentii* Amshoff), emerging as sister to clade 9 sensu Mazine & al. (2014). This clade, named *E.* sect. *Speciosae* Bünger & Mazine, is found in both the Atlantic and Amazon forests. The biogeographical history of this clade is discussed in detail in Bünger & al. (2016a, b).

***Eugenia* sect. *Umbellatae*. —** Flowers in the exceptionally species-rich *E.* sect. *Umbellatae* clade appear to uniquely and exclusively possess a style that is approximately twice as long as the stamens (Vasconcelos & al., 2018). Morphological patterns within *E.* sect. *Umbellatae*, however, are difficult to discern and statistical support for relationships is often low. For these reasons, formal subdivision of this clade is premature and awaits both a wider sample and more molecular data. Instead, morphological or geographical characters common to the seven subclades are considered. Phylogenetic structure according to geography appears more pronounced than morphology, similar to some other large Neotropical genera such as *Miconia* Ruiz & Pav. (Goldenberg & al., 2008), and *Leandra* Raddi (Martin & al., 2008). These patterns suggest that sympatric speciation has played an important role in *Eugenia* evolution with high levels of speciation occurring within individual biomes. The

resulting groups represent hypothetical units that could be targeted in future taxonomic studies.

Clade A is the earliest diverging clade of *E.* sect. *Umbellatae* and is sister to the remainder of the section. In this study, it comprises *E. rotula* Sobral, *E. cerasiflora* Miq. and *E. punicifolia* (Kunth) DC. (Fig. 3G) (MLBS 100%; PP 1) and *E. melanogyna* (D.Legrand) Sobral (MLBS not recovered; PP 0.55). *Eugenia punicifolia* emerges from the oldest sect. *Umbellatae* node in Vasconcelos & al. (2017). *Eugenia rotula* and *E. cerasiflora* are both from the Chapada Diamantina, Bahia, Brazil and *E. punicifolia* is widespread, sampled here from Chapada dos Guimarães, Mato Grosso, suggesting a group associated with "Chapadas" or plateau areas and mountain ranges found in the Highlands of Brazil with similar geological histories (Conceição & al., 2016). *Eugenia melanogyna*, a coastal species occurring from Espírito Santo to Santa Catarina, is weakly associated with this group. Despite the possible link to chapadas, the fact that *E. punicifolia* and *E. cerasiflora* can occur in other biomes makes this pattern less clear. A larger sample from these areas could prove a possible link with certain old soils found in the plateaus of central Brazil where they are native. *Eugenia punicifolia* has solitary flowers or if more (2–4) then on very short axes. *Eugenia melanogyna* has 1–4 flowers grouped in fascicles in leafless branch nodes.

Clade B comprises *E. spruceana* O.Berg and *E. pisonis* O.Berg (Fig. 3E) (MLBS 24%; PP 0.74), two Amazonian species. *Eugenia pisonis* is currently a synonym of *E. moschata* (Aubl.) Nied. ex T.Durand & B.D.Jacks., however, examination of recently studied material support it as a distinct species. *Eugenia pisonis* is from Amazonas state and *E. spruceana* from French Guiana, also occurring in northern Brazil and Peru. *Eugenia spruceana* and *E. pisonis* are likely to share a common ancestor with *E. moschata* based on shared morphological characters such as partial calyx lobe fusion in the lower third of the bud, strongly deflexed, cucullate calyx lobes at anthesis and long, pale anthers. If this is the case, the clade may correspond to the name *Catinga* Aubl., a genus currently in the synonymy of *Eugenia*, diagnosed by calyx fusion in the bud, splitting into four longitudinal segments (Amshoff, 1951; Lemée, 1953), a character found elsewhere in *Eugenia*. The apparent Amazonian ancestral area suggests a relatively old migration to this biome, but a larger sample is required to fully explore these patterns.

All species of *E.* sect. *Umbellatae* from the Caribbean (e.g., Fig. 3F) emerge in the well-supported clade C (MLBS 98%; PP 1). Morphological characters of clade C species occur elsewhere in the section making the main defining character of clade C its geographical origin (Caribbean+Continental Central America). Caribbean species that do not come up in clade C, are *E. domingensis* O.Berg and *E. intermedia* O.Berg from the Dominican Republic that fall within *E.* sect. *Racemosae* and have flowers in racemes. *Eugenia lindahlli*, also from the Dominican Republic, emerges in *E.* sect. *Excelsae*. *Eugenia hiraeifolia* Standl., the only species endemic to Central America (deciduous tropical forest and dry-moist forest transitions in Nicaragua, Costa Rica and Panama) in this analysis, also emerges here. The high statistical support of this clade in

relation to the Atlantic Forest clades D to G suggest that this migration to the Caribbean was from the Atlantic Forest biome, as found for *Myrcia* s.l. (Santos & al., 2017). The age estimate for the root of this clade is close to estimated timings of a discrete pulse of plant migration during early Oligocene to early Miocene – 31 to 16.3 myr (Bacon & al., 2013, 2015); when dated using macrofossils, the age estimate of the root fits these dates more precisely. Myrtaceae have berries consumed by birds and bats (as well as mammals) and thus have high dispersal ability. This supports a scenario of long dispersal from South America to Central America and the Caribbean at a time when land connections between South America and Central America were still remote (Montes & al., 2015).

Clade D comprises *E. nutans* O.Berg, *E. pisiformis* Cambess., *E. subavenia* O.Berg, *E. prasina* O.Berg (Fig. 3B), *E. ellipsoidea* Kiaersk., *E. verticillata* (Vell.) Angely, *E. hirta* O.Berg (Fig. 3D), *E. umbrosa* O.Berg, *E. crassa* Sobral and *E. goiapabana* Sobral & Mazine (MLBS 51%; PP < 0.5). Again, geographical affinity is visible in this Brazilian Atlantic Forest clade. Most of these species share a characteristic inflorescence of clusters of flowers that superficially appear fasciculate but on closer inspection has a very short rachis, i.e., a bracteate shoot reduced so as to appear fasciculate, unlike in *E.* sect. *Racemosae* where the rachis is consistently racemose with flower internodes at least half as long as the pedicel. Exceptionally *E. verticillata* has clusters of sessile flowers. Other than these inflorescence characters, this clade is not morphologically cohesive; however, *E. umbrosa*, *E. crassa* and *E. goiapabana* share thick leaves, and large, yellowish fruits otherwise uncommon in *E.* sect. *Umbellatae*. Clade D is not recovered in the ML analysis (Fig. 1) and *E. bahiensis* DC. is recovered within it only in the BEAST analysis, highlighting the unstable relationships within and between this clade and the Caribbean clade (clade C). Further analysis and the inclusion of additional species associated to this group are likely to clarify relationships between these species allowing greater understanding of the biogeographical links between the Caribbean, continental Central America and the Atlantic Forest.
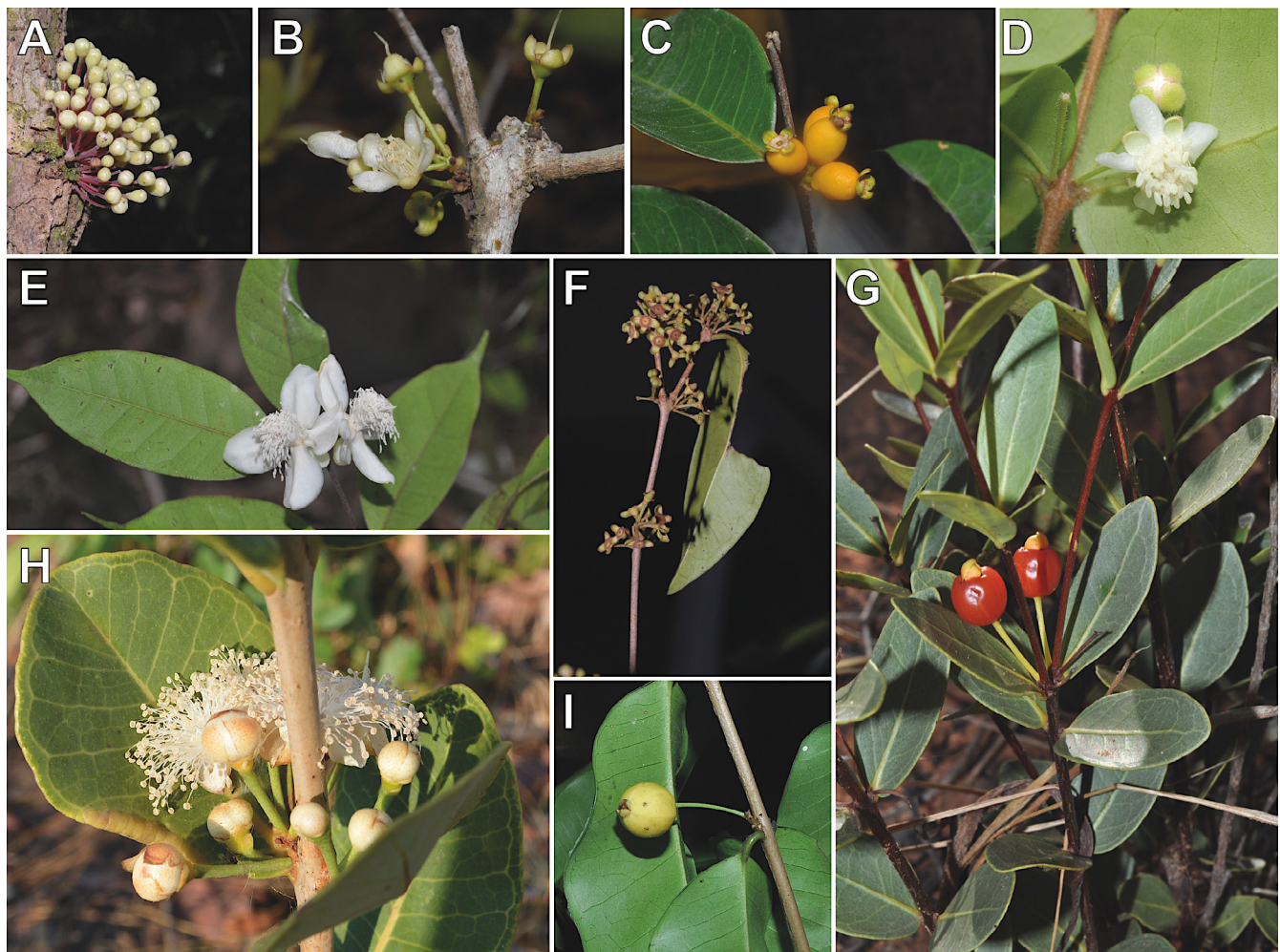

Fig. 3. Morphological diversity of: **A,** *Eugenia* sect. *Jossinia* and **B–I,** *Eugenia* sect. *Umbellatae* buds, flowers and fruits. **A,** *Eugenia brongniartiana* Guillaumin; **B,** *Eugenia prasina* O.Berg (clade D); **C,** *Eugenia lambertiana* DC. (clade E); **D,** *Eugenia hirta* O.Berg (clade D); **E,** *Eugenia pisonis* O.Berg (clade B); **F,** *Eugenia foetida* Pers. (clade C); **G,** *Eugenia punicifolia* (Kunth) DC. (clade A); **H,** *Eugenia bimarginata* DC. (clade E); **I,** *Eugenia egensis* DC. (clade G).

Clade E comprises *E. pluriflora* DC., *E. bacopari* D.Legrand, *E. astringens* Cambess., *E. neoglomerata* Sobral, *E. bimarginata* DC. (Fig. 3H), *E. stictopetala* DC., *E. unana* Sobral and *E. lambertiana* DC. (Fig. 3C) (MLBS 75; PP 0.77). The species of this clade also have clustered flowers, but largely in axils with deciduous leaves or leafless nodes; these species do not have solitary flowers. *Eugenia astringens*, *E. bacopari*, *E. pluriflora*, *E. neoglomerata* and *E. unana* are Atlantic Forest species. *Eugenia bimarginata*, *E. stictopetala* and *E. lambertiana* are widespread, while *E. bimarginata* and *E. stictopetala* occur more commonly in the Cerrado and *E. lambertiana* is mostly Amazonian although apparently also present in the Caribbean.

Clade F comprises *E. neoverrucosa* Sobral, *E. leptoclada* O.Berg and *E. sphenophylla* O.Berg (MLBS 97%; PP 1). These three species are from the Brazilian Atlantic Forests of Minas Gerais, São Paulo and Paraná. *Eugenia leptoclada* and *E. neoverrucosa* have axillary inflorescences with 2–6 flowers while in *E. sphenophylla* flowers are mostly on leafless nodes (as described for clade E, above). Once again, morphological characters are lacking to diagnose this clade but there is some overlap in distributions between some species.

Clade G comprises *E. flavescens* DC., *E. sparsa* S.Moore, *E. anastomosans* DC., *E. densiracemosa* Mazine & Faria, *E.* sp.3, *E.* sp.4, *E. protenta* McVaugh and *E. egensis* DC. (Fig. 3I) (MLBS 60 %; PP 1). This is a northern South American clade comprising mostly species from the Amazon forest. The only exception in this clade is *E. platysema* that has a North-eastern Atlantic Forest distribution range. *Eugenia flavescens* and *E. sparsa* are sister taxa and share the tendency for leaf blades to dry bright green. The leaves of *E. aurata* O.Berg, a species not included in the present study, also dry to this distinctive colour and may be associated with this clade. Inflorescences in this group are consistently fasciculate with long pedicels although, again, this characteristic can be found in other clades.

■ NOMENCLATURAL ADJUSTMENT

In the following chapter subgenera and sections are ordered according to their position in the phylogenetic tree presented in Fig. 2.

Eugenia L., Sp. Pl.: 470. 1753.

Eugenia subg. *Pseudeugenia* (Mazine & Faria) Mazine & Faria, **stat. nov.** ≡ *Pseudeugenia* D.Legrand & Mattos in Arq. Bot. Estado São Paulo 4(2): 63. 1966, nom. illeg., non *Pseudoeugenia* Scort. in J. Bot. 23: 153. 1885 ≡ *Eugenia* sect. *Pseudeugenia* Mazine & Faria in Phytotaxa 289(3): 227. 2016 – Type: *Eugenia stolonifera* (D.Legrand & Mattos) Mazine (≡ *Pseudeugenia stolonifera* D.Legrand & Mattos).

Description. – Shrubs or trees, stem with smooth or rough bark, sometimes with rhytidome accumulation; flowers in auxotelic racemes, rarely dichasia or botryoids (rachis terminates in a flower); flowers 4-merous; bracteoles filiform and deciduous at anthesis or before so; calyx with free lobes in the bud, persistent in fruit; style approximately the same length as the stamens; ovary 2–4-locular, 1 to many ovules per locule, locules of ovary predominantly hairless internally, and when trichomes present, these are sparse; fruits large, usually greater than 2×2 cm when mature, mainly pyriform, edible, predominantly velutinous, yellow or yellowish when mature; embryo with cotyledons totally or partially fused.

Notes. – *Eugenia* subg. *Pseudeugenia* is composed of a single section, sect. *Pseudeugenia*, that emerges from the earliest node of *Eugenia* and is sister to the remainder of the genus. A list of synonyms, circumscription and nomenclatural notes can be found in Faria-Jr. (2014) and Mazine & al. (2016).

Distribution. – Ca. 25 species; exclusively found in South America, where it occurs from Guianas and Suriname to Bolivia, Paraguay, southern Brazil and northern Argentina (Mazine & al., 2016).

Eugenia [subg. *Pseudeugenia* (Mazine & Faria) Mazine & Faria] sect. *Pseudeugenia*
Notes. – For a list of synonyms, circumscription and nomenclatural notes, see Faria-Jr. (2014) and Mazine & al. (2016).

Eugenia subg. *Hexachlamys* (O.Berg) Mattos in Loefgrenia 105: 2. 1995 ≡ *Hexachlamys* O.Berg in Linnaea 27(2–3): 345. 1856 ("1854") ≡ *Eugenia* subsect. *Hexachlamys* (O.Berg) Nied. in Engler & Prantl, Nat. Pflanzenfam. 3(7): 82. 1893 ≡ *Eugenia* sect. *Hexachlamys* (O.Berg) Mazine in Phytotaxa 289(3): 228. 2016 – Type: *Hexachlamys humilis* O.Berg (= *Eugenia anomala* D.Legrand).

Description. – Shrubs or trees up to 15 m; inflorescence an axillary bracteate shoot with an abbreviated axis with 2 to several flowers; flowers 5- or 6-merous; bracteoles filiform or lanceolate and deciduous at anthesis; calyx with free lobes in the bud, deciduous or persistent in fruit; style approximately the same length as the stamens; ovary 2- or 3-locular, locules generally internally hairy, 1–3 ovules per locule; fruit crowned by the calyx-lobes or by a circular scar; seed with an embryo with a small but visible and exerted hypocotyl, testa woody.

Notes. – The type *Hexachlamys humilis* is currently accepted as *Eugenia anomala* (WCSP, 2017). *Eugenia* subg. *Hexachlamys* comprises a single section, sect. *Hexachlamys*.

Distribution. – Ca. 10 species; distributed in southern and southeastern Brazil, Bolivia, Paraguay, Argentina and Uruguay (Mazine & al., 2016).

Eugenia [subg. *Hexachlamys* (O.Berg) Mattos] sect. *Hexachlamys*
Notes. – For a list of synonyms and nomenclatural notes, see Cruz & al. (2013) and Mazine & al. (2016). For circumscription (as *Hexachlamys*), see Soares-Silva (2000).

Eugenia L. subg. *Eugenia*, Sp. Pl.: 470. 1753 – Type: *Eugenia uniflora* L.
Description. – Shrubs or trees; flowers single or arranged in glomerules, fascicles, diplobotrys, racemes, dichasia, botryoids (rachis terminates in a flower) or auxotelic racemes; flowers

4-merous; bracteoles various, generally persistent, sometimes deciduous at anthesis; calyx free or fused in bud, deciduous or persistent in fruit; style approximately the same length, to twice as long as the stamens; ovary 2(–4)-locular, locules internally glabrous or sometimes pilose, 1 to numerous ovules per locule; fruit usually smaller when mature, commonly red or purplish when mature but sometimes yellow, crowned by the calyx-lobes or by a circular scar; seed with an embryo with cotyledons usually firmly fused in an homogeneous mass, less frequent embryos with plano-convex, completely separate cotyledons.

Notes. – This is the most diverse subgenus in *Eugenia*, containing the large majority of species. Nine sections are recognised here.

Distribution. – The distribution of the subgenus is basically the distribution of the whole genus, from southern Mexico, Cuba and the Antilles to Uruguay and Argentina, with ca. 120 species in Africa and neighbouring islands, and ca. 71 species in Southeast Asia and the Pacific (Wilson, 2011).

Sections in *Eugenia* subg. *Eugenia* are ordered below according to their relative position in Fig. 2.

Eugenia [subg. *Eugenia*] sect. **Eugenia**
Notes. – For circumscription, a list of synonyms and nomenclatural notes, see Mazine & al. (2016).

Eugenia [subg. *Eugenia*] sect. **Pilothecium** (Kiaersk.) D.Legrand in Bradea 2(8): 37. 1975 ≡ *Myrtus* sect. *Pilothecium* Kiaersk., Enum. Myrt. Bras.: 39. 1893 ≡ *Pilothecium* (Kiaersk.) Kausel in Ark. Bot., n.s., 4: 401. 1962 – Type: *Myrtus beaurepairiana* Kiaersk. (≡ *Eugenia beaurepairiana* (Kiaersk.) D.Legrand).
Notes. – The type *Myrtus beaurepairiana* is currently accepted as *Eugenia beaurepairiana* (Kiaersk.) D.Legrand (Faria-Jr., 2014). For a list of synonyms, circumscription and nomenclatural notes, see Faria-Jr. (2014) and Mazine & al. (2016).

Eugenia [subg. *Eugenia*] sect. **Phyllocalyx** Nied. in Engler & Prantl, Nat. Pflanzenfam. 3(7): 82. 1893 – Type: *Phyllocalyx involucratus* (DC.) O.Berg (≡ *Eugenia involucrata* DC.).
Notes. – The type *Phyllocalyx involucratus* is currently accepted as *Eugenia involucrata* DC. (Bünger & al., 2016b; WCSP, 2017). For a list of synonyms, circumscription and nomenclatural notes, see Bünger & al. (2016b, c) and Mazine & al. (2016).

Eugenia [subg. *Eugenia*] sect. **Excelsae** Mazine & E.Lucas, **sect. nov**. – Type: *Eugenia excelsa* O.Berg.
Diagnosis. – Inflorescences axillary fasciculate (short racemes) with very short internodes (except in *Eugenia coffeifolia*, with glomerate inflorescence, in leafless or axillary nodes), bracts triangular and persistent; flowers with pedicels (sessile flowers in *Eugenia coffeifolia*); bracteoles usually linear and filiform and often equal the flower bud in length, usually caducous before fruits are formed (bracteoles of *Eugenia coffeifolia* unusually persistent in the fruit); sepals triangular, reflexed on the opened flower but erect on the fruit (regular sepals in *Eugenia coffeifolia*); style approximately the same length as the stamens; hypanthium glabrous (densely pubescent in *Eugenia coffeifolia*); ovary bilocular.

Assigned species. – *Eugenia coffeifolia* DC., *E. excelsa* O.Berg, *E. lindahlii* Urb. & Ekman., *E. pistaciifolia* DC. and *E. platyphylla* O.Berg.

Distribution. – *Eugenia excelsa* and *E. platyphylla* are from the Brazilian Atlantic Forest and *E. pistaciifolia* is from Caatinga (dry habitats, in the Brazilian states of Bahia and Minas Gerais). *Eugenia lindahlii* is endemic to Haiti and the Dominican Republic.

Eugenia [subg. *Eugenia*] sect. **Schizocalomyrtus** (Kausel) Mattos in Loefgrenia 120: 3. 2005 ≡ *Schizocalomyrtus* Kausel in Lilloa 32: 367. 1967 – Type: *Schizocalyx pohliana* O.Berg.
Notes. – It corresponds to the "clade 7" of Mazine & al. (2014) and to the *Eugenia* sect. *Calycorectes* of Mazine & al. (2016). For a list of synonyms and nomenclatural notes, see Giaretta & al. (unpub. data in prep.).

Eugenia [subg. *Eugenia*] sect. **Jossinia** (DC.) Nied. in Engler & Prantl, Nat. Pflanzenfam. 3(7): 81. 1893 ≡ *Jossinia* Comm. ex DC., Prodr. 3: 237 ["337"]. 1828 – Type: *Jossinia tinifolia* (Lam.) DC. (≡ *Eugenia tinifolia* Lam.).
= *Myrtopsis* O.Hoffm. in Linnaea 43: 133. 1881, nom. illeg.
= *Chloromyrtus* Pierre in Bull. Mens. Soc. Linn. Paris, n.s., 1: 71. 1898.
= *Meteoromyrtus* Gamble in Bull. Misc. Inform. Kew 1918: 241. 1918.
= *Monimiastrum* J.Guého & A.J.Scott in Kew Bull. 34(3): 483. 1980.
Notes. – The type *Jossinia tinifolia* is currently accepted as *Eugenia tinifolia* (WCSP, 2017). For a description of *Eugenia* sect. *Jossinia*, see Blume (1850: 119), Diels (1921: 531, 1922: 376) and Merrill (1950: 330, 1951: 356), under *Jossinia*. For nomenclatural notes and synonyms, see Mazine & al. (2016) under "Old World *Eugenia*".

This section corresponds to the "Old World" clade of Mazine & al. (2014). As noted by Merrill (1950: 330), Niedenzu (1893: 81) defined sect. *Jossinia* of the subgenus "*Eueugenia*", but did not include any of the species on which the genus *Jossinia* (1828) was based; despite this, that section is valid. *Eugenia* sect. *Jossinia* can be distinguished from *Eugenia* sect. *Umbellatae* by its exclusively extra-American distribution, a tendency for increased numbers of locules and ovules, common cryptic dioecy, and the style that is approximately the same length as the stamens.

Eugenia [subg. *Eugenia*] sect. **Racemosae** O.Berg in Linnaea 27(2–3): 278. 1856 ("1854") – Type: *Eugenia racemosa* DC. (= *Eugenia biflora* (L.) DC.).
Notes. – The type *Eugenia racemosa* is currently accepted as *Eugenia biflora* (Mazine & Souza, 2015; WCSP, 2017). For a list of synonyms and nomenclatural notes and circumscription, see Mazine & al. (2016).

Eugenia [subg. *Eugenia*] sect. *Speciosae* Bünger & Mazine in
Phytokeys 61: 75. 2016. – Type: *Eugenia speciosa* Cambess.
Notes. – For a list of synonyms, nomenclatural notes and
circumscription, see Bünger & al. (2016c).

Eugenia [subg. *Eugenia*] sect. *Umbellatae* O.Berg in Linnaea
27(2–3): 204. 1856 – Type: *Eugenia umbellata* DC.
(= *Eugenia bimarginata* DC.).
Notes. – The type *Eugenia umbellata* is currently accepted
as *Eugenia bimarginata* (Mazine & al., 2016; WCSP, 2017). For
a list of synonyms and nomenclatural notes, see Mazine & al.
(2016) and Giaretta & al. (unpub. data in prep.). In the sense
used here, *Eugenia* sect. *Umbellatae* can be circumscribed
according to the description provided by Berg (1856) and
Mazine & al. (2016) with the additional diagnostic characters
that the distribution of these species is exclusively Neotropical
and that the style is consistently and exclusively twice as long
as the stamens. The Caribbean genera *Calyptrogenia*, *Hottea*
and *Pseudanamomis* feature in the phylogenetic analysis of
Vasconcelos & al. (2017) and are nested in *Eugenia*. These
genera require nomenclatural transfer to *Eugenia* that is in
preparation elsewhere.

■ **CONCLUSION**

A new subgenus, *Eugenia* subg. *Pseudeugenia*, and new
section of *Eugenia*, *E.* sect. *Excelsae*, are described above.
Eugenia sect. *Jossinia* is also reviewed. The systematic position
of *E.* sect. *Eugenia*, *E.* sect. *Hexachlamys*, *E.* sect. *Phyllocalyx*
and *E.* sect. *Schizocalomyrtus* (previously *E.* sect. *Calycorectes*
sensu Mazine & al., 2016) reported by Mazine & al. (2014)
are confirmed and the subgeneric classification of *Eugenia* is
further stabilised. *Eugenia* sect. *Umbellatae* sensu Mazine &
al. (2016) is shown not to be monophyletic, with non-Ameri-
can species emerging in a sister clade to *E.* sect. *Racemosae*.
The division of Old World species into groups X and Y as
suggested by Van der Merwe & al. (2005) is not supported by
the molecular evidence presented here, preventing further com-
ment on their breeding systems. *Eugenia* sect. *Umbellatae* as
circumscribed in this study can be distinguished from *E.* sect.
Racemosae based on the nature of the inflorescence. Within
E. sect. *Umbellatae* taken in this current sense, some clades
can be interpreted with morphology and can serve as manage-
able units for subsequent taxonomic analysis, but many remain
morphologically unsupported and more accurate species rela-
tionships await new analyses based on more data.

Geographic structuring is evident, both at the level of the
genus and within *E.* sect. *Umbellatae*. It appears that from a
dry biome origin, the common ancestor of modern *Eugenia* and
Myrcianthes was able to take advantage of the expansive humid
forests of the Oligocene and early Miocene where *E.* subg.
Eugenia subsequently underwent high levels of rapid speciation
(Vasconcelos & al., 2017). After rapid Miocene speciation in the
contiguous forests linking today's Atlantic coastal and Amazon
forests, the formation of the Cerrado (<9 to ca. 16 Ma accord-
ing to Simon & al., 2009 and Ratter & al., 1997, respectively)

divided this distribution. Subsequently species continued to
thrive in both forest biomes with subsequent dispersal or vi-
cariance events leading to *Eugenia* migrating to the Caribbean
on at least three occasions, to Asia and the Pacific apparently
only once and to species exchange between the Atlantic and
Amazon forests and Cerrado. Evidence suggests that the areas
in which most speciation occurred were the eastern forests
now known as the Atlantic Forest, making this the cradle of
Eugenia diversity. Elevated levels of *Eugenia* speciation in the
Oligocene and Miocene correspond to rapid diversifications
in other species-rich clades of fleshy fruited Myrtaceae (e.g.,
Myrcia; Santos & al., 2016) and of Neotropical mammals and
birds (Hoorn & al., 2010). These vertebrate guilds favour fleshy
Myrtaceae berries and likely acted as highly efficient dispersal
vectors, driving new niche colonisation and accelerated specia-
tion (Vasconcelos & al., 2017). Accompanying these ecological
changes were morphological changes such as from cymose
inflorescences, i.e., often dichasial in *Myrcianthes*, to racemose,
widely found in Neotropical *Eugenia* in extended or reduced
forms (e.g., glomerules and fascicles), and reproductive changes
from functional bisexual flowers to dioecy in some species.
Furthermore, there is a tendency for persistent bracteoles in spe-
cies from more recent nodes, almost entirely absent outside of
clade PB. Inflorescence characters display some trends within
and between the groups of *E.* sect. *Umbellatae* but it is clear that
this character is homoplastic and inflorescence development
requires further investigation before use for reliable distinction
of groups within the genus. Developmental studies of reproduc-
tive units may provide a further source of systematic characters
with which to understand and interpret *Eugenia* evolution. This
should be the focus of further studies alongside more detailed
analysis of a larger sample of *E.* sect. *Jossinia* to determine its
emigration from the Neotropics. Further studies are required
to (1) conclusively understand the relationship of the *Eugenia*
sections to each other and the monophyly or otherwise of *E.*
sect. *Eugenia*, (2) determine positions of as yet unclassified
species and (3) test the consistency or otherwise of preliminary
groupings within *E.* sect. *Umbellatae*.

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Appendix 1. DNA sequences used in the phylogenetic study.

Species name and authority, country (Brazilian states in parenthesis), voucher's collector and collector number (herbarium code in parenthesis). After semi-colon, GenBank numbers of DNA sequences (ITS, *psbA-trnH*, *rpl16*, *rpl32-trnL*, *trnQ-rps16*). Brazilian states: AM = Amazonas, BA = Bahia, DF = Distrito Federal, ES = Espírito Santo, GO = Goiás, MG = Minas Gerais, MT = Mato Grosso, PR = Paraná, RJ = Rio de Janeiro, RR = Roraima, SP = São Paulo. An n-dash (–) indicates a missing sequence; partial sequences are marked as "partial".

Acca sellowiana (O.Berg) Burret, RBG Kew (cultivated), *Lucas 205* (K), AM234067, AM489807, MH446098*, MH446190*, MH446280*; *Algrizea macrochlamys* (DC.) Proença & NicLugh., Brazil (BA), *Giulietti 1648* (K), AM234126, AM489809, MF954310, MF954310, KP722283; *Campomanesia ilhoensis* Mattos, Brazil (BA), *Ibrahim 122* (HUEFS), MH445990*, MH446047*, MH446133*, MH446226*, MH446316*; *Eugenia anastomosans* DC., Marie Selby Bot. Gard. (cultivated), *Holst 9383* (SEL), MH445996*, MH446053*, MH446145*, MH446238*, MH446328*; *Eugenia angustissima* O.Berg, Brazil (BA), *Vasconcelos 405* (K, UB), MF954032, MF954289, MF954332, MF954217, MF954096; *Eugenia arenosa* Mattos, Brazil (SP), *Mazine 1043* (ESA, K, MBM), KJ187605, KJ469654, MH446118*, MH446211*, MH446301*; *Eugenia astringens* Cambess., Brazil (SP), *Mazine 782* (ESA, K), KJ187606, KJ469655, MH446113*, MH446206*, MH446296*; *Eugenia axillaris* (Sw.) Willd., Turks & Caicos, *Hamilton 553* (FTG, K), KJ187607, KJ469656, MH446132*, MH446225*, MH446315*; *Eugenia bacopari* D. Legrand, Brazil (PR), *Mazine 967* (ESA, HUEM, K, MBM), KJ187608, KJ469657, MH446102*, MH446195*, MH446285*; *Eugenia bahiensis* DC., Brazil (ES), *Faria 4229* (K, UB), MH446018*, MH446076*, MH446169*, MH446260*, MH446352*; *Eugenia bimarginata* DC., Brazil (MG), *Mazine 469*(ESA, K), KJ187611, KJ469660, MH446106*, MH446199*, MH446289*; *Eugenia binata* Mazine & Sobral, Brazil (SP), *Colletta 1208* (ESA), MH446016*, MH446074*, MH446167*, MH446258*, MH446350*; *Eugenia bojeri* Baker, Mauritius, *Page 32* (MAU), MH445985*, MH446042*, MH446126*, MH446219*, MH446309*; *Eugenia brasiliensis* Lam., Brazil (PR), *Lucas 126* (ESA, K), KJ187613, KJ469662, MH446120*, MH446213*, MH446303*; *Eugenia brevistyla* D.Legrand, Brazil (PR), *Mazine 993* (ESA, K, SORO), KJ187614, KJ469663, MH446099*, MH446191*, MH446281*; *Eugenia brongniartiana* Guillaumin, New Caledonia, *Pillon 176* (K, NOU), KJ187615, KJ469664, MH446161*, MH446253*, MH446344*; *Eugenia cerasiflora* Miq, Brazil (BA), *Vasconcelos 419* (K, UB), MH446019*, MH446077*, MH446170*, MH446261*, MH446353*; *Eugenia coffeifolia* DC., French Guiana, *Holst 9516* (SEL), MH445992*, MH446049*, MH446141*, MH446234*, MH446324*; *Eugenia crassa* Sobral, Brazil (ES), *Giacomin 1860* (BHCB), KX789269, KX789296, KX789321, KX789350, KX910671; *Eugenia densiracemosa* Mazine & Faria, Brazil (MT), *Mazine 1072* (ESA, SORO), KJ187642, KJ469691, MH446101*, MH446193*, MH446283*; *Eugenia dictyophylla* Urb., Dominican Republic, *Clase 8180* (K), MH446012*, MH446069*, MH446162*, MH446254*, MH446345*; *Eugenia domingensis* O.Berg, Dominican Republic, *Lucas 1127* (K), MH446008*, MH446065*, MH446157*, MH446249*, MH446340*; *Eugenia dysenterica* DC., Brazil (MG), *Mazine 466* (ESA, K), KJ187620, KJ469669, MH446114*, MH446207*, MH446297*; *Eugenia egensis* DC., Brazil (AM), *Vasconcelos 319* (K, UB), MH446026*, MH446084*, MH446177*, MH446268*, MH446360*; *Eugenia ellipsoidea* Kiaersk., Brazil (ES), *Lucas 879* (K), MH445991*, MH446048*, MH446137*, MH446230*, MH446320*; *Eugenia erythrophylla* Strey, South Africa, *Maurin 1801* (JRAU), MH445976*, MH446033*, MH446091*, MH446183*, MH446273*; *Eugenia excelsa* O.Berg, Brazil (PR), *Lucas 125* (ESA, K), KJ187621, KJ469670, MH446121*, MH446214*, MH446304*; *Eugenia expansa* Spring ex Mart., Brazil (PR), *Mazine 950* (ESA, K, SORO), KJ187619, KJ469668, MH446124*, MH446217*, MH446307*; *Eugenia flavescens* DC., Brazil (ES), *Zappi 415* (K), MH445982*, MH446039*, MH446097*, MH446189*, MH446279*; *Eugenia florida* DC., Brazil (PR), *Mazine 965* (ESA,

Appendix 1. Continued.

K, UEC), KJ187622, KJ469671, MH446112*, MH446205*, MH446295*; ***Eugenia foetida*** Pers., Marie Selby Bot. Gard. (cultivated), *Holst 8865* (SEL), MH445997*, MH446054*, MH446146*, MH446239*, MH446329*; ***Eugenia goiapabana*** Sobral & Mazine, Brazil, *Bünger s.n.* (BHCB), KX789270, KX789300, KX789325, KX789354, KX910675; ***Eugenia hamiltonii*** (Mattos) Mattos, Brazil (SP), *Mazine 1033* (ESA, K), KJ187653, KJ469703, MH446109*, MH446202*, MH446292*; ***Eugenia handroi*** (Mattos) Mattos, Brazil (PR), *Mazine 951* (ESA, MBM), KJ187654, KJ469704, MH446104*, MH446197*, MH446287*; ***Eugenia hiraeifolia*** Standl., Brazil (RJ), *M.C. Souza 1142* (UB), MH445999*, MH446056*, MH446148*, MH446241*, MH446331*; ***Eugenia hirta*** O.Berg, Brazil (ES), *Faria 4227* (K, UB), MH446020*, MH446078*, MH446171*, MH446262*, MH446354*; ***Eugenia intermedia*** O.Berg, Dominican Republic, *Araújo 1788* (K), MH446014*, MH446071*, MH446164*, –, MH446347*; ***Eugenia inversa*** Sobral, Brazil (ES), *Faria 4230* (K, UB), MH446021*, MH446079*, MH446172*, MH446263*, MH446355*; ***Eugenia laevis*** O.Berg, Dominican Republic, *Lucas 1113* (K), MH446005*, MH446062*, MH446154*, MH446246*, MH446337*; ***Eugenia lambertiana*** DC., Brazil (RR), *Vasconcelos 382* (K, UB), MH446030*, MH446088*, MH446180*, partial, MH446364*; ***Eugenia leptoclada*** O.Berg, Brazil (SP), *Lucas 389* (K), MH446004*, MH446061*, MH446153*, –, MH446336*; ***Eugenia lindahlii*** Urb. & Ekman, Dominican Republic, *Clase 7839* (K), MH446013*, MH446070*, MH446163*, MH446255*, MH446346*; ***Eugenia melanogyna*** (D.Legrand) Sobral, Brazil (PR), *Mazine 969* (ESA, MBM, SORO), KJ187624, KJ469673, KJ469673, MH446194*, MH446284*; ***Eugenia modesta*** DC. (MG), *Mazine 854* (ESA, K), KJ187625, –, MH446108*, MH446201*, MH446291*; ***Eugenia monticola*** (Sw.) DC., Dominican Republic, *Lucas 1117* (K), MH446007*, MH446064*, MH446156*, MH446248*, MH446339*; ***Eugenia myrcianthes*** Nied., Brazil (GO), *Faria 2850* (UB), MH446003*, MH446060*, MH446152*, MH446245*, MH446335*; ***Eugenia natalitia*** Sond., South Africa, *Maurin 1796* (JRAU), MH445977*, MH446034*, MH446092*, MH446184*, MH446274*; ***Eugenia neofasciculata*** Bennet, Mauritius, *Page 105* (MAU), MH445987*, MH446044*, MH446129*, MH446222*, MH446312*; ***Eugenia neoglomerata*** Sobral, Brazil (SP), *Mazine 461* (ESA, K), KJ187626, KJ469674, MH446116*, MH446209*, MH446299*; ***Eugenia neoverrucosa*** Sobral, Brazil (PR), *Lucas 118* (ESA, K), KJ187628, KJ469676, MH446122*, MH446215*, MH446305*; ***Eugenia nutans*** O. Berg, Brazil (MG), *Lucas 281* (ESA, K), KJ187629, KJ469677, MH446105*, MH446198*, MH446288*; ***Eugenia orbiculata*** Lam., Mauritius, *Page 104* (MAU), KJ187631, KJ469679, MH446128*, MH446221*, MH446311*; ***Eugenia paracatuana*** O. Berg, Brazil (GO), *Faria 2928* (UB), MH446000*, MH446057*, MH446149*, MH446242*, MH446332*; ***Eugenia paracatuana*** O. Berg, Brazil (SP), *Silva 64* (SORO), MH446011*, MH446068*, MH446160*, MH446252*, MH446343*; ***Eugenia patens*** Poir., French Guiana, *Lucas 104* (ESA, K), KJ187633, KJ469681, KX789331, KX789361, KX910681; ***Eugenia patrisii*** Vahl, French Guiana, *Holst 9514* (SEL), MH445993*, MH446050*, MH446142*, MH446235*, MH446325*; ***Eugenia patrisii*** Vahl, Brazil (AM), *Vasconcelos 327* (K, UB), MH446027*, MH446085*, MH446178*, MH446269*, MH446361*; ***Eugenia pisiformis*** Cambess., Brazil (MG), *Lucas 232* (ESA, K), KJ187634, KJ469682, MH446119*, MH446212*, MH446302*; ***Eugenia pisonis*** O.Berg, Brazil (AM), *Giaretta 1419* (SPF), MH446032*, MH446090*, MH446182*, –, MH446366*; ***Eugenia pistaciifolia*** DC., Brazil (BA), *Faria 1782* (UB), MH446001*, MH446058*, MH446150*, MH446243*, MH446333*; ***Eugenia platyphylla*** O.Berg, Brazil (BA), *Lucas 1188* (K), MH446009*, MH446066*, MH446158*, MH446250*, MH446341*; ***Eugenia platysema*** O.Berg, Brazil (BA), *Mazine 3001* (K), MH446010*, MH446067*, MH446159*, MH446251*, MH446342*; ***Eugenia plicatocostata*** O.Berg, Brazil (BA), *Popovkin 1770* (HUEFS), MH446022*, MH446080*, MH446173*, MH446264*, MH446356*; ***Eugenia pluriflora*** DC., Brazil (PR), *Mazine 961* (ESA, K, MBM, SORO), KJ187636, KJ469684, MH446107*, MH446200*, MH446290*; ***Eugenia pollicina*** J.Guého & A.J.Scott, Mauritius, *Page 106* (MAU), MH445988*, MH446045*, MH446130*, MH446223*, MH446313*; ***Eugenia prasina*** O.Berg, Brazil (PR), *Mazine 959* (ESA, K), KJ187637, KJ469685, MH446111*, MH446204*, MH446294*; ***Eugenia protenta*** McVaugh, Brazil (RR), *Vasconcelos 350* (K, UB), MH446029*, MH446087*, MH446179*, MH446271*, MH446363*; ***Eugenia punicifolia*** (Kunth) DC., Brazil (MT), *Mazine 1065* (ESA, K, SORO), KJ187638, KJ469686, KX789332, KX789361, KX910682; ***Eugenia pyriformis*** Cambess., Brazil (SP), *Mazine 1028* (ESA, K, MBM, SPF), KJ187639, KJ469687, MH446117*, MH446210*, MH446300*; ***Eugenia reinwardtiana*** (Blume) DC., Singapore Bot. Gard. (cultivated), *Zappi s.n.*; (K), MH445995*, MH446052*, MH446144*, MH446237*, MH446327*; ***Eugenia reinwardtiana*** (Blume) DC., Marie Selby Bot. Gard. (cultivated), *Holst 8870* (K, SEL), MH446015*, MH446073*, MH446166*, MH446257*, MH446349*; ***Eugenia repanda*** O.Berg, Brazil (SP), *Mazine 1090* (ESA, K, SORO), –, KJ469690, MH446140*, MH446233*, MH446323*; ***Eugenia rhombea*** (O.Berg) Krug & Urb., Marie Selby Bot. Gard. (cultivated), *Holst 8864* (K, SEL), MH445998*, MH446055*, MH446147*, MH446240*, MH446330*; ***Eugenia roseopetiolata*** N.Snow & Cable, RBG Kew (cultivated), probably from Madagascar, *Liv. Coll. 2007-2349* (K), MH446017*, MH446075*, MH446168*, MH446259*, MH446351*; ***Eugenia rotula*** Sobral, Brazil (BA), *Faria 4190* (K, UB), MH446023*, MH446081*, MH446174*, MH446265*, MH446357*; ***Eugenia sp. 2***, Dominican Republic, *Lucas 1115* (K), MH446006*, MH446063*, MH446155*, MH446247*, MH446338*; ***Eugenia sp. 3***, Brazil (RR), *Vasconcelos 348* (K, UB), MH446028*, MH446086*, –, MH446270*, MH446362*; ***Eugenia sp. 4***, French Guiana, *Holst 9435* (SEL), KJ187643, KJ469692, MH446134*, MH446227*, MH446317*; ***Eugenia sparsa*** S.Moore, Brazil (MT), *Mazine 1084* (K, SORO), –, MH446072*, MH446165*, MH446256*, MH446348*; ***Eugenia sphenophylla*** O.Berg, Brazil (MG), *Lucas 257* (ESA, K), KJ187644, KJ469693, MH446123*, MH446216*, MH446306*; ***Eugenia splendens*** O.Berg, Brazil (BA), *Faria 4196* (K, UB), MH446024*, MH446082*, MH446175*, MH446266*, MH446358*; ***Eugenia spruceana*** O.Berg, French Guiana, *Holst 9465* (SEL), MH445994*, MH446051*, MH446143*, MH446236*, MH446326*; ***Eugenia stictopetala*** DC., Brazil (MT), *Mazine 1077* (ESA, K, SORO), KJ187641, KJ469689, MH446115*, MH446208*, MH446298*; ***Eugenia stipitata*** McVaugh, French Guiana, *Holst 8872* (CAY, SEL), KJ187645, KJ469694, MH446136*, MH446229*, MH446319*; ***Eugenia subavenia*** O.Berg, Brazil (SP), *Mazine 805* (ESA, K), KJ187646, KJ469695, MH446110*, MH446203*, MH446293*; ***Eugenia subterminalis*** DC., Brazil (PR), *Mazine 974* (ESA, HUEFS, SORO), –, KJ469696, MH446139*, MH446232*, MH446322*; ***Eugenia supraaxillaris*** Spring, Brazil (PR), *Mazine 994* (ESA, K), KJ187618, KJ469667, MH446100*, MH446192*, MH446282*; ***Eugenia tetramera*** (McVaugh) M.L.Kawas. & B.Holst, French Guiana, *Holst 9422* (CAY), KJ187648, KJ469698, MH446135*, MH446228*, MH446318*; ***Eugenia tinifolia*** Lam., Mauritius, *Page 25* (MAU), MH445984*, MH446041*, MH446125*, MH446218*, MH446308*; ***Eugenia umbrosa*** O.Berg, Brazil (MG), *Mazine 1085* (ESA, K, SORO), KJ187649, KJ469699, MH446138*, MH446231*, MH446321*; ***Eugenia umtamvunensis*** A.E.van Wyk, South Africa, *Maurin 1794* (JRAU), MH445978*, MH446035*, MH446093*, MH446185*, MH446275*; ***Eugenia unana*** Sobral, Brazil (BA), *Faria 4221* (K, UB), MH446025*, MH446083*, MH446176*, MH446267*, MH446359*; ***Eugenia uniflora*** L., RBG Kew (cultivated), *Lucas 207* (K), AM234088, AM489828, KX789338, KX789367, KX910688; ***Eugenia vaughanii*** J.Guého & A.J.Scott, Mauritius, *Page 69* (MAU), MH445986*, MH446043*, MH446127*, MH446220*, MH446310*; ***Eugenia verticillata*** (Vell.) Angely, Brazil (SP), *Duarte ESA85678* (ESA, K), MH446031*, MH446089*, MH446181*, MH446272*, MH446365*; ***Eugenia wentii*** Amsh., French Guiana, *Holst 9421* (CAY, SEL), KJ187651, KJ469701, KX789339, KX789368, KX910689; ***Eugenia woodii*** Dummer, South Africa, *Maurin MvdB26* (JRAU), MH445979*, MH446036*, MH446094*, MH446186*, MH446276*; ***Eugenia zeyheri*** (Harv.) Harv., South Africa, *Maurin 1800* (JRAU), MH445980*, MH446037*, MH446095*, MH446187*, MH446277*; ***Eugenia zuluensis*** Dummer, South Africa, *Abbott 9188* (JRAU), MH445981*, MH446038*, MH446096*, MH446188*, MH446278*; ***Myrcia tomentosa*** (Aubl.) DC., Brazil (SP), *Savassi ESA 85681* (ESA), MH446040*, MH446103*, MH446196*, MH446286*; ***Myrcianthes fragrans*** (Sw.) McVaugh, Turks & Caicos, *Hamilton 552* (FTG, K), MH445989*, MH446046*, MH446131*, MH446224*, MH446314*; ***Myrcianthes pungens*** (O.Berg) D.Legrand, Brazil (DF), *Faria 2759* (UB), MH446002*, MH446059*, MH446151*, MH446244*, MH446334*; ***Myrtus communis*** L., RBG Kew (cultivated), *Lucas 211* (K), AM234149, AM489872, KX789342, MF954420, KP722221.